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An evaluation is a statement of the accuracy of some measure. Thus one should evaluate a measure of mortality by determining how close the measure comes to the true mortality. The obvious consequence of this statement is that some measure of true mortality must be available, a problem that may be insurmountable. The purpose of the present review of techniques of measuring mortality is to present some basic definitions that should clarify the use of terms and also to indicate some possibilities for use of some measures in the field. This presentation will omit mathematical details that are best given in other places. There will be no discussion of the problem of diagnosis of the cause of death. Fortunately, it is relatively easy to decide whether the animal is dead or alive. Lastly, this summary will not include lists of data about mortality rates which are available in the literature.

Mortality Rates

The problem of definitions of mortality rates is central to an evaluation because, as indicated above, the real problem is to determine how close a measure comes to the true rate of mortality. Definitions can be separated into two big groups, biological and mathematical. The biological definitions are concerned with problems of the causes of death which present very complex difficulties since an animal may die while simultaneously suffering a number of afflictions. Thus, it is extremely difficult to assign the cause of death, even in humans where information is abundant. The result of this situation is that one should not attempt to assign the cause of death in wild animals but just simply state under what conditions the animal died. However, for some purposes, as will be seen later, it is desirable to attempt to indicate what condition is frequently associated with death.

Another aspect of the biological definitions is the relation of various factors such as the age and sex as well as habitat conditions and social rank to the life of the individual. Again, these aspects are very complex and require individual studies for almost each species or condition.

Among the mathematical definitions the term mortality rate is widely used, often without a clear definition. Perhaps it is best to let the term mortality rate be a useful, sloppy term simply to indicate that one is concerned with some sort of a rate of dying. It may be that the term is useful when one wants for example to talk about a high or low mortality rate of foxes or of mosquitoes. In these two cases, the numerical values would be very different but most persons have a general idea of the meaning of such a statement. However, for evaluation of techniques a much more rigorous definition is necessary. The first term to be defined[2] is the probability of dying. This term (usually represented by q) is the number of individuals dying during some time interval divided by the number in the initial population. The time interval is usually a year, borrowed from demographic studies. If some other time interval is desired, as would be the case in studies of mosquitoes,

then it should be indicated. The complement of q is the probability of survival or p; hence, $q = 1 - p$. A mathematical transformation of time units is easily followed by remembering an individual can survive for more than one time period but of course cannot die in more than one successive time period. Hence, p_a is equal to $(p_m)^{12}$ where p_a is annual probability of surviving and p_m is the monthly probability of surviving. This definition can be cast in terms of the population by stating it as the population decay formula $n_t = n_0 (1-q)^t$. This formulation simply says that the number at sometime t is equal to the original number multiplied by the proportion surviving raised to a power to represent the number of time units. Numerous methods have been devised for calculation of the standard error but perhaps the one devised by Haldane[6] is the best:

$$SE = q\sqrt{p/D}$$ where D is number of deaths.

A different definition is called the death rate (usually represented by d). It is the number of deaths during a time unit divided by the average population during this time. Thus, if 60 individuals die during a year when the average population was a 100, then $d = 60/100 = 0.6$. This definition is probably best expressed in reference to the population as $n_t = n_0 e^{-dt}$. It will be noted that this statistic, d, is an instantaneous value and refers to an infinitesimally small period of time t. The relation of d and p are complex.[2] Simply stated it can be noted that $p = n_t/n_0$ which, of course, $= e^{-dt}$. In this way $\ln p = -d$.

A figure of great utility for studies of mortalities is the expectation of life. It is true that this figure is a projection from past events and suffers all of the inadequacies of such assumptions. Nevertheless, for comparison and for projection it is useful. The mathematical derivations described above allow the conclusion that $E = 1/q$ and also $E = 1/d$, from which of course one would conclude that $q = d$. This relation can be true from the definitions above only under certain circumstances. The difficulty lies in the fact that d is an instantaneous rate and applies only to very small time intervals whereas q refers to a finite period of time. However, when q is very low then q and d are very nearly equal since whatever the time interval, little difference occurs between the two values. An anomally, pointed out by Farner[5] occurs (Fig. 1). The graph gives a simple line of the calculated relationship between p or q and the expectation of life. In the lower part of the curve where q is low,
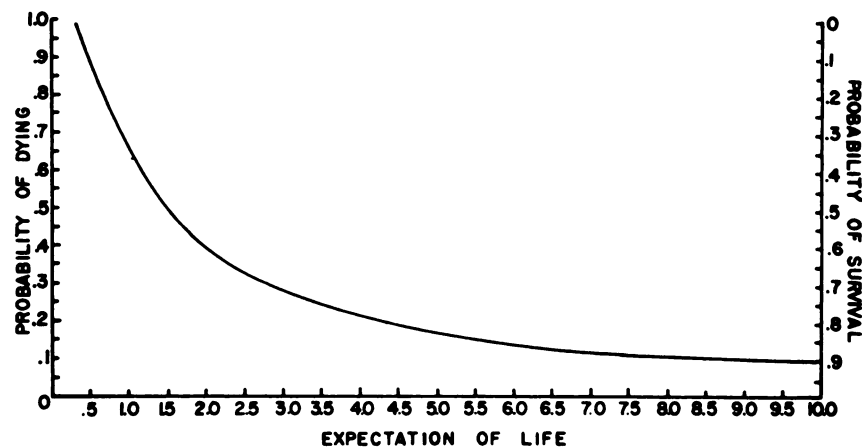

FIGURE 1. *Relation of probability of dying[2] and expectancy of life. When q is above 0.5 then serious discrepancies occur between the values of E calculated by two definitions (see text).*

this line represents equally well both $E = 1/d$ and $E = 1/q$. However, in the left-hand part of the curve where q is rather large an inreconcilable situation occurs. Consider, for example, a hypothetical situation in which a number of foxes are born on January 1 and all die that day. The value of q is, of course, 1 since all individuals died during a year and the value of d is almost zero since the average population during the year had to be almost zero. However, in contrast, suppose that these foxes born on January 1 all lived until December 31 and then died on that date. The value of q would, of course, again be 1.0 but the value of d would be almost 1.0 since the average population had been large during that time. Considering figure 1, the first case would essentially move the upper part of the line to the left so that it met the vertical axis at $E = 0$; whereas, the second case would move the line to the right to meet the vertical axis at $E = 1$.

The essential point in considering definitions is to recognize that the same data when put into different mathematical formulae can give different answers. Thus, the evaluation of a measure of mortality must pay great attention to the mathematical derivations and assumptions in the definitions. Clearly a measure of mortality based on one set of assumptions cannot be evaluated by a measure of mortality based on a different set of assumptions. Definitions, of course, are conventions and a scientist has a right to define his terms in any way that he wishes. There are advantages to using somewhat different definitions since some changes may represent progress. However, the scientist is obliged to define clearly his terms so that another reader can understand the assumptions underlying the definitions. Lamentably, many papers fail to define the terms[4] and inevitably produce confusion.

The use of different letters to represent these terms is, of course, understandable and regularly occurs in the fishery literature. Ricker,[7] for example, clearly defines his terms but uses different symbols. However, the clear statement of definitions will prevent confusion. Except for the use of mortality rate as a good, sloppy term, there is no excuse for failure to define the meaning of the mathematical derivations.

Methods of Getting Data

The above statements have been concerned with the treatment of information after it has been obtained. It has been assumed that somehow or other a knowledge of the numbers of deaths in some time period had been obtained. This knowledge in field work may be hard to obtain and, hence, provide little material for the above calculations. Nevertheless, the methods of getting the data can be divided into several different categories.

Actual Deaths

In nature, it is rare to find dead animals simply because their remains are so quickly dispersed by scavengers. Nevertheless, under certain special circumstances one may find a number of dead individuals or their remains such as jaws or teeth. In other cases, animals may be tagged somehow and subsequently found. Under these circumstances one can create a tabulation giving the time since marking in the following manner (Table 1). In this generalized case, the age at marking is not known, but of course in a special case, the age may be known and hence the age at death is known. The first column gives the units (years, months, etc.) since marking in which a number of animals were found dead. The total of 60 individuals can be converted to 100 per cent and thus the percentage alive or the probability of survival can be easily calculated. Clearly, this same table can be constructed for individuals whose ages at death are known. An essential assumption in drawing conclusions from a table of this type is that the animals not found have the same rate of mortality as those found. This assumption is difficult to test.

TABLE 1. *Tabulation of data on deaths after marking.*

Time Unit	Number Dying	Alive at start	
		Number	Percent
0	16	60	100
1	11	44	73
2	13	33	55
3	11	20	33
4	5	9	15
5	4	4	7
6	0	0	0

A different manner of getting data is simply to average the yearly rates.[5] Suppose that the time of death since banding is known for 597 robins of which 291 died during the first year. All of these robins were banded as nestlings and, hence their ages were known. From these data q = 291 divided by 597 = 0.49. This method, however, does not give adequate weight to variations between years. Possibly a year of high mortality is under represented or over represented. The following formula corrects for this problem.

$$q = \frac{D_1 + D_2 + \ldots + D_m}{D_1 + 2D_2 + \ldots + nD_m} = \frac{597}{1148} = 0.52$$

Another method of obtaining data is to assume that the population is stationary, that is, numerically the same throughout the time period. Under these circumstances the number of young individuals will have to equal the number that died during the year. Hence, in the above table 1 it is clear that 16 individuals had to die during the year to allow the 16 young to join the group. Under these circumstances q = 16 divided by 60 = 0.27. This example assumes a closed population. To account for movements, immigration can be added to births and emigration can be added to deaths.

The above examples illustrate the point that somehow an age of the animal must be assigned to give the death rate. The "age" can be represented simply as time since marking. This approach is particularly useful for birds, some mammals, and for fish. However, the true age can be determined for a large number of species and then the appropriate tabulation can be prepared. This paper is not the place to attempt a discussion of methods of determining age of animals. However, a vast storehouse of data is available.[6] While for many species methods of determining age have not yet been developed, enough is now known to be confident that some character can be found in nearly every species. The list of possible characters is long and can be the source of possibilities in the case of a species not yet examined.

The generality of these techniques is illustrated (Fig. 2) in the calculation of mortality rates for muskrat houses. In this case, the houses were marked when they were constructed and followed at monthly intervals to see whether they were "alive". Note that the survival as expressed on semi-log scale was not constant, but decreased with the age of the muskrat house. This graph illustrates that the definitions of q are general and can be used for many processes. Indeed, as pointed out[2] these definitions are the same as those for a decay process. Figure 2 also illustrates that q may not be constant as was assumed for figure 1.
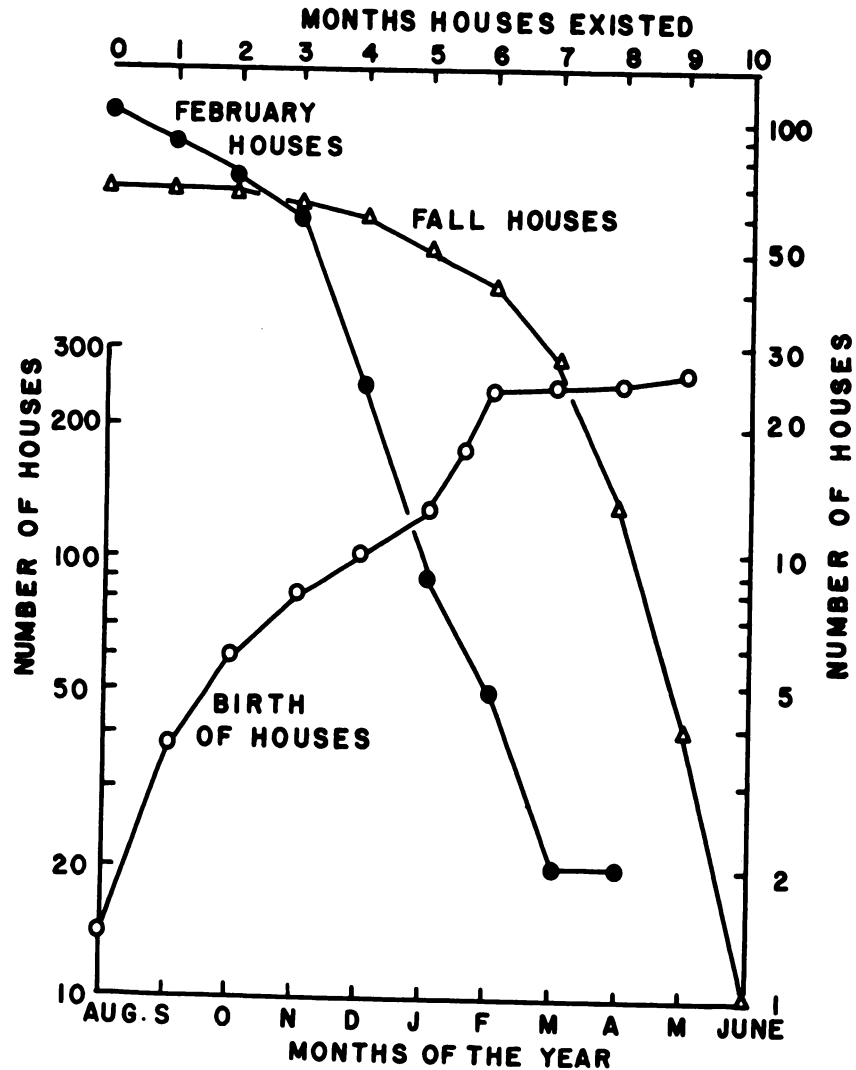
FIGURE 2. *The history of decay of muskrat houses marked in fall and in February. Note that survival was high for fall houses for 4 months and then declined rapidly. Houses constructed in February had short lives.*

Recapture Methods

A different approach is to recapture individuals thereby finding out how long they have lived rather than when they died. This method, of course, makes certain assumptions about the length of life after last recapture. One can assume that it is a constant fraction of the total life or one can make different claims. This method

can be combined with the recapture census method to provide additional information about the population. The procedure is as follows. Suppose that in the spring of the year 269 animals were tagged and released. Then in the summer, 253 individuals were captured. In addition a few young individuals which were not yet alive or large enough to be marked in the spring were also captured. Of these 253 individuals, a total of 52 had been marked (recaptured) and 201 were not marked. Now suppose that some method is available for independently estimating the summer population at 891 individuals. Hence,

$$52/253 = X/891 \quad X = 183 \text{ (marked and alive)}$$

Then: $\quad\quad\quad\quad p = 183/269 = 0.68 \text{ and } q = 0.32.$

Another approach to recaptured individuals really uses basically the same concepts but the arithmetic is somewhat different.[8] Suppose that c is the probability of being captured and f is the fraction of the total population caught in the t-th year. Then f_t is equal to cp^t which simply says that the fraction captured equals a constant times the probability of survival for t intervals of time. The data can be plotted on semilog paper with f_t, on the logarithmic axis and t on the arithmetic axis. The slope then is log p, because $\log f_t = \log c + t \log p$.

In still another version, this method can be easily used with banded birds.[1] In the year 1956, 483 birds were banded and in the year 1958, 81 of these were recaptured. In the year 1957, 200 birds were banded and in the year 1958, 35 of these were recaptured. Clearly, the birds banded in 1956 and recaptured in 1958 had to survive two years while those banded in 1957 and recaptured in 1958 had to survive only one year. Hence, the following proportion 483 p^2 / 200 p = 81/35 and p = 0.57.

Disappearance Rate

For some purposes the objective of the study is satisfied by a comparison of two groups. In these cases, while it might be nice to know the mortality rate, the difficulty of obtaining the data may force one to be content with "disappearance rate". The definitions for the rates are the same as above but one simply knows that the animal has disappeared; whether it is dead or alive is assumed to have no significance. For example, a comparison of two treatments may be possible as in Table 2. It can be seen that the adult males disappeared from the population more rapidly than did the adult females. From this it may be concluded by making several assumptions that the mortality rate for adult males is higher than that of females.

TABLE 2. *A comparison of disappearance of males and of females.*

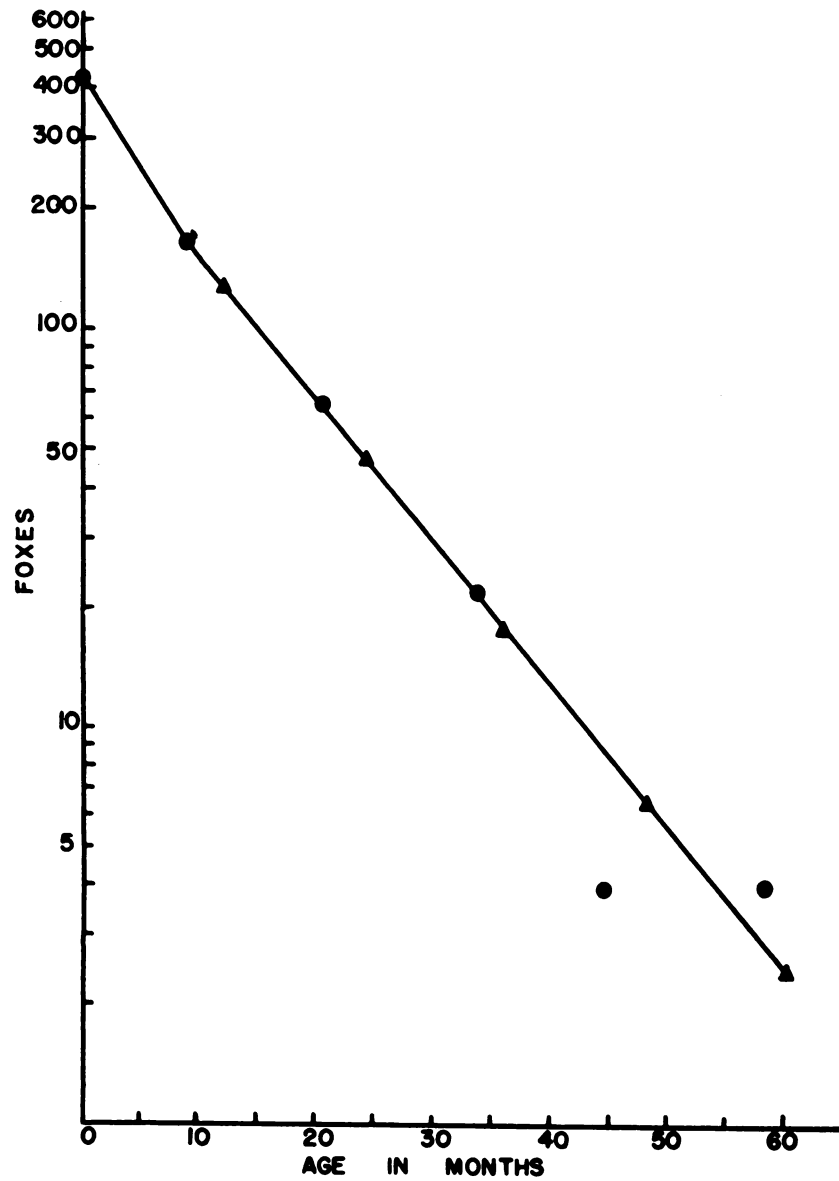| Time after marking	Recaptured at various times			
	Males		Females	
	Number	percent	Number	percent
0	115	100	134	100
1	73	62	101	75
2	42	37	70	52
3	26	23	38	28
4	6	5	15	11
5	3	2	8	6
6	0	0	0	0

FIGURE 3. *Representation of mortality of foxes.[10] The number of foxes is given on logarithmic scale on the ordinate and the age on arithmetic scale on the abcissa. The straightness of the line indicates constant probability of dying after the first year.*

Life Table

The above arrangements of data present many similarities of course to the life table so widely used in human affairs. The life table is a very convenient technique for recording the data about mortalities and has many important uses that have been amply described.[2,3,4] However, for studies of wild animals the life table in its extensive form suffers a number of deficiencies. In the first place, adequate data are rarely available for wild species since it is extremely difficult to find dead individuals and to know the age of the individuals at death. Secondly, the life table of course is retrospective and simply gives the history of the deaths that have occurred in the past. Thirdly, groups or cohorts of animals are combined that have had different exposures to risks of mortality. Thus, animals born five years ago and ten years ago would suffer different risks of mortality but would be included in one life table. For these reasons the more simplified versions, given above, perhaps protect the reader from unjustified assumptions concerning the possibilities of predictions. Nevertheless, the life table is a convenient and concise method of describing the findings about mortalities of animals.

Data of the type used in life tables can be graphed easily to give a vivid picture of mortality (fig. 3). In this case the age of trapped foxes[10] was analyzed. The data were collected during 5 years and thus foxes 20 months old when trapped were not all born in the same year. Thus, yearly differences in mortality are smothered. These data are the same kind as those in the third column of table 1. When plotted on semilogarithm paper it is clear that mortality is higher in the first year but lower and constant thereafter since the slope is constant.

Analysis and Evaluation

We now return to the original problem of the evaluation of methods of measuring mortality. There are only three basic methods of collection of data. (1) Time since marking. (2) Recapture information. (3) The proportion surviving. Indeed, in many ways the last two overlap. Evaluation of a measure of mortality obviously requires that the data be collected in at least two different manners. It is clear that simply recalculating the same data by a slightly different arithmetical procedure is not an evaluation of the measure of mortality; it is simply an indication of whether or not the arithmetic was correctly performed. Thus, if one wishes to evaluate a measure of mortality of foxes by some age criterion it is necessary to use a recapture procedure rather than simply some different age measure. (Using two techniques for determination of age only evaluates the techniques). Thus, the only way really to evaluate a method of determining mortality rates is to collect data in a different manner.

Some similar problems arise in the calculations of the data. Here again, simply calculating the figures by a different method from the same data is merely an exercise in checking arithmetic. However, another problem arises. As indicated above the use of different definitions can give different numerical values when using the same data. It will be remembered from above that when values of q are low then there is little difference between the use of d and of q. Let us follow through (Fig. 1) a numerical example when q is rather high such as 0.7. Under these circumstances E calculated from d would equal 0.9 whereas E calculated from q would equal 1.6. A person naively attempting to evaluate a measure of mortality would think that these different answers meant that the measure was unsatisfactory. Obviously, the difference arises simply from the mathematical definitions related to the duration of the time unit. These remarks apply equally well to the life table tabulations.

The use of these approaches in the field cannot easily be discussed since the variety of techniques depends so greatly upon the details of the life history of the individual species. In general, one has to collect information about the age of death or at least number dying in a particular time period. Clearly, the possibilities of obtaining satisfactory data depend upon the life history of the species and the time available. Before planning a study to evaluate mortality rates one should be sure that adequate time is allotted to get a satisfactory amount of data. A thorough knowledge of the life history of individuals is absolutely necessary to evaluate the assumptions concerning differences in mortality between seasons, between ages, between sexes. There is no easy road to this aspect; the investigator will simply have to use his ingenuity to avoid the pitfalls. At least in some cases the differences may not be important but they should be recognized and some statement about their relative importance made.

The separation of causes of mortality has been neglected in the above discussions primarily because it is difficult to diagnose different causes of death of wild animals. The simple statement that a fox was found dead with a high level of parasitic worms is by no means proof that the worms caused the death of the fox. However, in some cases, especially hunting or trapping mortality, it is possible to divide the causes of death into natural causes and hunting causes. Fortunately, a mathematical device allows a very easy calculation in this situation. It will be remembered that $n_t = n_n e^{-dt}$ where d, of course, is the death rate from all causes. A fortunate property of exponents is that they can be added and thus d can be subdivided into $d_1 + d_2 + \ldots + d_x$. Under these circumstances if the number of deaths due to cause 1 or 2 or x can be determined then the death rate for that particular cause can be calculated and put into the formula. Thus, for example, if the total mortality for the year is known and the hunting mortality is also known then the natural mortality for the year can be calculated from $d = d_h + d_n$. However, since compensation may occur in that an animal killed by a hunter might have died the next week of natural causes, a factor must be added to apportion this compensation properly.

Conclusions

The evaluation of mortality data presents several opportunities. In the first place, data have been obtained from literally hundreds of studies of natural populations so that generalizations and detailed studies are now available. For example, many studies of adult songbirds show that q = 0.5. And thus, E = 1.5 years. Another encouraging aspect is that birthrates or the number born is known for a large number of vertebrates and thus, using the assumption of a stationary population, the death rate can be easily calculated since b, the birthrate, under these circumstances has to equal d, the death rate.

The existence of several methods for collecting data and also for calculating the results provides assurance that for a particular species some combination of techniques will be available. Thus, a person embarking on the study of mortality rates of some hitherto unstudied species could from the literature first get an approximation of what the mortality rate might be from data on related species and secondly, find some methods that had reasonable assurance of producing results. In addition, he may be so fortunate as to learn of some pitfall in assumptions that might trap the unwary investigator.

Lastly, as in all such studies, the problem of assumptions, both biological and mathematical, must be confronted. Of course, all of the figures mentioned above have been obtained by a sample from a population. Thus, the appropriate tests of significance of differences must be applied in making comparisons from one group to another, from one season to another, or from one area to another. Fortunately,

several different statistical techniques are available for testing the null hypothesis in respect to a particular mortality rate. The other assumptions deal primarily with differences in seasons and sex or age composition. The only way to test these assumptions is by astute collection of information and careful consideration of the life history of the species.

In the introductory statement the term accuracy was used. Perhaps it is necessary to distinguish between the terms accuracy and precision. The latter term refers primarily to the repeatability of results whereas the former term refers to the correctness of the value. To cite a simple example, a person might measure the length of a table with a ruler that was incorrectly marked. His accuracy would be very poor because of a defect in his instrument but his precision might be very high because it always gave him the same answer even though wrong. In studying mortality rates in nature, the precision of a measure can usually be estimated simply by doing the study several times or by using somewhat different methods. However, the accuracy of the value may be extremely difficult to determine because it is possible that under no circumstances can the true mortality be determined for comparison.

The mechanics of computation of mortality rates, fortunately, are relatively minor. Indeed, even without computers the arithmetic can usually be done easily by simply using tables of natural logarithms. However, computer programs are available and can save time in many cases. Nevertheless, as is always true, the computer itself does not add any virtues to the analysis other than speed of calculation.

A final statement is necessary concerning the objectives of the study. Let us assume that the investigator wishes to determine something about the mortality rate of foxes. Before his field work starts he should outline in quantitative terms the objectives of the study. Let us assume that he, in a general way, is interested in whether the mortality of foxes in areas where rabies is known to exist is greater than that of foxes in areas where rabies is not known to exist. It is known that q for foxes equals about 0.5 and hence, he can be sure that the observed values will be somewhere in that neighborhood.[10] Now to plan his collection of data properly, he needs to have some idea of how great a difference he wishes to be able to detect. It would be absurd to attempt to detect a difference between 0.49 and 0.51 since the amount of data necessary would be astronomical in number. However, suppose that the investigator is content to show that q for foxes in rabies areas is 0.6 or higher whereas in nonrabies areas it is 0.4 or lower. With these quantitative objectives in mind he can examine the possible procedures for obtaining data, determine how many traps must be set for foxes and hence purchased and how many years he must study the problem. By this means, the costs of the program can be determined. If the investigator finds that his quantitative objectives cannot be met within the budget allowed then he should courageously state that he will not embark upon such a study because it would simply be a waste of time. All too frequently, data are collected but conclusions cannot be drawn because the precision is too low.

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