THE GROWTH OF STARLING, *STURNUS VULGARIS*, POPULATIONS

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INTRODUCTION

BECAUSE of the newness of the studies of bird populations, considerable confusion exists concerning the theory and data relating to increases in numbers. This paper attempts to clarify at least certain aspects and to stimulate studies of bird populations. First the theory of growth of populations will be presented briefly, and then the data available for avian species. I am indebted to Dr. R. V. Rider for advice on the mathematical aspects of this paper.

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At the beginning we should have a clear idea of the subject being discussed. A population of birds may grow just the same as a population of cells (an individual bird) grows. This population will increase until it reaches the maximum number that the area can support. Although in the laboratory, conditions can be kept constant so that an area will support a certain number, in nature the conditions change every year so that the area can support a different number every year. These changes in conditions cause frequent changes in the size of the population. It is essential to distinguish between two entirely different problems: (1) the growth of a population under stationary conditions; and (2) the changes in a population due to changing conditions. The first problem is the concern of this paper; the second problem will be discussed only in reference to the first.

As might be expected, the theory of populations was developed by studies of human beings and then checked by laboratory experiments. The literature on the subject is tremendous, but Pearl (1940) gave a recent summary of theory and a list of references. It was found that the growth of the human population of the United States could be described by a curve called the logistic (Fig. 1). This curve is characterized by slow initial growth, then rapid growth, and then stability at the upper asymptote. Laboratory work on fruit flies, bacteria, and protozoa confirm this relationship. In nature, however, birds do not show these relations very satisfactorily. Data for the lower part of the curve are hard to get because a species is seldom far enough below the upper asymptote to be suitable for study, and it is impracticable to reduce a species to such a low level. Data for the asymptotic part of the curve are scarce because in nature the asymptote varies from year to year and confuses the analysis by superimposing the changes caused by the environment upon changes due to growth. Hence for practical purposes the central and upper section of the curve is the only part that can readily be observed in nature. When a population is in the central part of the curve, it is so far below the capacity of the

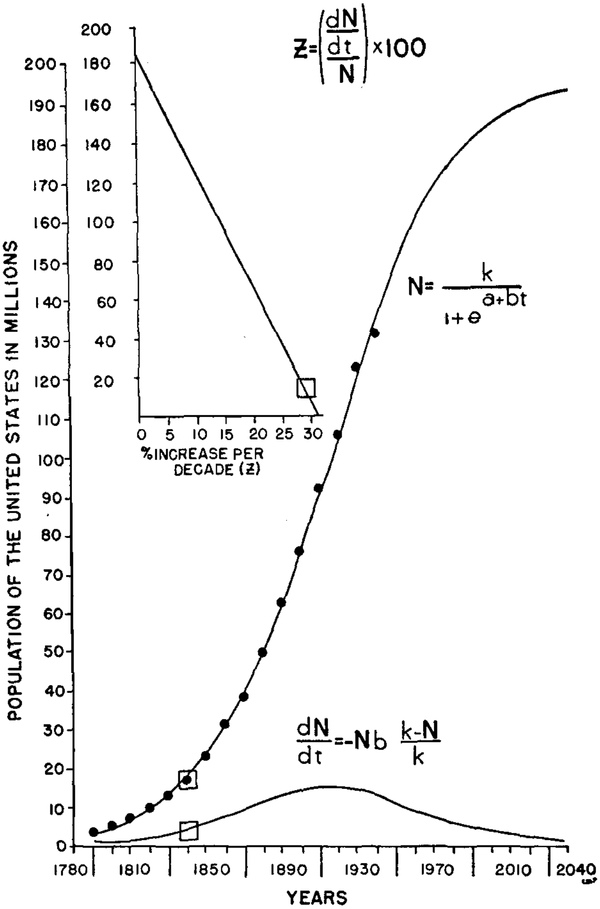

FIGURE 1. The growth of the human population of United States, the rate of growth (first derivative) and the percentage increase.

area (the asymptote) that its growth is independent of usual annual variations in food and shelter. It should be noted that the central section can be drawn as a straight line without altering the curve significantly.

Thus far we have considered the increase in numbers (N). Now let us consider the rate of increase per unit time (dN/dt) as shown in the lower curve (Fig. 1). The rate is low at first, increases to a maximum, and then decreases to zero at the upper asymptote.

Now lastly let us consider the percentage increase (Z) given in Figure 1. These values are obtained by dividing the rate of increase (dN/dt) by the population (N) at that date. The result is a descending straight line (Fig. 1). Consider a specific example. In the year 1840 the population of the United States was about 17 million; the rate of increase was about 5 million per year, and the percentage increase was about 29 (compare squares in Fig. 1). Consideration of another year, for example 1940, shows a high population, a high but declining rate of increase, and a low percentage increase.

The descending straight line (Z) requires special attention because it agrees with the "inverse ratios" so frequently referred to in ornithological literature. Its meaning is clear. At high populations the percentage increase is low. At low populations the percentage increase is high. Thus, the percentage increase is inversely proportional to the population. Now let us consider data for some species of birds.

Increasing Populations

The European Starling, *Sturnus vulgaris*, is a suitable species for analysis. The Christmas census data from 'Bird Lore' (Audubon Magazine) were generously supplied by Dr. Leonard Wing for the Starlings seen per hour for various states. These data, smoothed by moving averages of threes, are plotted on semilogarithm paper by years for New York, Massachusetts, and Ohio (Fig. 2). It is at once apparent that the populations increase logistically to an asymptote of about 40 Starlings per hour for New York, 35 for Massachusetts, and perhaps 20 for Ohio. The fluctuations are great, but the flocking habits of the species and variations in census methods, as well as usual annual changes in weather and food, probably are adequate to explain much of the fluctuation. However, it should be mentioned parenthetically that a more elaborate treatment of the theory of the logistic predicts inherent oscillations about the asymptote.

The Starling was introduced essentially into a vacuum in the sense that the environment permitted the birds to increase. Basically the same situation would be obtained if a species, for example Robins, were reduced by poisoning to a small fraction of their present population. Note especially in this hypothetical (and impossible) reduction that the environment was not altered. In other words the upper asymptote was not changed for the Robins. The asymptote for the Starlings was far above their population level until about 1930 in New York.

Data for other introduced species are not available or suitable except for Einarsen's (1942, 1945) reports on the increase of Pheasants on an island. In 1937, two males and six females were introduced. A spring census in succeeding years gave 40, 100, 426, 844, 1540, and 1898 birds or a percentage increase of 400, 230, 438, 118, and 43 per cent, respectively. Although the data are meager, there is a suggestion of a decline in the rate of increase with increasing populations.

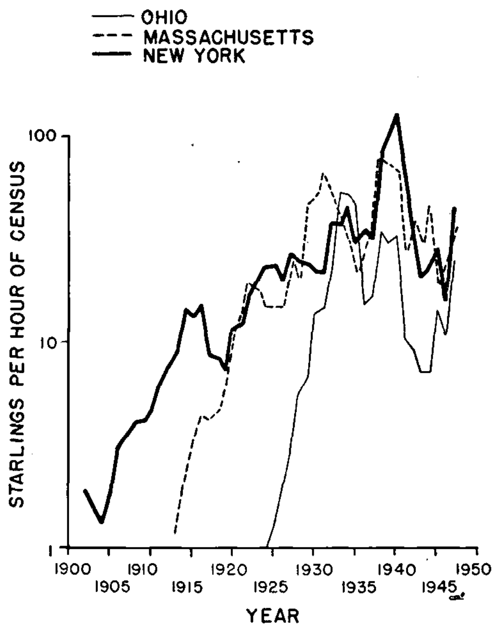

FIGURE 2. The number of Starlings seen per hour in three states, calculated by moving averages of threes.

Perhaps the best documented observations are by Errington (1945) on Quail. He was dealing with a natural population in an environment which was changing, that is, the upper asymptote was moving up and down. If we assume that each phase discussed by Errington has a different level for the asymptote, then the expected relation of population and the rate of increase is fairly clear. For example, from his Figure 6 we can set up a table for population density and per cent gain: 45 (262%); 97 (228%); 122 (188%); 196 (112%); 236 (69%); 288 (43%); 290 (40%); and 339 (28%). Errington also summarized from other authors' data which, although usually meager, agreed with this inverse relationship.

Lack (1946) presented data for 19 years on the Heron population in England. Generally the increases vary inversely with the population.

Fisher and Venables (1938) plotted data for the increase in Gannets at a gannetry. These data agree with the theory of the logistic.

Kendeigh (1934: 309) presented data about House Wrens from which he concluded that "the number of broods per female per season tends to vary inversely with the total population" although his data are not statistically convincing. However, Kendeigh (1937: 103) remarked later that "percentage increase in number was found not to be correlated with number of adults present." It must be emphasized that Kendeigh's data refer to annual fluctuations of a supposedly asymptotic population. It is, therefore, not surprising that the "inverse ratio" does not occur because the fluctuations do not depend upon population as much as upon environmental factors.

Discussion

This paper makes no pretense of covering the literature for every possible evidence of inverse ratios. Actually suitable data are practically non-existent for a sufficient period of time. The data from the Christmas censuses are fine for introduced species, and some game management studies have data for almost enough years. But it is necessary to have data on spring and fall populations or on spring population and success in nesting for a period of 20 to 30 years before suitable analysis can be done. It is hoped that the presentation of the theory and the meager data will stimulate studies of this fundamental problem.

Another aspect requires clarification. We have referred to a fluctuating environment and asymptotic population. To know something about the capacity of the environment to support birds it is necessary actually to measure the environment. We should have data, not on Starlings per hour or Quail per acre, but on Starlings per pound of food or Quail per nesting site. The bewildering complexity of this task should not daunt us but should stimulate a concerted effort towards a solution even though several generations of ornithologists will be required for completion.

Summary

The rate of increase of a population may be described by the logistic curve which predicts a slow initial increase, then a rapid growth, followed by a stationary population at the upper asymptote. The number of Starlings per hour recorded by the Christmas bird census for New York, Massachusetts, and Ohio fits the logistic curve reasonably well. It is of primary importance to distinguish between changes of asymptotic populations which depend upon the environmental

capacity and, on the other hand, changes of growing populations, which depend upon the population level.

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