institution was re-modelled and co-ordinated in 1893, when the first principal was appointed, but it was not until 1901 that the educational work was organised for development on the lines of a university college with the provision of a curriculum for the external examinations of the University of London.

The College was placed upon the list of university institutions in receipt of grant from H.M. Treasury as from August 1, 1922, when it was incorporated under its present name as a company limited by guarantee, and the college buildings and halls of residence were transferred to it by the Exeter City Council. From that time its progress has been rapid, the number of degree students in the four years ending 1924–25 having been 96, 139, 187, and 211 respectively. The total number of full-time students in 1924–25 was 332, of whom 221 were in the teachers' training department. Residential halls provide accommodation for 134 women and 110 men students. Part-time students numbered 38 and occasional students 40. There are departments of biology, chemistry, classics, education, English, geography, history and economics, law, pure and applied mathematics, modern languages, music, philosophy, physics, and extra-mural studies. The total income was 29,067*l.*, including parliamentary grants 12,317*l.*, grants from local education authorities 10,384*l.*, tuition and examination fees 5040*l.*, income from endowment 674*l.*, and from other sources 1112*l.* The book value of its land, buildings, and permanent equipment is 81,433*l.*, and its endowment investments 11,603*l.*

These figures do not suggest that the College is likely to qualify soon for full university status, but it might conceivably join with the Technical Schools, Plymouth, the Seale - Hayne Agricultural College, Newton Abbot, and the Camborne School of Mines, to form a federal university. An important scheme for co-operation with the Technical Schools, Plymouth, has been worked out providing for degree and diploma courses in civil, electrical, marine, and mechanical engineering and in commerce at Plymouth, and the extension of the law teaching and extra-mural work already carried on there by the College. An appeal was launched in October 1925 for 100,000*l.* for the equipment and endowment.

UNIVERSITY COLLEGE, HULL.

The plans for the proposed University College for Hull, for which the Right Hon. T. R. Ferens gave 250,000*l.*, provide for an organisation somewhat similar in scope to that of University College, Southampton, with the addition of a department of agriculture and, eventually, departments of shipbuilding and applied chemistry of the oil, colour, gas, and spirit industries.

Lest the account already given of the policy of the University Grants Committee in regard to proposals for establishing new universities should be misunderstood, it must be added that the Committee is careful to point out that its "view of what is prudent at one particular stage of our history betokens no lack of sympathy with the general desire for a wider avenue to university education, or with the ambitions of certain large and populous cities to rival the more fortunate communities which already possess universities of their own." The Committee hopes that "as returning prosperity enables the schemes of local education authorities under the Education Act to be carried into effect, the local colleges will play an increasingly distinguished part in the higher education of the people, and will steadily raise the level of national knowledge and culture. It may well be that some of these will, in course of time, establish a claim to university rank and receive charters as independent universities."

Fluctuations in the Abundance of a Species considered Mathematically.[1]

By Prof. VITO VOLTERRA, For. Mem. R.S., President of the R. Accademia dei Lincei.

A CONSIDERATION of biological associations, or of the mutual interactions between two or more species associated together, has led me to certain mathematical results which may be set forth as follows.

The first case I have considered is that of two associated species, of which one, finding sufficient food in its environment, would multiply indefinitely when left to itself, while the other would perish for lack of nourishment if left alone ; but the second feeds upon the first, and so the two species can co-exist together.

The proportional rate of increase of the eaten species diminishes as the number of individuals of the eating species increases, while the augmentation of the eating species increases with the increase of the number of individuals of the eaten species. Having determined the laws of this increase and diminution, it is possible to establish two differential equations of the first order, non-linear, which can be integrated. The integrals reveal the fact that the numbers of individuals of the two species are periodic functions of the time, with equal periods but with different phases, so that each species goes through a cycle relative to the other during a period, a process which may be called the 'fluctuation of the two species.' Figs. 1 and 2 give representations of different possible cycles, corresponding to different initial values of the number of individuals of the two species : ordinates representing the eating, and abscissæ the eaten species.

The co-ordinates of a point on a cycle are the concurrent values of the numbers of individuals of the two species, those of the central point Ω being the mean values ; and the following laws have been deduced from integration of the differential equations which represent the fluctuation :

I. The fluctuation of the two species is periodic, the period depending only on the coefficients of increase and of destruction of the two species, and on the initial numbers of the individuals of the two species.

II. The average numbers of the two species tend to constant values, whatever the initial numbers may have been, so long as the coefficients of increase or of destruction of the two species and also the coefficients of protection and attack remain constant. (Laws I. and II. are illustrated in Fig. 2.)

III. If we try to destroy individuals of both species uniformly and proportionately to their number, the average number of individuals of the *eaten* species grows and the average number of the eating species diminishes (see Fig. 1). But increased protection of

[1] V. Volterra.—Variazioni e fluttuazioni del numero di individui in specie animali conviventi.—*Memorie della R. Accademia dei Lincei* (Cl. di Sci. Fis. etc.), ser. 6, vol. ii. fasc. 3, 85 pp., 1926.

the eaten species increases the average numbers of both.

In the case of small fluctuations, we have the following approximate laws :

(1) Small fluctuations are isochronous, *i.e.* their period is not sensibly affected either by the initial
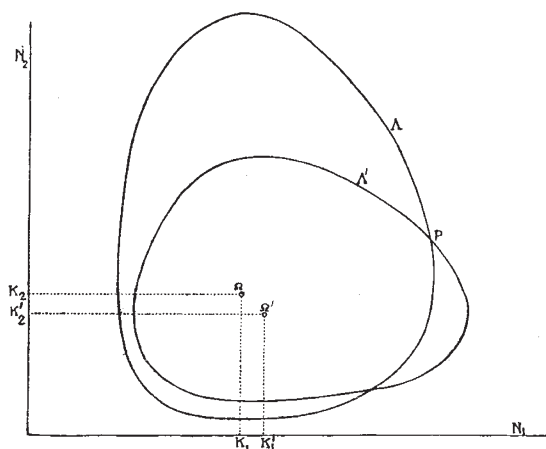

FIG. 1.

number of individuals, or by the conditions of protection and offence.

(2) The period of fluctuation is proportional to the product of the square roots of the time required for the first species to double itself, and for the second species to reduce itself to half. If the first species doubles itself in the time t_1 and the second species is reduced to half in the time t_2, the period is $T = \dfrac{2\pi}{\log_e 2}\sqrt{t_1 t_2} = 9 \cdot 06 \sqrt{t_1 t_2}$.

(3) The steady destruction of individuals of the eating species accelerates the fluctuation, and the destruction of individuals of the eaten species retards it.

With the contemporaneous and uniform destruction of individuals of the two species, the ratio between the amplitude of the fluctuation of the eaten species and that of the eating species tends to increase.

In Fig. 1 are represented two cycles, the second of which corresponds to a perturbation produced in the first by a constant and proportionate destruction of the individuals of the two species. The centre Ω' of the perturbed curve is displaced, in respect to the centre Ω of the primitive curve, downwards and to the right ; this reveals an augmentation of the average number of individuals of the first species, and a diminution of the average number of the second.

Law III. is undoubtedly the most interesting of all, because it affords the best actual verification so far found of the theory. For Dr. U. d'Ancona, comparing fishery statistics in the Adriatic Sea before the War, during the War (when fishing almost ceased), and after fishing was resumed at the end of the War, has ascertained that the voracious species (selachians), which feed on other fishes, had increased during the War as compared with the preceding and following periods, while the contrary had been the case for the number of individuals of the eaten species.[2]　In other words, a complete closure of the fishery was a form of

[2] U. d' Ancona.—Dell' influenza della stasi peschereccia del periodo 1914-1918 sul patrimonio ittico dell' Alto Adriatico.—*Memorie del R. Comitato Talassografico Italiano* (in course of publication).

'protection' under which the voracious fishes were much the better and prospered accordingly, but the ordinary food-fishes, on which these are accustomed to prey, were worse off than before. This is in agreement with Fig. 1, and with Law III. My theoretical researches, which I was induced to undertake by the statistical studies begun by Dr. d'Ancona, correspond accordingly with his results.

Charles Darwin had an intuition of these phenomena in relation to the struggle for existence when in Chap. iii. of his "Origin of Species" he wrote : "The amount of food for each species of course gives the extreme limit to which each can increase ; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average number of a species. Thus there seems to be little doubt that the stock of partridges, grouse, and hares on any very large estate depends chiefly on the destruction of vermin. If not one head of game were shot during the next twenty years in England, and at the same time if no vermin were destroyed, there would in all probability be less game than at present, although hundreds of thousands of game animals are now annually shot."

Law III. is, however, true only up to a certain limit. It is evident that if the destruction of both species continue, their exhaustion will ensue. It is therefore necessary to ascertain up to just what point it is profitable to destroy both species in order to obtain the greatest augmentation in the average number of the eaten species. We arrive in this manner at a curious example of a mathematical *upper limit* without the existence of a *maximum*. There is in fact a limit of destruction beyond which both species are exhausted. If we remain below it, the average number of the eaten species grows as this limit is approached ; but once the limit is reached, the eating species tends to exhaustion and the fluctuation ceases, while the number of individuals of the eaten species tends asymptotically
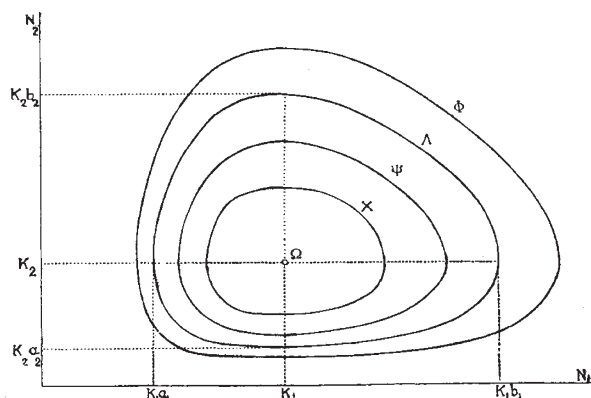

FIG. 2.

towards a value which is less than the average formerly reached.

Besides the case dealt with above, a study of variations in the number of individuals of two associated species can also be made in all cases in which the species interact either favourably or injuriously, in all possible degrees or combinations. All such cases can be classified in distinct types, and in each of these it is possible to

follow the numerical variations of the two species by the help of formulæ, or of diagrams to correspond. It is easy to see from these diagrams *which species is winning in the struggle for existence, and which of them is in process of extinction.*

Again, it is certain that many facts of medical interest may be classed among phenomena resulting from concurrent and reciprocal action between different species—between the human species and pathogenic germs, between parasitic species and those on which they are parasites. The periodicity of epidemics may be connected with the same phenomena.

A second part of my investigation is devoted to a general study of biological association, where any number of species may be living together. I have studied two types of association, and have called them *conservative* and *dissipative associations.*

For the first or conservative association, equivalent values may be assigned to the different species so that the destruction of a certain number of individuals belonging to one species by another species, to its own benefit, corresponds to an increase in numbers of the latter species, in the precise ratio which the said equivalents express. Moreover, in a conservative association, the number of individuals of every species has no influence on its own augmentation. The case of two species, already dealt with : the case of *n* species, where individuals of the first eat those of the second, and the latter those of the third, and so on to the *n*th ; the case of four species so connected that the first eats the second and the second is also eaten by the third, which in its turn is eaten by the fourth ; all these cases are examples of biological conservative associations, if we neglect actions between individuals of the same species. The variation in numbers of the conservative associations depends on a system of differential quadratic equations associated with a skew-symmetric determinant.

Owing to the peculiar properties of these skew-symmetric determinants, and to the differences between those of odd and those of even order, we must treat in different ways the cases where odd and where even numbers of biological species are associated together. When the number is odd, then, if the coefficients allow a 'stationary state,' we shall always have fluctuations such as to maintain the number of individuals of each species between positive limits. These limits are dependent on initial conditions, which may be so assumed as to restrict these limits to any extent we please.

The average numerical values of the different species tend, in periods of time of infinite duration, towards the corresponding values for the stationary state, and are therefore independent of the initial values.

The case of an odd number of species does not correspond to a condition of stability for a strictly conservative system.

In the case of associations which I call *dissipative,* if a stationary state exists, the variations will be fluctuations which slowly extinguish themselves, or are asymptotical. From an analytical point of view, the dissipative association is characterised by a definite positive quadratic form.

The analogous form is null in the case of a con-

servative system. The dissipative actions work in a way analogous to friction in a mechanical system.

Therefore the terms conservative and dissipative may also be applied to the fluctuations, which in the first case continue to exist, and in the second are dissipated. It will be observed that to prove the existence of the fluctuations, we follow an analysis different from that used in elastic or electric vibrations, the equations here employed being not linear but quadratic.

Applying this theory to a particular case, suppose three different species living together in a limited area, such as an island. Of these three species the first eats the second, which in turn eats the third. We may take for example a carnivorous species, feeding upon a herbivorous animal, which in turn feeds on a certain plant species—assuming that for the last the same method may be used which we apply to animals. The same method may also be employed in the case of insects parasitic upon plants, and of parasites of such parasites.

If we suppose that system to be conservative, that is, if we neglect the actions between individuals of the same species, we may have two different cases which are distinguished by the values of the coefficients occurring in the equations :

(1) The food which reaches the carnivorous species through the herbivorous is not sufficient to maintain the carnivorous species ; and so the latter is exhausted, while the herbivorous animal and the plant tend to a periodical fluctuation.

(2) The vegetable species grows indefinitely. This case is, however, incompatible with the limitation of the island, which does not allow the indefinite multiplication of the plant. It is therefore necessary in this case to suppose the system to be dissipative, admitting that the coefficient of increase of the vegetable species is dependent on the number of existing plants, and then we have three cases : Either (1) both animal species are exhausted ; or (2) only the carnivorous species is exhausted, while the herbivorous and the plant tend to a fluctuation of gradually diminishing amplitude or to an asymptotic variation ; or (3) all three species live together without exhausting themselves, but vary asymptotically in a common fluctuation of gradually diminishing amplitude, the characteristic elements of which can be determined.

Side by side with the general theory, we may make various special inqu ies. Thus, for example, we may suppose the coefficient of increase of the species to have an annual period, a supposition tending to establish a law of forced fluctuations superposed on the free fluctuations of the biological association considered.

We may also study how exhaustion takes place of a species in a biological conservative association of an uneven number of species ; or in general how exhaustion takes place of species in dissipative associations ; or what perturbation is produced when a new species is introduced into an association in equilibrium.

Seeing that a great number of biological phenomena are characteristic of *associations* of species, it is to be hoped that this theory may receive further verification and may be of some use to biologists.