Notes on the Estimation of Survival Rates
from Age Distributions of Deer

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The widespread use of the Severinghaus (1949) method for determining deer ages has resulted in knowledge of the age distribution in a number of deer herds. Under certain conditions the rate of survivals may be estimated from these age distributions.

In the following discussion those familiar with the paper by W. E. Ricker (1948) entitled "Methods of estimating vital statistics of fish populations" will soon recognize the very heavy use we have made of this important work. It is to be hoped that Dr. Ricker is successful in his plans to reissue this publication, for aside from its importance in the field of fisheries, it contains much which is directly applicable to research on game animals.

Certain terms used here need explanation. A "year-class" comprises all deer born during a certain fawning season, while an "age-class" refers to all animals of a stated age. Thus each year-class passes through successive age-classes, year by year. The term "recruitment" refers here to the addition of deer to the <u>hunted</u> herd. Under a buck law, for example, a year-class is not recruited to the hunted herd until its second fall, and then recruitment may be only partial.

Samples showing the age distribution of deer are generally taken to reflect a parallel distribution of ages in at least part of the herd, revealing what is known as the "age structure." Thus, as a start, we assume

1. That at least some ages of deer are equally vulnerable to hunters, and,

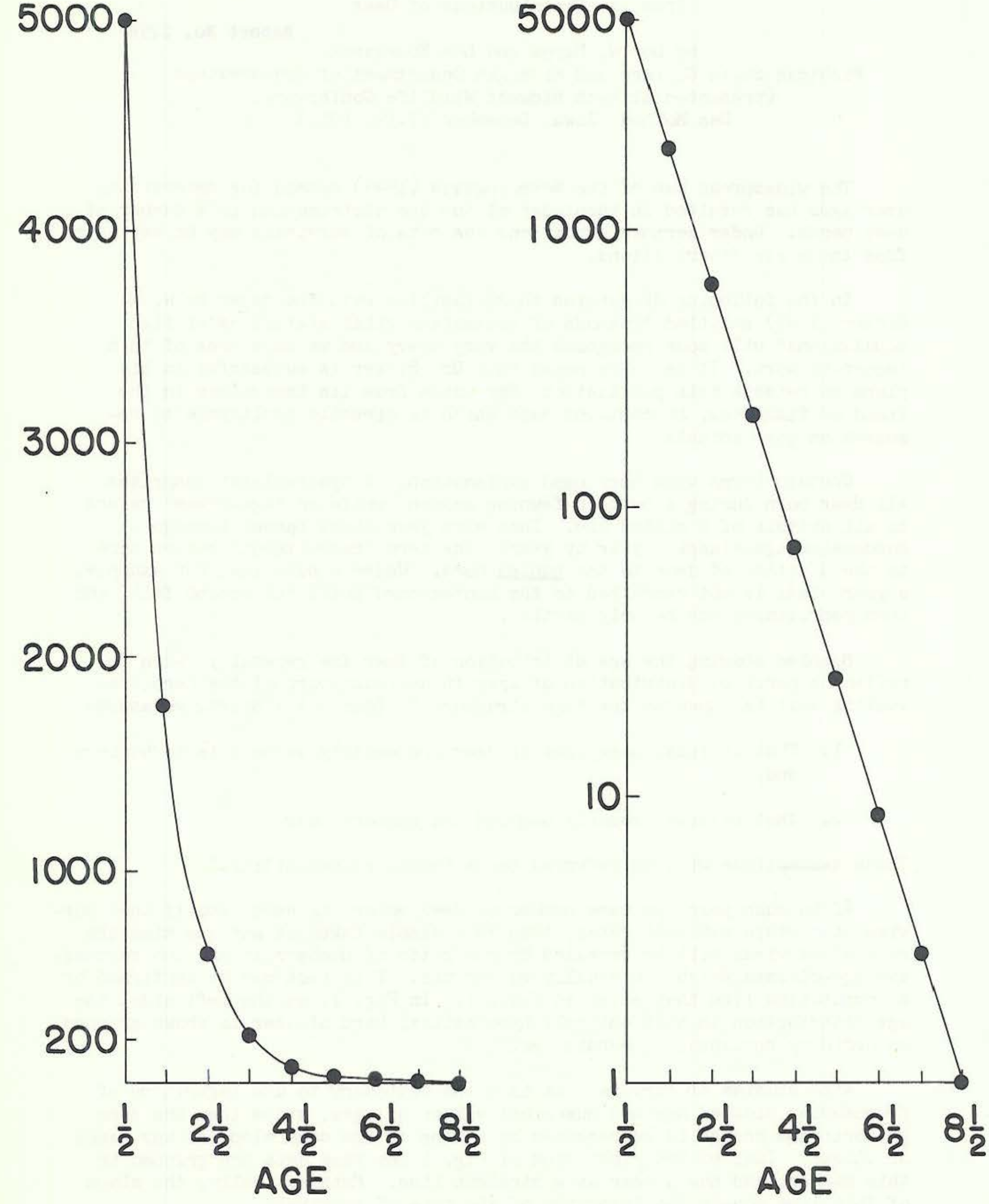
2. That we have properly sampled the hunters' bag.

These assumptions will be referred to as "equal vulnerability."

If in each year the same number of deer enter the herd, and if they survive at certain constant rates, then in a sample taken at any one time the rate of survival will be revealed by the ratio of numbers in any two successive age-classes which are equally vulnerable. This fact may be confirmed by a computation like that shown in Table 1. In Fig. 1, on the left side, the age distribution in this entirely hypothetical herd of deer is shown graphed on ordinary rectangular coordinates.

With studies of survival, it is often customary to use logarithms of frequencies plotted against numerical values of ages, since then the same proportioned change is represented by a line of the same slope at any range of values. Thus on the right side of Fig. 1 the same data are graphed in this manner, and now appear as a straight line. Mathematically, the slope of this line equals the logarithm of the rate of survival.

FIG. 1



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Repeating the comparison, now with actual data, Fig. 2 shows on rectangular coordinates the age distributions for bucks from two areas of New York State in 1947 stated as percentages for comparison purposes (data used here by courtesy of C. W. Severinghaus). These same data are shown in Fig. 3, plotted on the semilogarithmic scale. A major difference stands out as one in trend of the two lines, implying different survival rate.

When graphed in this manner, these age distributions closely resemble the "catch curves" of fisheries research, as discussed by Ricker (1948). In particular, the distribution relating to Adirondack deer shows an "ascending left limb, a dome-shaped upper portion, and a long descending right limb," described by Ricker as representing, respectively, the lesser vulnerability of younger animals, increasing vulnerability with age, and then, with equal vulnerability of older animals, the decreasing numbers with passage of time. A parallel situation appears to exist for deer, with the younger age-classes being represented in lesser proportion as compared with older classes. Reasons for this situation, which have been discussed by Severinghaus (1951) and Shaw and McLaughlin (1951), may include poor antler development and a buck law, hunter discrimination against small deer, and reticence about shooting such, and habits of the deer. Quite clearly, there are areas where the younger age-classes are not included in the samples in as great proportion as are older animals in the same herd. We use here the term "kill-curve" in reference to an age distribution of deer, plotted, as in Fig. 3, on a semilogarithmic scale.

The estimate of apparent survival rate may be made in several ways, once it appears that there is a reasonably straight line in at least the right limb of the curve. The data should first be plotted on semilogarithmic paper to identify the straight portion of the curve, if it exists. Then, to evaluate the survival rate, one may:

1. Use a protractor constructed of transparent plastic (or of thin paper, oiled) upon which have been drawn several lines of different slopes, corresponding to several rates of survival. This protractor, laid over a kill curve drawn to the same scale, allows rapid, if approximate, evaluation of the apparent rate.

2. Draw an eye-fitted line and compute the survival rate as the ratio of the numbers at two points on the line, spaced one year apart, the older divided by the younger.

3. If there appears to be a straight line beyond a certain age class, then divide the sum of the numbers in all age classes older than this class by the same sum plus the number in this class.

4. Fit a line by formal methods, and the slope will equal the logarithm of the rate of survival. Since the rate is always a fraction, its logarithm is negative.

By the second method above, starting with the $2\frac{1}{2}$ year animals, the survival rate among the Adirondack animals appears to have been about 0.5. For the deer from the Catskills, a straight line appears from the youngest animals, and indicates survival to have been about 0.2 per year.

FIG. 2

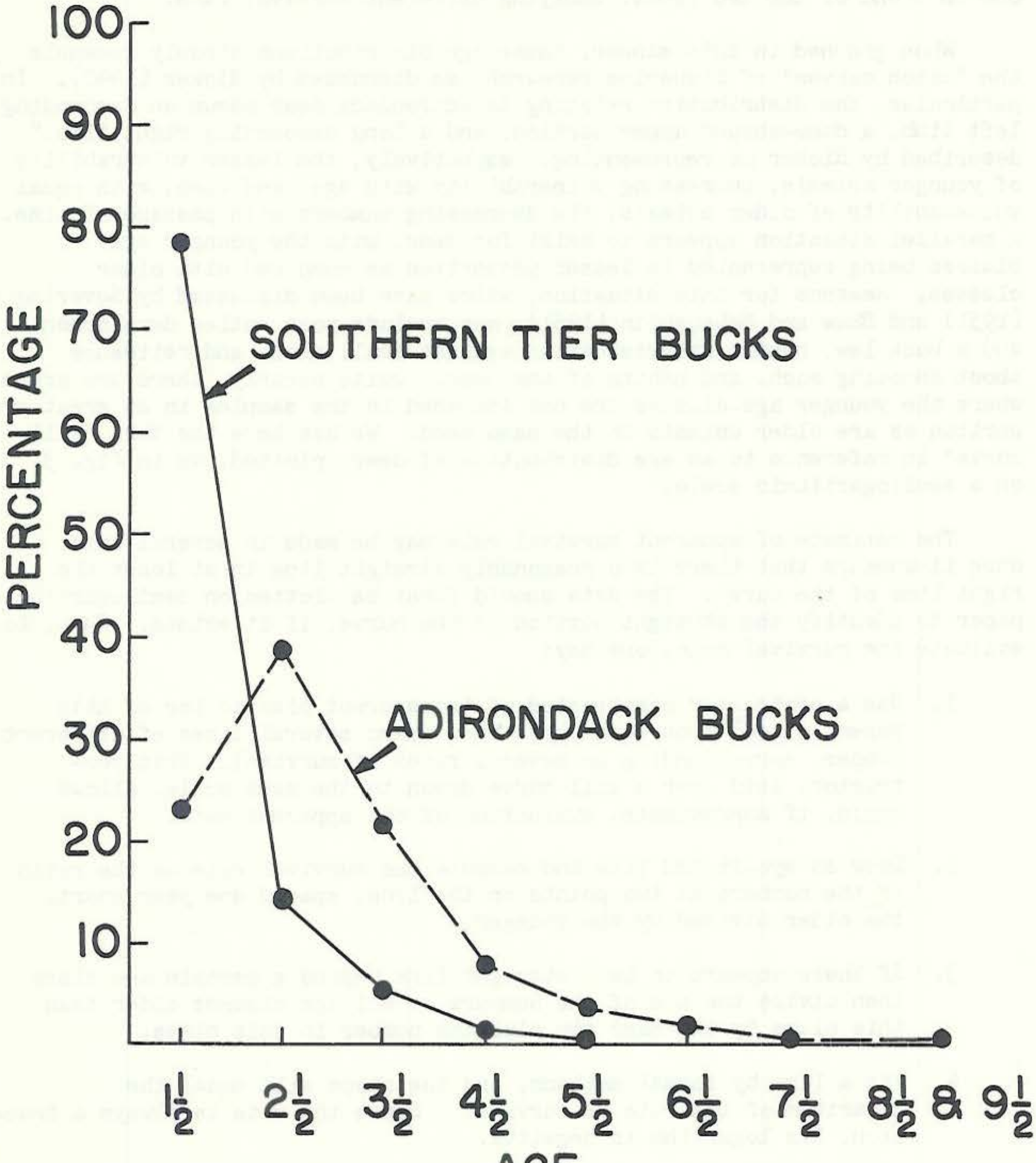

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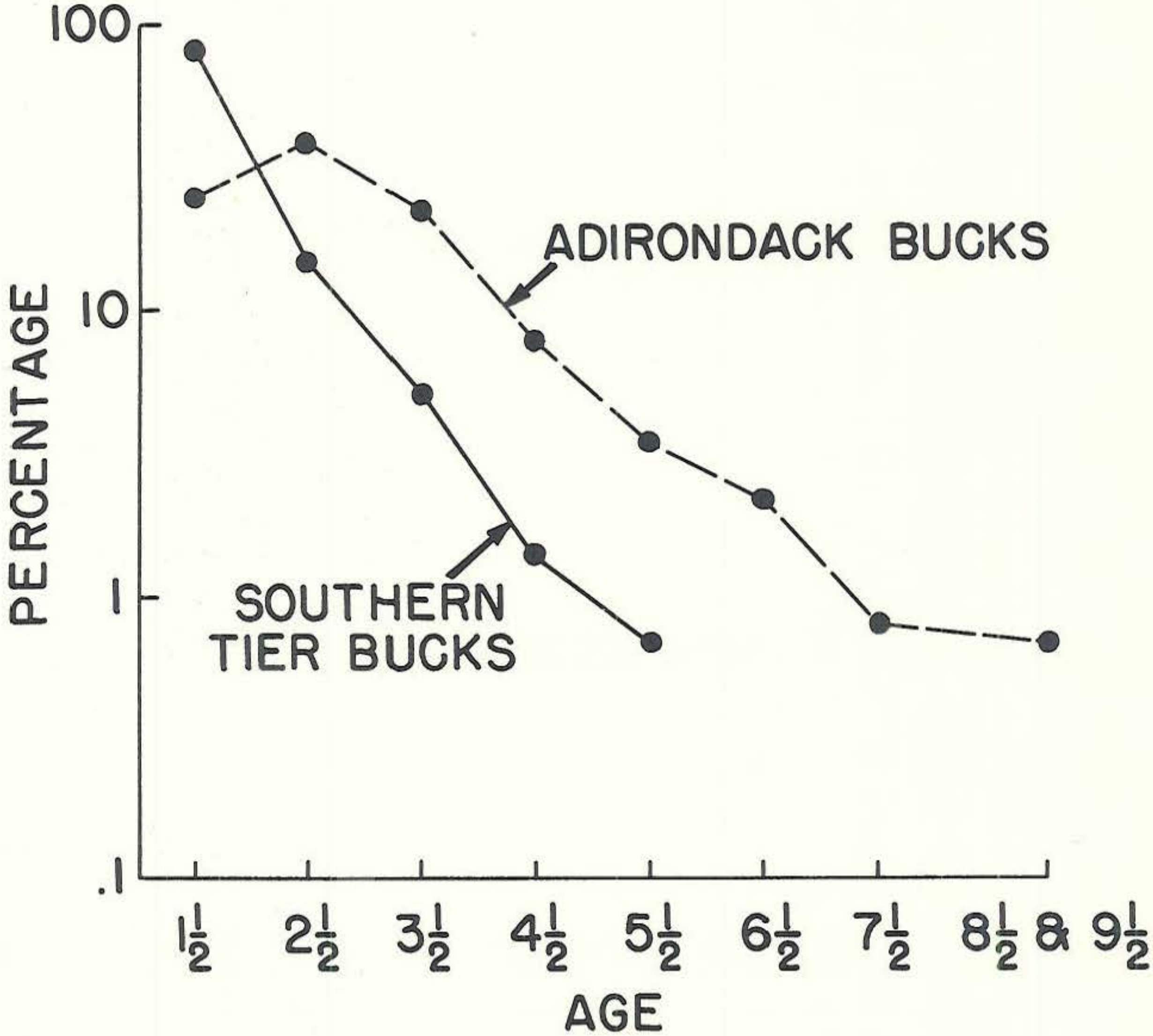
FIG. 3



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There are certain conditions required for estimation of survival rate from the descending right limb of the kill curve. The slope of this right limb equals the logarithm of the rate of survival and an estimate of rate of survival may legitimately be made from the trend of the data when:

1. There is equal recruitment to the hunted herd each year.

2. There is equal vulnerability to hunting for the age classes being considered.

3. The survival rate experienced by these age classes is constant with respect to both time and age.

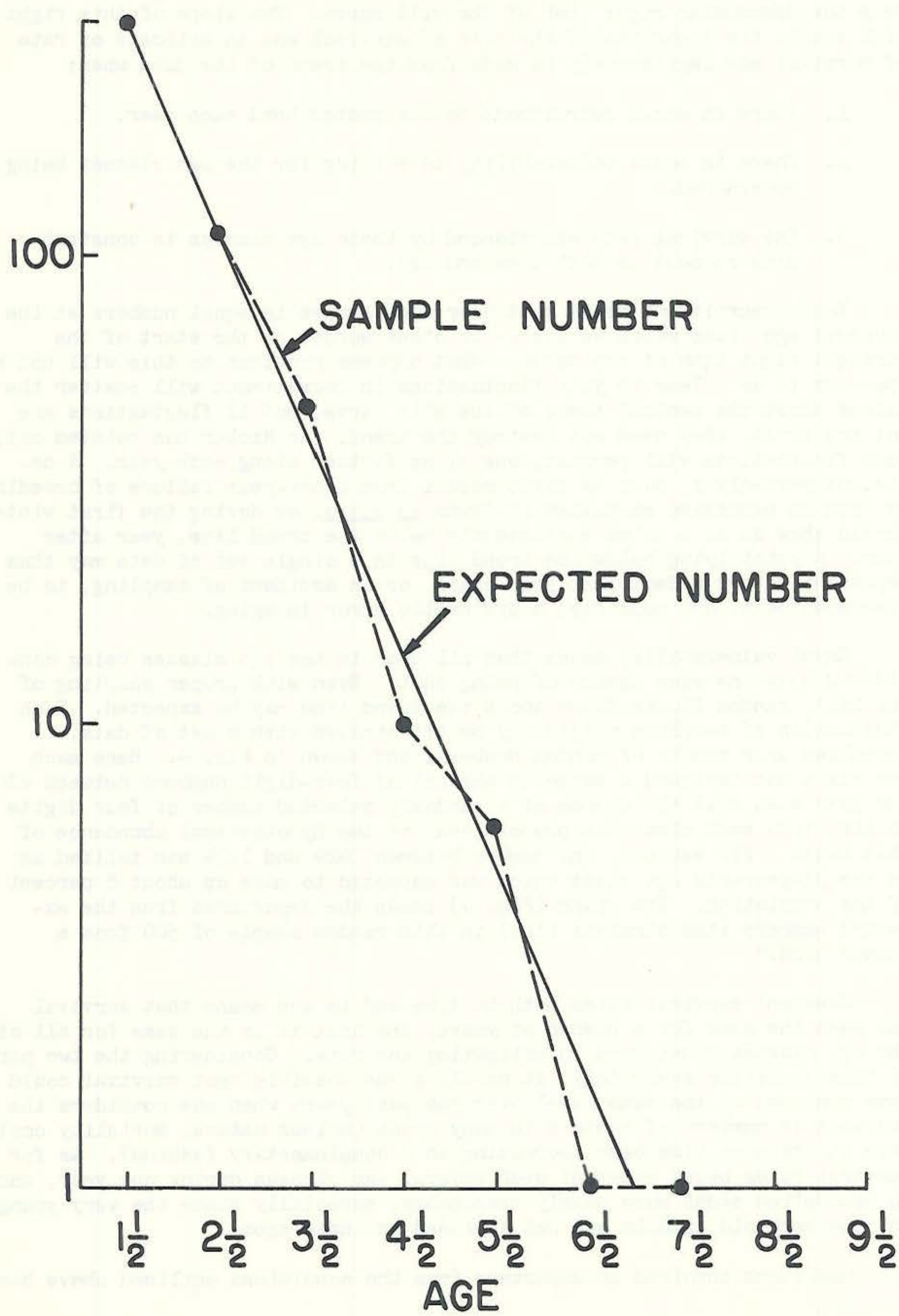
Equal recruitment means that deer must arrive in equal numbers at the youngest age class which we use -- in other words, at the start of the straight right limb of the curve. What happens previous to this will not be apparent to us. Year to year fluctuations in recruitment will scatter the values about the central trend of the kill curve, but if fluctuations are not too great, they need not destroy the trend. As Ricker has pointed out, such fluctuations will persist, one class farther along each year. A deficient year-class, such as might result from a one-year failure of breeding or from an excessive mortality of fawns _in utero_, or during the first winter, should show up as a point consistently below the trend line, year after year. A point lying below the trend line in a single set of data may thus represent either a deficient year class, or an accident of sampling, to be discussed next, or, possibly, a systematic error in aging.

Equal vulnerability means that all deer in the age classes being considered have the same chance of being shot. Even with proper sampling of the kill, random fluctuations about the trend line may be expected. Such fluctuation of sampling origin may be illustrated with a set of data, assembled as a sample of random numbers, and shown in Fig. 4. Here each age class was assigned a range in the set of four-digit numbers between 0000 and 9999 such that the chance of a randomly selected number of four digits falling into each class was proportional to the hypothetical abundance of that class. For example, any number between 0429 and 1224 was tallied as in the $3\frac{1}{2}$-year-old age class which was supposed to make up about 8 percent of the population. The graph (Fig. 4) shows the departures from the expected numbers (the straight line) in this random sample of 500 from a "paper herd."

Constant survival rates both in time and in age means that survival has been the same for a number of years, and that it is the same for all of the age classes considered in estimating the rate. Considering the two parts of this condition separately, it hardly seems possible that survival could have remained at the same level over the past years when one considers the increase in numbers of hunters in many areas (unless natural mortality could have at the same time been decreasing in a complementary fashion). As for survival rates being constant over several age classes during one year, such an assumption seems more nearly reasonable, especially since the very young and the very old animals are not included in these ages.

Questions involved in departure from the conditions outlined above have

FIG. 4



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been discussed in some detail by Ricker (1948) and cannot even be mentioned here except to state:

1. That a straight right limb is possible by combination of certain departures from these conditions.

2. That a changing rate of recruitment is likely to appear as a change in the slope without visibly affecting the straightness of the line.

3. That the effect of a decreasing survival rate is, in general, to produce a right limb concave upward, with an opposite effect for an increasing rate.

The last point above is illustrated in Fig. 5, which is drawn from a set of computed data, where the rate of survival was changed from 0.65 to 0.35, and the animals of the $1\frac{1}{2}$ year age-class were only half as vulnerable to hunting as older animals.

One of the very interesting points relating to such a change in survival rate is the fact that the survival rate apparent from comparison of two adjacent age classes relates largely not to the present but to the period in the past when these age classes were becoming vulnerable to hunting. This point is apparent in Fig. 4. An explanation is apparent if the annual survival rate may be considered to be the product of these two component survival rates with these characteristics:

First, a rate which is constant for any one age-class from year to year, although the level of survival may vary from age-class to age-class. As an approximation, this may be termed "survival of natural mortality", although a more precise term is "age-specific survival rate."

Second, a rate which, in any one year, is constant for all age classes being considered, but which may vary from year to year in its overall effect. This rate will be termed here "survival of hunting mortality" even though natural catastrophes would also show their effect here. Again, a more precise term is "time-specific survival rate."

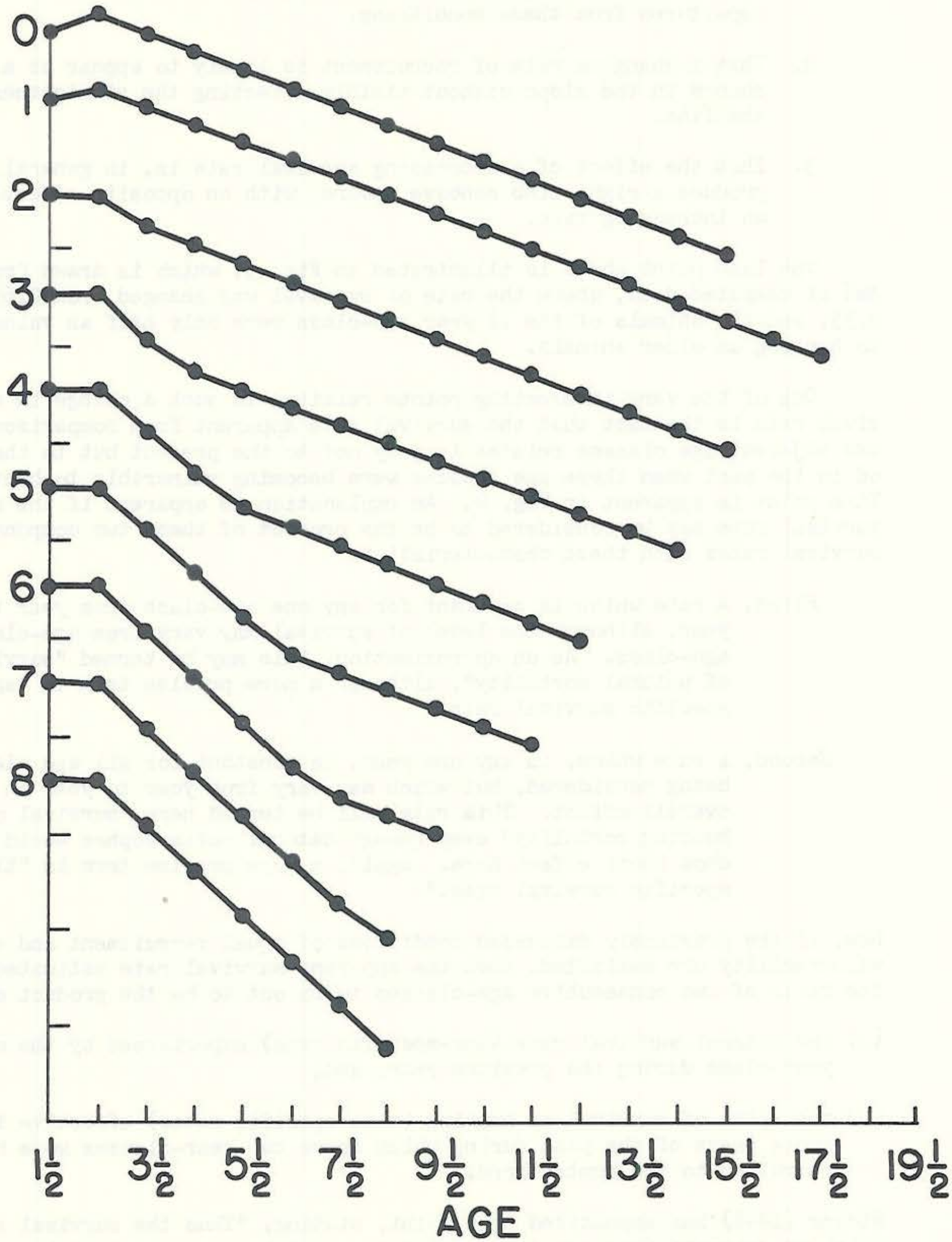
Now, if the previously discussed conditions of equal recruitment and equal vulnerability are satisfied, then the apparent survival rate estimated from the ratio of two consecutive age-classes turns out to be the product of

(a) the natural survival rate (age-specific rate) experienced by the older year-class during the previous year, and,

(b) the rates of survival of hunting (time specific rates) effective in those years of the past during which these two year-classes were being recruited to the hunted herd.

Ricker (1948) has emphasized this point, stating, "Thus the survival rates which we estimate from age-frequencies in a catch are ancient history."

FIG. 5



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Conclusions

1. Rates of survival may conveniently be judged from a "kill curve," a graph constructed by plotting the logarithm of the frequency (on the ordinate) against the numerical value of the age (on the abscissa). Lines of equal slope on such a graph indicate equal rates of proportional change. The following points relate to such a curve.

2. A common characteristic of catch curves from fish populations and of some kill curves from deer, is the presence of an ascending left limb, reflecting a vulnerability lesser in the younger age classes, and increasing with age.

3. A straight line relationship among the age classes under consideration, under certain conditions reflects the survival rate and allows its estimation. The required conditions are:

   (a) Equal recruitment to the hunted herd each year.

   (b) Equal vulnerability to hunting (for those classes considered).

   (c) Survival rates both constant in time (from year to year) and constant in age (from age class to age class for those classes considered).

4. It is possible for a linear relationship to exist in the absence of these conditions, and therefore a straight line is not, of itself absolute proof of a uniform survival rate.

5. Under certain conditions less demanding than those above, a survival rate may be estimated from the representation of two adjacent age-classes, and this rate is a compound quantity, the product of both:

   (a) The natural survival rate (age-specific rate) experienced by the older year class during the previous year, and

   (b) The rate of survival of hunting (time-specific rate) experienced by the two year classes during the years of the past when they were becoming fully vulnerable to hunting.

The first two of the conditions necessary here are identical to those listed above, but the third differs. The conditions stand as:

1. Equal recruitment to the hunted herd each year.

2. Equal vulnerability to hunting for those age classes being considered.

3. Survival rate being divided into two components:

   a. Survival to natural mortality factors possibly varying from age class to age class, but constant from year to year for any particular age class (age-specific), and,

b. Survival to hunting mortality possibly varying from year to year in overall effect, but in any one year being constant for all age classes considered (time-specific).

These latter conditions may more nearly characterize deer herds in many areas, and under them the more important hunting becomes as a mortality factor, the more nearly the indicated survival rate reflects "ancient history."

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Table I. Numbers of survivors expected with unifrom recruitment (10,000) and uniform survival rate (0.35), all vulnerable during first season. The age distribution for any year reads across the table from right (younger animals) to left. The history of any year-class reads from the top downward.

	Year - Class									
Year	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
1944	3,500	10,000								
1945	1,225	3,500	10,000							
1946	429	1,225	3,500	10,000						
1947	151	429	1,225	3,500	10,000					
1948	52	151	429	1,225	3,500	10,000				
1949	18	52	151	429	1,225	3,500	10,000			
1950	6	18	52	151	429	1,225	3,500	10,000		
1951	2	6	18	52	151	429	1,225	3,500	10,000	
1952	---	2	6	18	52	151	429	1,225	3,500	10,000

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