# EXPERIMENTAL DEMONSTRATION OF VOLTERRA'S PERIODIC OSCILLATIONS IN THE NUMBERS OF ANIMALS

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(With Four Text-figures.)

FROM purely theoretical considerations Lotka (1920) and Volterra (1926) concluded that a biological system consisting of two interdependent species (predator and prey) will exhibit regular periodic fluctuations in respect to the absolute and relative abundance of each species, even when random fluctuations due to external environmental factors have been eliminated. So far as is known this conclusion has not been investigated by direct experimental methods.

Two types of inherent oscillation are conceivable. The first is that considered by Lotka and by Volterra. If $N_1$ is the density of population of the prey, and $N_2$ the density of population of the predator, then

$$\left.\begin{aligned}\frac{dN_1}{dt} &= b_1 N_1 - k_1 N_1 N_2 \\ \frac{dN_2}{dt} &= k_2 N_1 N_2 - d_2 N_2\end{aligned}\right\} . \qquad \ldots\ldots(1)$$

In these equations $b_1$ is the birthrate of the prey, and $d_2$ is the deathrate of the predator. The rate of increase of the population of the prey is decreased by the rate at which the prey is consumed by the predator ($k_1 N_1 N_2$) and if the rate of reproduction of the predator depends on the number of prey available for consumption the net rate of increase of the predator will be given by the difference of two factors one of which depends on the number of prey available ($k_2 N_1 N_2$) and another which represents the death rate of the predator population ($d_2 N_2$). The actual rate of increase of the population of either species can be positive or negative and a generalised solution of the equations (1) shows that, under the conditions laid down, a series of periodic fluctuations may be expected in the values of $N_1$ and $N_2$.

It is, however, necessary to consider a second type of fluctuation which is aperiodic. For example, an epidemic cannot start in a population containing a large number of immune individuals but if the concentration of the latter diminishes owing to a loss of immunity or the infiltration of non-immune individuals, then an epidemic is liable to start when a critical threshold of non-immune individuals has been reached. Once the epidemic has started it will continue until the original state of the immune population has been again reached—and the cycle will be repeated. This type of sudden fluctuation is obviously different from that discussed by Lotka and Volterra[1]. It has been shown experimentally (Gause, 1934) that in a population of two infusoria (*Didinium nasutum* as predator, and *Paramecium caudatum* as prey) the interaction of the two species is aperiodic and leads to a complete disappearance of both species. If immigration is allowed from external sources, fluctuations of the second theoretical type occur analogous to those described by Topley and Greenwood (Greenwood, 1932). The present paper on the other hand deals with populations which exhibit fluctuations of the type considered by Lotka and Volterra.

The first set of experiments were performed with *Paramecium bursaria* and the yeast *Schizosaccharomyses pombe*. The culture medium had the following composition:

| | | | |
|---|---|---|---|
| NaCl | 2·350 | KCl | 0·050 |
| $MgCl_2$ | 0·184 | $CaCl_2$ | 0·027 |
| $MgSO_4$ | 0·089 | Doubly distilled water 100 c.c. | |

This stock solution was diluted 225 times with doubly distilled water before use. The yeast was cultivated on solid beer wort in 1·5 per cent. agar in a Petrie dish. A fixed amount of yeast was removed by a platinum loop and placed in the salt solution containing the *Paramecium*. As *Paramecium* (1928) has pointed out, *S. pombe* is a perfectly satisfactory food for *Paramecium bursaria*. In order to avoid an accumulation of waste products the yeast and *Paramecium* were transferred to fresh salt solution every other day by means of a centrifuge. During the course of an experiment the yeast was prevented from settling on the bottom of the container by passing air bubbles through the salt solution. In order that the system should exhibit periodic fluctuations of the Lotka-Volterra type it is necessary that the yeast should be capable of reproduction. For experimental purposes it was convenient to control the density of the yeast population by doubling (or increasing 1·5 times) the unconsumed population of yeast cells at fixed intervals of time (one day). Alternatively the density of *Paramecium* could be varied.

Fig. 1 represents the results of one of these experiments carried out in an Ehrlenmeyer flask containing 30 c.c. of the salt solution (at a temperature of 25° C.). The curve for *P. bursaria* shows the change in the number of individuals in 0·5 c.c. and that of *S. pombe*, the change in the number of cells in a large square of a Buerker-Reichert camera ($\frac{1}{10}$ c.mm.). The coefficient of multiplication of yeast was such that $b_1 = 0{\cdot}65$ (with 24 hours as a unit of time), and the coefficient of mortality ($d_2$) of *P. bursaria* was 0·32. Quite clearly periodic fluctuations of the Lotka-Volterra type occurred.

It will be noted that the first cycle in these experiments was larger than the subsequent cycles. This seems to be associated with the fact that a relatively large number of *Paramecium* (24 individuals per 0·5 c.c.) were introduced.

The relative values of the density of population of *Paramecium* ($N_2$) and of the yeast $N_1$ are shown in Fig. 2. A similarity to the theoretical curves of Lotka and Volterra is obvious.

[1] A mathematical theory of these oscillations is given by the author elsewhere.

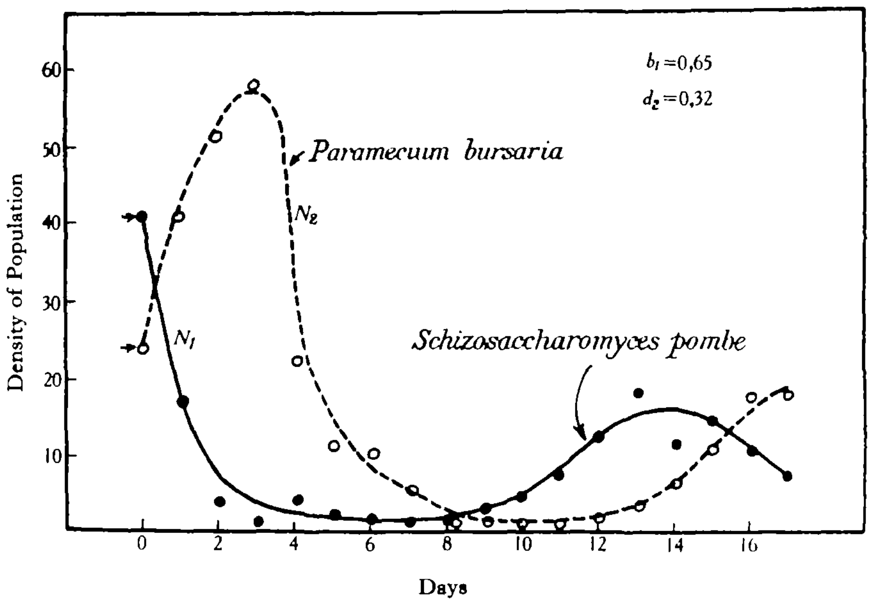


Fig. 1. Fluctuations in the density of population of *Paramecium bursaria* (number of organisms per 0·5 c.c.) and *Schizosaccharomyces pombe* (per 0·1 c.mm.).

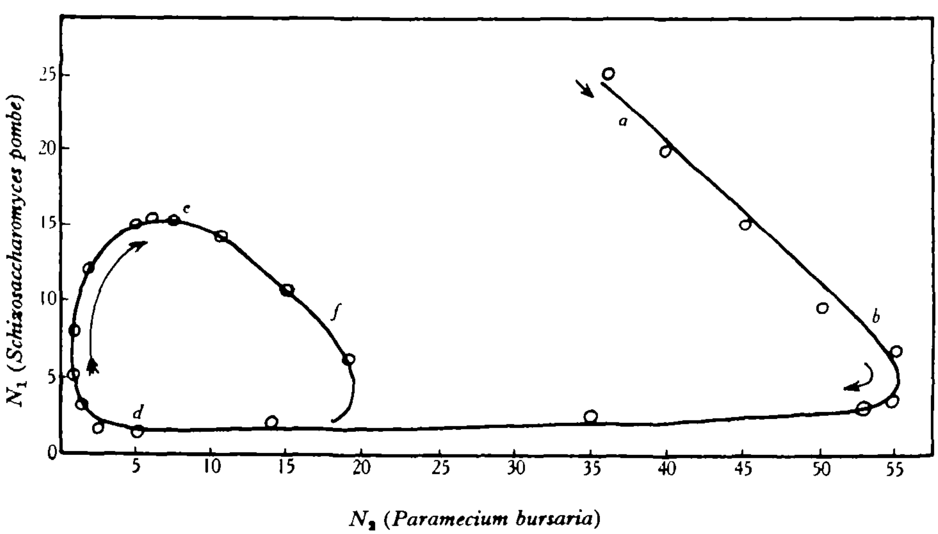


Fig. 2. Cyclical variations in the system: *Paramecium bursaria* → *Schizosaccharomyces pombe*.

From data of the type here presented it is possible to calculate the values of the constants $k_1$ and $k_2$ in equation (1). This has been done in Table I.

Table I

| $N_1$ | $N_2$ | $k_1$ | $k_2$ |
|---|---|---|---|
| 22 | 37 | 0·04 | 0·05 |
| 2 | 15 | 0·06 | 0·09 |
| 15 | 4 | 0·10 | 0·06 |
| 10 | 15 | 0·07 | 0·06 |

It will be noticed that the values of the constants do not change markedly over wide ranges of variation of population density; at the same time some variation undoubtedly occurs and requires further investigation.

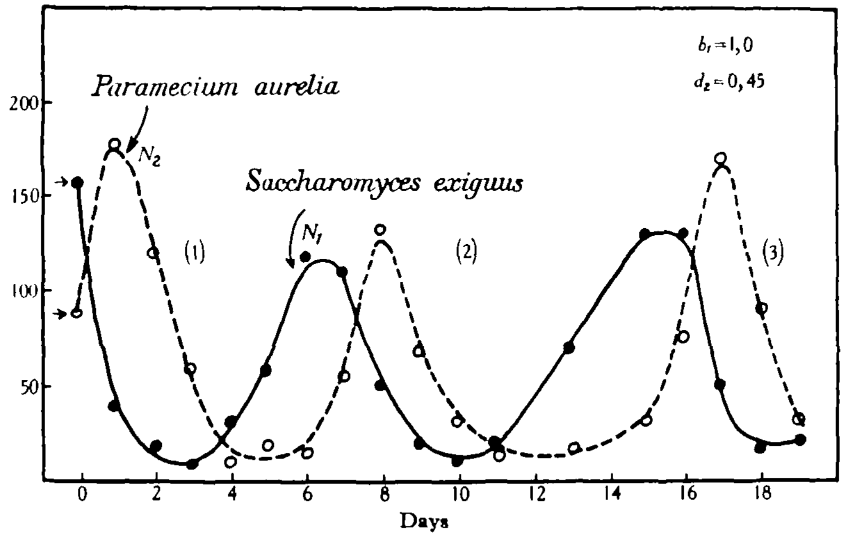


Fig. 3. Fluctuations in the density of population of *Paramecium aurelia* (per 15 c.c.) and *Saccharomyces exiguus* (per 0·1 c.mm.).

Similar periodic oscillations have been observed in mixed populations of *Paramecium aurelia* and *Saccharomyces exiguus*. In this case the Osterhout salt solution was buffered (3 c.c. $M/20$ $KH_2PO_4$ + 100 c.c. of water + $M/20$ KOH, giving $pH = 7{\cdot}5$). The coefficient of multiplication of the yeast ($b_1$) had an average value of 1·0, and the coefficient of daily dilution of *Paramecium* ($d_2$) was 0·45. The system was incubated at 25° C. in 25 c.c. of liquid, and the culture was stirred by gentle rotation of the flask. There appeared to be a slight deficiency of oxygen in these experiments and the rate of mortality of the *Paramecium* was somewhat high. As is shown in Figs. 3 and 4, however, typical fluctuations were observed whose period was approximately constant. Fig. 4 shows that the magnitude of the fluctuations was also approximately the same in all cases.

It now seems fairly clearly established that periodic fluctuations of the Lotka-Volterra type actually occur under controlled experimental conditions and it is of interest to consider the fluctuations observed by Cutler (1923) and others (Russell, 1927). In these cases it looks as though essentially the same factors were at work (Nicholson, 1933). The bacteria in the soil did not fluctuate in numbers when grown in sterilised soil, but rose to high population densities and remained at those levels. As soon as amoebae were introduced the number of bacteria fell but no constant level was reached, the numbers fluctuating markedly—with an inverse proportionality between the number of bacteria and amoebae. It is difficult to avoid the con-

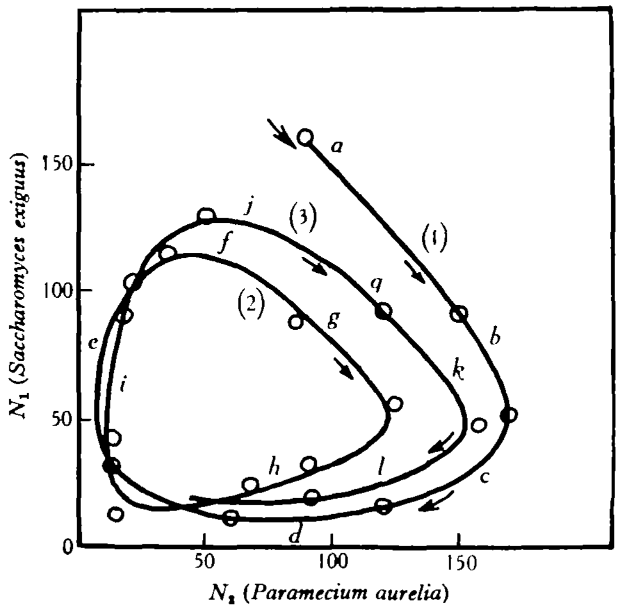


Fig. 4. Cyclical variations in the system: *Paramecium aurelia* → *Saccharomyces exiguus*.

clusion that the system is definable as a periodic fluctuation of the Lotka-Volterra type.

It is of interest to note, on the other hand, that recent observations on the vertebrates does not reveal similar fluctuations (Sewertzoff, 1933; Jensen, 1933). Further investigation of these cases would be of interest.

In conclusion I wish to express my sincere thanks to Dr W. W. Alpatov for interest in the present investigation.

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