

Variations and Fluctuations of the Number of Individuals in Animal Species living together.

By

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§ 1. Preliminary Considerations.

1. Many applications of mathematics have been made to biology. In the first place come the researches on physiological questions relative to the senses, to the circulation of the blood, to the movement of animals, which can be viewed as subjects of optics, of acoustics, of hydrodynamics or of the mechanics of solid bodies and hence have not called for new methods outside the scope of the classical mathematical physics. Biometry, on the other hand, with its own modes of procedure, has recourse to the use of calculus of probability and has created a mass of new and original studies¹). And too the recent geometrical researches on the form and growth of organized existence have a particular character. In them geometry has been used to describe the forms themselves and their development just as for a long time it has been employed in astronomy to describe the orbits and the motions of the celestial bodies²). Moreover it is to be hoped that the methods allied to the analysis used for heredity may be advantageously employed in questions concerning biology³).

Putting aside other applications of mathematics, these points, of

¹) Cf. VOLTERRA, *Saggi scientifici*. — I. Sui tentativi di applicazione delle matematiche alle Scienze biologiche e sociali, Bologna, Zanichelli, 1920. — For Biometry see the periodical "Biometrika" founded by KARL PEARSON in 1901.

²) D'ARCY THOMPSON WENTWORTH, *On Growth and Form*, Cambridge, 1917.

³) VOLTERRA, *Ibid.*, VII, L'evoluzione delle idee fondamentali del calcolo infinitesimale. — VIII, L'applicazione del calcolo ai fenomeni d'eredità.

which I shall speak in this article, I consider worthy of study and research, as being able to clarify various points actually interesting to biologists¹⁾.

2. Biological associations (biocoenosis) are established by many species which live in the same environment. Ordinarily the various individuals of such an association contest for the same food, or else some species live at the expense of others on which they feed. But nothing prevents them from being able to take advantage of each other. All this comes back again to the general phenomenon called the struggle for life.

The quantitative character of this phenomenon is manifested in the variations of the number of individuals which constitute the various species. In certain conditions such variations consist in fluctuations about a mean value, in others they show a continuous decrease or increase of the species.

The study of these variations and of these different tendencies is important theoretically, but often has also a practical importance worthy of notice, as in the case of the species of fish which live in the same seas and whose variations interest the fisheries²⁾. And also agriculture is

¹⁾ The complete work has been published by me in "Memorie della R. Accademia Nazionale dei Lincei", division on mathematical, physical and natural sciences, Series VI, vol. II, and in Memoria CXXXI, of R. Comitato Talassografico Italiano, with the title: *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*. After the publication of this note I received word that in the study of parasites relative to malaria there existed the equations of Ross, and I learned that in the volume: *Elements of physical Biology*, New York 1925, Doctor LOTKA had considered the case of two species developed by me in § 3 of part 1, arriving by other methods at the integral, to his diagram, and to the period of small oscillations. However the general laws obtained by me in this same section, the various cases developed in the other sections of the first part, as likewise all the other three parts of my Memoir, in which I consider the applications of the aforesaid laws and the cohabitation of n species in the hypothesis of conservative and dissipative associations, are new and treated for the first time.

²⁾ Doctor UMBERTO D'ANCONA has many times spoken to me about the statistics which he was making in fishery in the period during the war and in periods before and after, asking me if it were possible to give a mathematical explanation of the results which he was getting in the percentages of the various species in these different periods. This request has spurred me to formulate the problem and solve it, establishing the laws which are set forth in § 7. Both D'ANCONA and I working independently were equally satisfied in comparing results which were revealed to us separately by calculus and by observation, as these results were in accord; showing for instance that man in fisheries, by disturbing the natural condition of proportion of two species, one of which feeds upon the other, causes diminution in the quantity of the species that eats the other, and an increase in the species fed upon. See: D'ANCONA, *Dell'influenza della stasi peschereccia del periodo 1914-18 sul patrimonio ittico dell' Alto Adriatico*. Memoria CXXVI R. Comitato Talassografico Italiano.

interested in the fluctuations of parasites of plants when these parasites are attacked by parasites of these parasites. Also infective diseases (malaria etc.) show fluctuations which are probably of an analogous nature.

The question presents itself in a very complex way. Certainly there exist periodic circumstances relating to environment, as would be those, for example, which depend upon the changing of the seasons, which produce forced oscillations of an external character in the number of individuals of the various species.

These actions of external periodic nature were those which were specially studied from the statistical point of view, but are there others of internal character, having periods of their own which add their action to these external causes and would exist even if these were withdrawn?

Observation inclines to an affirmative reply and mathematical calculation confirms it, as we shall see in this article. But on first appearance it would seem as though on account of its extreme complexity the question might not lend itself to a mathematical treatment, and that on the contrary mathematical methods, being too delicate, might emphasize some peculiarities and obscure some essentials of the question. To guard against this danger we must start from hypotheses, even though they be rough and simple, and give some scheme for the phenomenon.

For that we shall begin by studying that which could be called the purely internal phenomenon, due only to the reproductive power and to the voracity of the species as if they were alone. Later we shall study the addition of foreign or forced periodic actions which are the result of environment.

3. And what mathematical methods will it be convenient to use? Perhaps the methods founded on the calculus of probability which might suggest themselves first? Let me say at once it is not these which lead us to the goal.

Permit me to indicate how the question can be considered: Let us seek to express in words the way the phenomenon proceeds roughly: afterwards let us translate these words into mathematical language. This leads to the formulation of differential equations. If then we allow ourselves to be guided by the methods of analysis we are led much farther than the language and ordinary reasoning would be able to carry us and can formulate precise mathematical laws. These do not contradict the results of observation. Rather the most important of these seems in perfect accord with the statistical results¹⁾. The road followed is thus

¹⁾ D'ANCONA establishes from the examination of the statistics of the markets of Trieste, Venice and Fiume that during the war there took place in the Upper Adriatic

clearly indicated with these few words. We shall see after a little how the difficulties met were overcome.

4. On the basis of the ideas expressed above, in order to simplify the treatment, we shall assume that the species increase or decrease in a continuous way, that is to say we shall assume that the number which measures the quantity of individuals of a species is not an integer, but any real positive number whatever which varies continuously. In general the hatchings take place in definite periods separated from each other by an interval of time; we shall neglect these particulars assuming that births may take place with continuity every moment and that, on a parity with all the other conditions, they may be verified proportionally to the number of living individuals of the species. Let the same assumption be made on death and, according as births may prevail over deaths, or vice versa, an increase or diminution of individuals will occur. Thus we shall assume the homogeneity of the individuals of each species neglecting the variations of age and size.

If there is only one species or if the others have no influence on it, so that the circumstances of birth and death do not vary, we shall have, if N denotes the number of individuals,

$$\frac{dN}{dt} = nN - mN = (n - m)N$$

where t denotes time and n and m are constants, respectively the coefficients of birth and mortality. Letting $n - m = \epsilon$ we shall have

$$(I) \quad \frac{dN}{dt} = \epsilon N, \qquad (II) \quad N = N_0 e^{\epsilon t}$$

where N_0 denotes the number of individuals at the time zero. ϵ will be called the coefficient of increase of the species and if it is positive there will be a true increase, otherwise a decrease. If the circumstances of birth and death change, ϵ will vary with time or with N or with other elements. In such a case (I) will always exist, but evidently we shall no longer have (II).

a change of the proportions of the individuals of the various species of fish to the advantage of the Selacians which must be considered among the most voracious. This result agrees with the law of the disturbances of the average which we express farther along.

§ 2. Biological Association of two Species which contend for the same Food.

1. Let us suppose we have two species living in the same environment: let the numbers of the individuals be respectively N_1 and N_2 and let ϵ_1 and ϵ_2 be the values which their coefficients of increase would have if the quantity of the common food were always such as to amply satisfy their voracity. We shall have

$$\frac{dN_1}{dt} = \epsilon_1 N_1, \quad \frac{dN_2}{dt} = \epsilon_2 N_2 \quad (\epsilon_1 > 0, \quad \epsilon_2 > 0).$$

Let it be admitted now that the individuals of the two species, continually increasing in number, diminish the quantity of food of which each individual can dispose. Let us suppose that the presence of the N_1 individuals of the first species diminishes this quantity by an amount $h_1 N_1$ and the presence of the N_2 individuals of the second species diminishes it by the amount $h_2 N_2$ and that therefore by the combination of the two, the diminution amounts to $h_1 N_1 + h_2 N_2$ and that by virtue of the unequal need of food of the two species, the two coefficients of increase are reduced to

$$[1] \quad \epsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2), \quad \epsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)$$

We shall then have the differential equations

$$[2_1] \quad \frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2)) N_1$$

$$[2_2] \quad \frac{dN_2}{dt} = (\epsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)) N_2$$

in which we must suppose $\epsilon_1, \epsilon_2, h_1, h_2, \gamma_1, \gamma_2$ to be positive constants.

2. From the preceding equations it follows that

$$[3_1] \quad \frac{d \log N_1}{dt} = \epsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2)$$

$$[3_2] \quad \frac{d \log N_2}{dt} = \epsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)$$

and hence

$$[4] \quad \gamma_2 \frac{d \log N_1}{dt} - \gamma_1 \frac{d \log N_2}{dt} = \varepsilon_1 \gamma_2 - \varepsilon_2 \gamma_1$$

that is to say

$$[5] \quad \frac{d \log \frac{N_1^{\gamma_2}}{N_2^{\gamma_1}}}{dt} = \varepsilon_1 \gamma_2 - \varepsilon_2 \gamma_1$$

and integrating and passing from logarithms to numbers,

$$[6] \quad \frac{N_1^{\gamma_2}}{N_2^{\gamma_1}} = C e^{(\varepsilon_1 \gamma_2 - \varepsilon_2 \gamma_1) t}$$

where C is a constant quantity.

3. If the binomial $\varepsilon_1 \gamma_2 - \varepsilon_2 \gamma_1$ is not zero we can suppose it positive, for if it were not positive it would suffice to exchange species 1 with species 2 to make it positive.

In this case

$$\lim_{t=\infty} \frac{N_1^{\gamma_2}}{N_2^{\gamma_1}} = \infty.$$

For N_1 equal to or greater than $\frac{\varepsilon_1}{\gamma_1 h_1}$, by virtue of [2₁], the differential coefficient $\frac{dN_1}{dt}$ is negative, hence N_1 can not exceed a certain limit.

N_2 then must approach zero.

It is easy to compute the expression asymptotic to N_1 .

In fact when N_2 becomes small enough to remain negligible, equation [2₁] will become

$$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 h_1 N_1) N_1$$

or, separating the variables

$$dt = \frac{dN_1}{N_1(\varepsilon_1 - \gamma_1 h_1 N_1)}$$

and integrating and passing from logarithms to numbers,

$$\frac{N_1}{\varepsilon_1 - \gamma_1 h_1 N_1} = C_0 e^{\varepsilon_1 t}$$

C_0 being a constant. Hence

$$N_1 = \frac{C_0 \varepsilon_1 e^{\varepsilon_1 t}}{1 + \gamma_1 h_1 C_0 e^{\varepsilon_1 t}} = \frac{C_0 \varepsilon_1}{e^{-\varepsilon_1 t} + \gamma_1 h_1 C_0}$$

Therefore N_1 approaches asymptotically the value $\frac{\varepsilon_1}{\gamma_1 h_1}$ for increasing or decreasing values according as C_0 is positive or negative.

We can sum up the results we have obtained, in the following proposition: If $\frac{\varepsilon_1}{\gamma_1} > \frac{\varepsilon_2}{\gamma_2}$ the second species continually decreases and the number of individuals of the first species approaches $\frac{\varepsilon_1}{\gamma_1 h_1}$.

§ 3. Association of two Species one of which feeds upon the other.

1. Let N_1 and N_2 be the numbers of individuals of the two species. Let $\varepsilon_1 > 0$ represent the coefficient of increase which the first would have if the other did not exist. Let us suppose that the second would die out because of lack of food if it were alone; therefore let its coefficient of increase be negative and equal to $-\varepsilon_2$ (ε_2 can be considered as a coefficient of decrease). If each of the two species were alone we should have

$$[7_1] \quad \frac{dN_1}{dt} = \varepsilon_1 N_1, \quad [7_2] \quad \frac{dN_2}{dt} = -\varepsilon_2 N_2.$$

But if they are together and the second species feeds upon the first ε_1 will diminish and $-\varepsilon_2$ will increase, and evidently the more numerous the individuals of the second species become the more ε_1 will diminish, and the more the individuals of the first species increase, the more will $-\varepsilon_2$ increase. To represent this fact in the simplest manner let us suppose that ε_1 diminishes proportionally to N_2 , that is by the amount $\gamma_1 N_2$, and that $-\varepsilon_2$ increases proportionally to N_1 , that is by the amount $\gamma_2 N_1$.

We shall have then the differential equations

$$(A_1) \quad \frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1, \quad (A_2) \quad \frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1) N_2.$$

The assumption that the coefficients of increase and of decrease be respectively linear in relation to N_2 and N_1 may seem very loose, but

it is justified as we shall see in § 5, if we compute these coefficients by means of the probable number of encounters of the individuals of the two species. And even if we take for the coefficients any functions whatever of N_2 and N_1 respectively, the mode of integration used in this section, in which they are supposed linear, works out just the same.

2. While the constants ϵ_1 and ϵ_2 sum up the conditions of birth and death of the two species, the coefficients γ_1 and γ_2 measure in a numerical way the aptitude of the first species to defend itself and the means of offense of the second species. In fact if we increase these means of offense then γ_1 and γ_2 must increase, and if we increase the means of protection of the first species then a diminution of these coefficients must follow.

In order to have a method of measuring ϵ_1 and ϵ_2 it will be sufficient to integrate $[7_1]$ and $[7_2]$; we should have if each of these two species were alone

$$N_1 = C_1 e^{\epsilon_1 t}, \quad N_2 = C_2 e^{-\epsilon_2 t},$$

where C_1 and C_2 are respectively the values of N_1 and N_2 for $t = 0$. Let us place $N_1 = 2C_1$, $N_2 = \frac{1}{2}C_2$ and denote by t_1 and t_2 the times necessary respectively for the first species to double itself and the second to be reduced by half. We shall have

$$\epsilon_1 = \frac{\log_e 2}{t_1} = \frac{0.693}{t_1}, \quad \epsilon_2 = \frac{\log_e 2}{t_2} = \frac{0.693}{t_2}.$$

From this it follows that ϵ_1 and ϵ_2 have the dimensions —1 with respect to time. It would always be possible to take the units of time in such a way that $\epsilon_1 = 1$. In fact if we take as the unit of time the time necessary for the first species to increase in the ratio $e = 2.728$, we shall have $e = e^{\epsilon_1}$ and hence $\epsilon_1 = 1$. ϵ_2 could be treated similarly.

Letting

$$[8] \quad \frac{\epsilon_2}{\gamma_2} = K_1, \quad \frac{\epsilon_1}{\gamma_1} = K_2,$$

the equations (A_1) and (A_2) show us that if

$$N_1 = K_1 \quad N_2 = K_2 \quad \text{then} \quad \frac{dN_1}{dt} = \frac{dN_2}{dt} = 0,$$

that is to say the two species are in a stationary state.

We shall have then

$$\gamma_1 = \frac{\varepsilon_1}{K_2}, \quad \gamma_2 = \frac{\varepsilon_2}{K_1}.$$

Now let us pass to the integration of equations (A₁) and (A₂).

From (A₁) and (A₂) it follows that

$$[9] \quad \frac{d \frac{N_1}{K_1}}{dt} = \varepsilon_1 \left(1 - \frac{N_2}{K_2}\right) \frac{N_1}{K_1}, \quad \frac{d \frac{N_2}{K_2}}{dt} = -\varepsilon_2 \left(1 - \frac{N_1}{K_1}\right) \frac{N_2}{K_2},$$

whence, by placing

$$[10] \quad N_1 = K_1 n_1, \quad N_2 = K_2 n_2,$$

the preceding equations may be written

$$(A'_1) \quad \frac{dn_1}{dt} = \varepsilon_1 (1 - n_2) n_1, \quad (A'_2) \quad \frac{dn_2}{dt} = -\varepsilon_2 (1 - n_1) n_2.$$

Multiplying these equations respectively by ε_2 and ε_1 and adding we have

$$[11] \quad \frac{d}{dt} (\varepsilon_2 n_1 + \varepsilon_1 n_2) = \varepsilon_1 \varepsilon_2 (n_1 - n_2).$$

Multiplying them respectively by $\frac{\varepsilon_2}{n_1}$ and $\frac{\varepsilon_1}{n_2}$, and adding, we find

$$\frac{\varepsilon_2}{n_1} \frac{dn_1}{dt} + \frac{\varepsilon_1}{n_2} \frac{dn_2}{dt} = \varepsilon_1 \varepsilon_2 (n_1 - n_2),$$

that is to say

$$[12] \quad \frac{d}{dt} (\log n_1^{\varepsilon_2} + \log n_2^{\varepsilon_1}) = \varepsilon_1 \varepsilon_2 (n_1 - n_2).$$

Equating the first members of [11] and [12] there follows

$$\frac{d}{dt} (\varepsilon_2 n_1 + \varepsilon_1 n_2) = \frac{d}{dt} (\log n_1^{\varepsilon_2} + \log n_2^{\varepsilon_1}),$$

and integrating and passing from logarithms to numbers

$$n_1^{\varepsilon_2} n_2^{\varepsilon_1} = C e^{\varepsilon_2 n_1 + \varepsilon_1 n_2}$$

where C is a positive constant. Whence

$$[13] \quad \left(\frac{n_1}{e^{n_1}}\right)^{\epsilon_2} = C \left(\frac{n_2}{e^{n_2}}\right)^{-\epsilon_1}.$$

From (A'_1) and (A'_2) it follows that

$$dt = \frac{dn_1}{\epsilon_1(1-n_2)n_1} = \frac{dn_2}{-\epsilon_2(1-n_1)n_2}.$$

If by means of the integral [13] we express n_2 in terms of n_1 or n_1 in terms of n_2 and substitute respectively these values in the preceding equations the variables remain separate, and the integration is reduced to a quadrature.

3. But we wish to examine directly the solution, and especially the integral [13].

Therefore let us place

$$[14] \quad x = \left(\frac{n_1}{e^{n_1}}\right)^{\epsilon_2} = C \left(\frac{n_2}{e^{n_2}}\right)^{-\epsilon_1}$$

and let us consider the curve Γ_1 , which has n_1 and x for abscissa and ordinate, and the curve Γ_2 , which has n_2 and x for abscissa and ordinate (fig. 1).

We shall have

$$[15] \quad \frac{d}{dn_1} \left(\frac{n_1}{e^{n_1}}\right) = e^{-n_1} (1-n_1)$$

which is positive for $n_1 < 1$ and negative for $n_1 > 1$. Then while n_1 varies between 0 and ∞ , x increases from 0 to its maximum value $\left(\frac{1}{e}\right)^{\epsilon_2}$ for $n_1 = 1$, and then approaches 0 as n_1 increases indefinitely.

Whereas while n_2 varies between 0 and ∞ , x decreases from ∞ to its minimum value Ce^{ϵ_1} for $n_2 = 1$, then increases without limit becoming ∞ for $n_2 = \infty$. The nature of the curves Γ_1 and Γ_2 appears then as shown in figure 1.

The constant C is determined from [13] whenever the initial values of n_1 and n_2 are known, and it is

$$C \leq e^{-(\epsilon_1 + \epsilon_2)}.$$

If $C < e^{-(\epsilon_1 + \epsilon_2)}$, that is if $e^{-\epsilon_2} > Ce^{\epsilon_1}$, for every value of x between Ce^{ϵ_1} and $e^{-\epsilon_2}$ there correspond two values of n_1 and two of n_2 , excluding the two values corresponding to the points C_1 and C_2 of maximum and minimum ordinates of the two curves Γ_1 and Γ_2 . Having

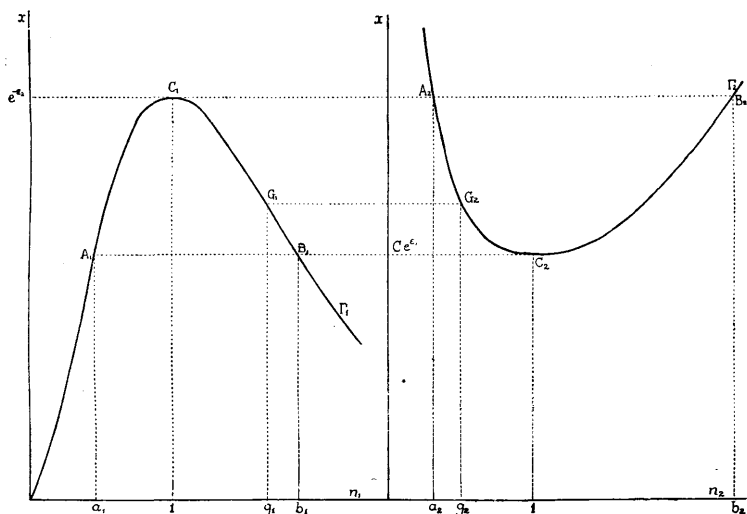


Fig. 1.

arranged the two curves as in fig. 1, with one axis of abscissas the continuation of the other, let us draw the normals to x from the vertices C_1 and C_2 and consider the sections $A_1C_1B_1$, $A_2C_2B_2$ of the two curves lying between these two parallels. Let $a_1 < 1$ and $b_1 > 1$ be the abscissas of A_1 and B_1 , $a_2 < 1$, $b_2 > 1$ the abscissas of A_2 and B_2 .

Then let us try to construct the curve λ having n_1 for abscissa and n_2 for ordinate. First let us make the point A_2 correspond to the point C_1 and trace the arc C_1B_1 with the point G_1 . Then in the curve Γ_2 let us trace the arc A_2C_2 , and, corresponding to G_1 on Γ_1 we shall have G_2 on Γ_2 , on the same perpendicular to x . Then the value $n_2 = g_2$ will correspond to $n_1 = g_1$, g_1 and g_2 being respectively the abscissas of G_1 and G_2 . Then while n_1 increases from 1 to b_1 , n_2 will increase from a_2

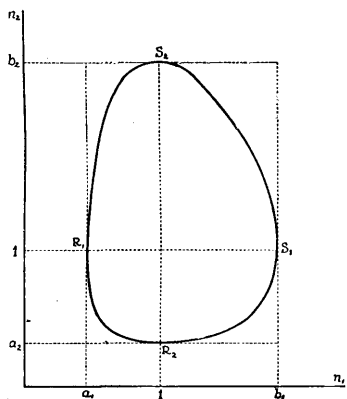


Fig. 2.

to 1, that is the curve of figure 2 will be traced from the point R_2 of coordinates $(1, a_2)$ to the point S_1 of coordinates $(b_1, 1)$. Continuing, while n_1 decreases from b_1 to 1, n_2 will increase from 1 to b_2 , that is we shall move in figure 2 from the point S_1 of coordinates $(b_1, 1)$ to the point S_2 of coordinates $(1, b_2)$; and as n_1 decreases from 1 to a_1 , n_2 decreases from b_2 to 1, that is in figure 2 we move from point S_2 of coordinates $(1, b_2)$ to the point R_1 of coordinates $(a_1, 1)$. Finally when n_1 increases from a_1 to 1, n_2 will decrease from 1 to a_2 and in figure 2 we go from the point R_1 of coordinates $(a_1, 1)$ to the point R_2 of coordinates $(1, a_2)$.

On our return to the point of departure there begins again the periodic tracing of the closed cycle of figure 2, and by virtue of [14], (as follows also from figure 1), when n_1 and n_2 take again the same values x also takes the same value.

4. From [14] it follows that $\log x = \varepsilon_2 (\log n_1 - n_1)$, and then, taking the derivative with respect to t and using (A'_1) ,

$$\frac{1}{x} \frac{dx}{dt} = \varepsilon_2 \left(\frac{1}{n_1} - 1 \right) \frac{dn_1}{dt} = \varepsilon_1 \varepsilon_2 (1 - n_1) (1 - n_2)$$

that is

$$dt = \frac{dx}{\varepsilon_1 \varepsilon_2 x (1 - n_1) (1 - n_2)}.$$

From which it follows that each time we trace with n_1 and n_2 the closed cycle of fig. 2, t will increase by a constant quantity T . From this it follows

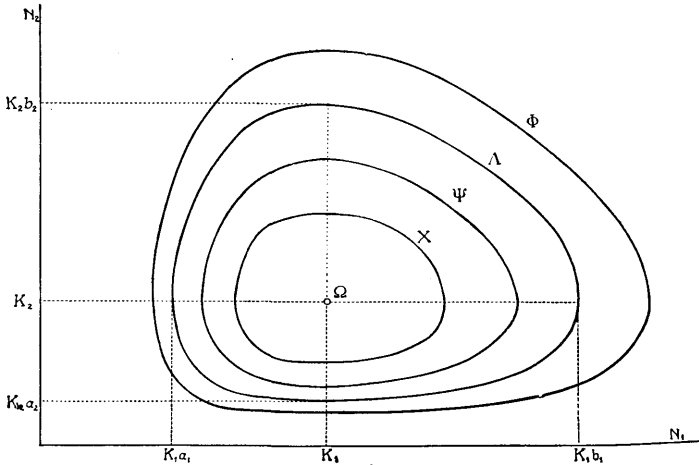


Fig. 3.

that n_1 and n_2 , and by virtue of [10] also N_1 and N_2 will be periodic functions of the time, with the period T . The curve \mathcal{A} of fig. 3 obtained from fig. 2 by multiplying the abscissas by K_1 , and the ordinates by K_2 , namely the curve which gives us the diagram of the cycle which relates N_1 to N_2 may be called the cycle of fluctuation and $K_1(b_1 - a_1)$, $K_2(b_2 - a_2)$ the amplitudes of the fluctuations of the two species. In general the cycle of fluctuation will not have a centre of symmetry, yet the point Ω whose coordinates are K_1 and K_2 stands inside all the possible cycles of fluctuation Φ , \mathcal{A} , Ψ , X , dependent upon all the possible initial conditions of the two species as is indicated in fig. 3. The name centre of fluctuation may be given then to the point Ω . All the curves of diagram 3 will be obtained by keeping ϵ_1 , ϵ_2 , γ_1 , γ_2 constant and letting the constant C take different values. These curves do not meet each other, but lie one within the other.

We have then in this case a periodic fluctuation of the number of individuals of the two species, with period T , or the phenomenon will have a cyclically periodic character.

Let us represent the fluctuation of n_1 and n_2 as functions of the time and we shall have figure 4.

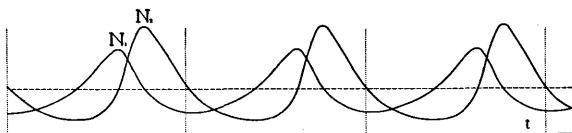


Fig. 4.

5. To determine the period T we shall need to calculate the integral

$$\int \frac{dx}{\epsilon_1 \epsilon_2 x (1 - n_1) (1 - n_2)}$$

extending it in succession over the four arcs $R_2 S_1$, $S_1 S_2$, $S_2 R_1$, $R_1 R_2$.

The sum of the four integrals will give us the period T .

The function under the integral sign becomes infinite at the four vertices R_1 , R_2 , S_1 , S_2 , but as is easily recognized, the order of infinitude is such that the integrals are convergent.

The preceding integral proves that the period T depends only on ϵ_1 , ϵ_2 and C .

In the following section we shall calculate approximately this period, assuming that the fluctuations are small¹⁾.

6. The approximate case in which the fluctuations are small can be treated easily by starting with equations (A_1) and (A_2).

In fact placing

$$[16] \quad n_1 = 1 + v_1, \quad n_2 = 1 + v_2$$

we shall have

$$[17] \quad N_1 = K_1 (1 + v_1), \quad N_2 = K_2 (1 + v_2).$$

Equations (A'_1), (A'_2) will become

$$(A''_1) \quad \frac{dv_1}{dt} = -\varepsilon_1 v_2 - \varepsilon_1 v_1 v_2, \quad (A''_2) \quad \frac{dv_2}{dt} = \varepsilon_2 v_1 + \varepsilon_2 v_1 v_2.$$

If the fluctuations are small v_1 and v_2 can be considered as small quantities of the 1st order, whence, if we neglect all terms of the 2nd order in the preceding equations, we shall have

$$\frac{dv_1}{dt} = -\varepsilon_1 v_2, \quad \frac{dv_2}{dt} = \varepsilon_2 v_1$$

which are integrated by the formulas

$$v_1 = L \sqrt{\varepsilon_1} \cos (\sqrt{\varepsilon_1 \varepsilon_2} t + a), \quad v_2 = L \sqrt{\varepsilon_2} \sin (\sqrt{\varepsilon_1 \varepsilon_2} t + a)$$

where L and a are both constants.

We shall have then, by using equations [8], [10], [16] and placing

$$L \frac{\varepsilon_1 \varepsilon_2}{\gamma_1 \gamma_2} = E,$$

$$[18] \quad N_1 = \frac{\varepsilon_2}{\gamma_2} + \frac{\gamma_1}{\sqrt{\varepsilon_1}} E \cos (\sqrt{\varepsilon_1 \varepsilon_2} t + a)$$

$$N_2 = \frac{\varepsilon_1}{\gamma_1} + \frac{\gamma_2}{\sqrt{\varepsilon_2}} E \sin (\sqrt{\varepsilon_1 \varepsilon_2} t + a)$$

whence N_1 and N_2 appear periodic with the period $\frac{2\pi}{\sqrt{\varepsilon_1 \varepsilon_2}}$.

We should have arrived at this same value by calculating directly

¹⁾ For the exact calculation of the period T , I refer to the article already cited, "Memoria della R. Accademia dei Lincei". Part 1st, § 3, No. 5.

the integral T of the preceding section and neglecting terms of infinitesimal order.

We can assume then that the period of the cycle of fluctuations of the two species is given approximately by

$$T = \frac{2\pi}{\sqrt{\epsilon_1 \epsilon_2}}.$$

If, as in article 2, we call t_1 and t_2 the two times in which respectively the first species doubles itself and the other is reduced by half, we shall have

$$T = \frac{2\pi \sqrt{t_1 t_2}}{0.693} = 9.06 \sqrt{t_1 t_2}.$$

The cycle of fluctuation will become an ellipse having its centre at the centre of fluctuation and having for semiaxes

$$E \frac{\gamma_1}{\sqrt{\epsilon_1}}, \quad E \frac{\gamma_2}{\sqrt{\epsilon_2}}$$

whence the amplitudes of the fluctuations will be

$$f_1 = 2E \frac{\gamma_1}{\sqrt{\epsilon_1}}, \quad f_2 = 2E \frac{\gamma_2}{\sqrt{\epsilon_2}}.$$

The ratio of the amplitudes of the two fluctuations will be

$$\frac{f_1}{f_2} = \frac{\gamma_1}{\gamma_2} \sqrt{\frac{\epsilon_2}{\epsilon_1}}.$$

The family of cycles of fluctuation will in this case consist of a group of homothetical ellipses having for common centre the centre of fluctuation. (See fig. 5.)

7. Now let us consider the average number of individuals of the two species during a cycle.

For that let us take equations (A'_1) , (A'_2) . Dividing both members respectively by n_1 and n_2 we shall have

$$\frac{d \log n_1}{dt} = \epsilon_1 (1 - n_2), \quad \frac{d \log n_2}{dt} = -\epsilon_2 (1 - n_1),$$

and integrating between the times t' and t'' at which times n_1 and n_2 assume respectively the values $n_1', n_1''; n_2', n_2''$, the following equations will be obtained:

$$\log \frac{n_1''}{n_1'} = \epsilon_1 \left[(t'' - t') - \int_{t'}^{t''} n_2 dt \right], \quad \log \frac{n_2''}{n_2'} = -\epsilon_2 \left[(t'' - t') - \int_{t'}^{t''} n_1 dt \right].$$

If we extend the integrals to a period T the first members vanish and we have

$$T = \int_0^T n_1 dt = \int_0^T n_2 dt$$

which is equivalent to saying

$$\frac{1}{T} \int_0^T n_1 dt = \frac{1}{T} \int_0^T n_2 dt = 1.$$

Then the averages of the values of n_1 and n_2 in a period are equal to 1 and by [10]

$$\frac{1}{T} \int_0^T N_1 dt = K_1 = \frac{\epsilon_2}{\gamma_2}, \quad \frac{1}{T} \int_0^T N_2 dt = K_2 = \frac{\epsilon_1}{\gamma_1},$$

that is the coordinates of the centre of fluctuation are the average values of the numbers of individuals of the species during a cycle. From this it follows that if $\epsilon_1, \epsilon_2, \gamma_1, \gamma_2$ stay constant, the averages of the individuals of the two species during a cycle of fluctuation will always be the same whatever may be the initial numbers of individuals of the two species.

Let us see how these averages change with variation of ϵ_1 and ϵ_2 , supposing γ_1 and γ_2 constants. It is seen at once that the average of the first species increases in proportion with ϵ_2 , and that of the second species decreases in proportion with ϵ_1 so long as this quantity remains positive.

Now to make ϵ_2 increase means destroying uniformly individuals of the second species in a quantity proportional to their number, and to make ϵ_1 decrease means destroying uniformly individuals of the first species in a quantity proportional to their number; from which it follows that if we try to contemporaneously destroy individuals of both species in the aforesaid manner but always keeping ϵ_1 positive, there will be an increase in the average of the individuals of the first species (those fed upon) while there will be a decrease in the average of the individuals of the second species (those feeding upon others). In figure 6 we have

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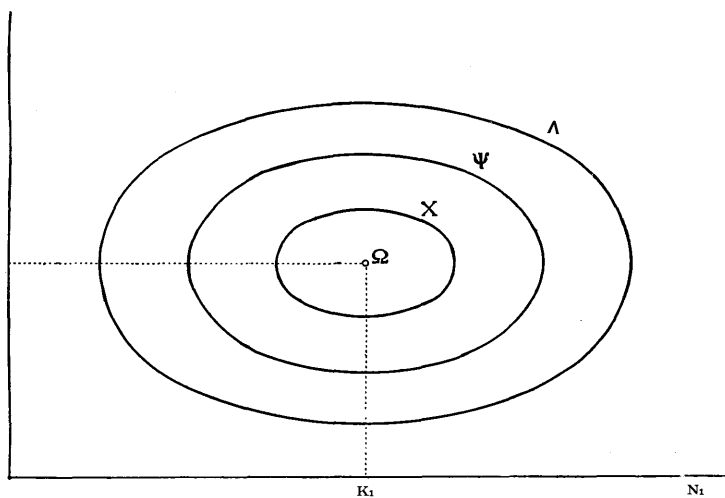


Fig. 5.

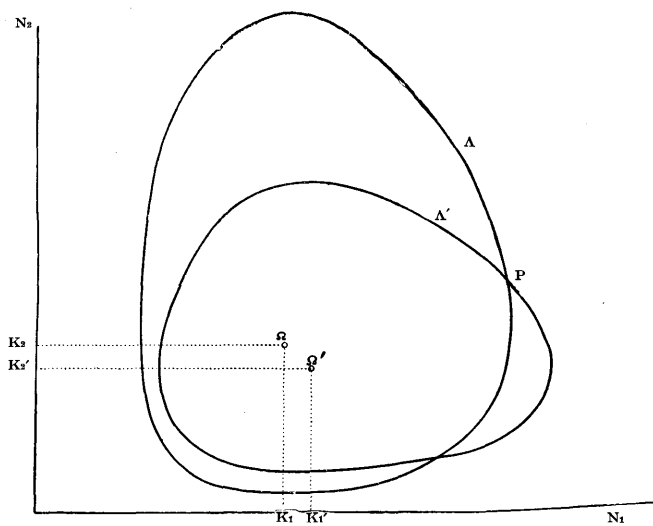


Fig. 6.

2*

represented the transition from a cycle \mathcal{A} corresponding to the parameters ϵ_1 and ϵ_2 to a cycle \mathcal{A}' corresponding to parameters $\epsilon'_1 < \epsilon_1$, $\epsilon'_2 > \epsilon_2$ (the parameters γ_1 and γ_2 are supposed invariable and $\epsilon'_1 > 0$). We may conceive of this transition as occurring in an instant corresponding to the point P of intersection of the two cycles, that is to say, without having any sensible change at that instant in the number of the individuals of the two species, although a change is disclosed with the passage of time by virtue of the constant action due to the variation of the parameters ϵ_1 and ϵ_2 . The centre Ω' of \mathcal{A}' is moved to the right of and below Ω which indicates a diminution in the average value of N_2 and an increase in the average value of N_1 .

To increase the protection of the species that is eaten from the voracity of the other means to diminish γ_1 and γ_2 and this corresponds to an increase in the average quantity of the two species.

8. We can sum up the various results obtained in the following laws which we shall call, the fundamental laws of the fluctuations of the two species living together:

1st) **Law of the periodic cycle.** The fluctuations of the two species are periodic and the period depends only upon ϵ_1 , ϵ_2 and C , (namely upon the coefficients of increase and decrease and the initial conditions).

2nd) **Law of the conservation of the averages.** The averages of the numbers of individuals of the two species are constant whatever may be the initial values of the numbers of individuals of the two species just so long as the coefficients of increase and decrease of the two species and those of protection and of offense (ϵ_1 , ϵ_2 , γ_1 , γ_2) remain constant.

3rd) **Law of the disturbance of the averages.** If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the average of the number of individuals of the species that is eaten increases and that of the individuals of the species feeding upon the other diminishes¹⁾.

Increasing the protection of the species fed upon increases, however, both the averages.

¹⁾ It is understood that this law is valid within certain limits as is explicitly said in N. 7, that is as long as the coefficient of increase ϵ_1 remains positive. In § 5 a special study will be made of the limit within which an element destructive of two species assists the species that is eaten.

In the case in which the fluctuations are small, we have the following approximate laws:

1st) The small fluctuations are isochronous, that is to say their period is not affected perceptibly either by the initial number of individuals or by the conditions of protection and offense.

2nd) The period of fluctuation is proportional to the geometric mean of the times in which the first species, alone, would double itself and the second, by itself, would be reduced by half. ($T = 9.06 \sqrt{t_1 t_2}$).

3rd) The uniform destruction of individuals of the species feeding upon the other accelerates the fluctuations, and the destruction of individuals of the species eaten retards them.

If the individuals of the two species are destroyed, contemporaneously and uniformly, the ratio of the amplitude of the fluctuation of the species eaten to the amplitude of the fluctuation of the species feeding upon the other increases.

It seems that the animal species for which in their natural state the verifications of these laws can most easily be carried out are fish, of which there are in fact species which feed upon others. Continual fishing constitutes a uniform destruction of individuals of the various species.

The cessation of fishing during the period of the recent war and its resumption after the war established transitions comparable to those considered above, from one cycle to another. Besides, the greater or less abundance of fish of various species determined by statistics gives a measure of the abundance of the individuals of the various species; hence the statistics of fishery furnish data on the fluctuations.

The results of the statistics are seen to be in accord with the mathematical predictions¹⁾.

¹⁾ Cf. the note for the 1st section Page 2, in which the statistics of Doctor D'ANCONA are spoken of.

CHARLES DARWIN had an intuition of the phenomena connected with the law of disturbance of averages, when, speaking of the struggle for life, he said:

"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 numbers of a species. Thus, there seems to be little doubt that the stock of partridges, grouse and hares on any 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 ver-

§ 4. Effects of the Various Actions which two Species living together can have on each other.

1. Let us suppose we have two species living together, and let N_1 and N_2 be respectively the numbers of individuals in each. The number of encounters of individuals of the first species with those of the second species, which occur in a unit of time, will be proportional to $N_1 N_2$ and can therefore be assumed equal to $\alpha N_1 N_2$, α being a constant. Let λ_1 and λ_2 be the coefficients of increase, positive or negative, of the two species when each is alone. In the case which we have already treated λ_1 is positive and λ_2 is negative. Moreover these meetings are unfavorable to the first species (the species fed upon), while they are favorable to the second species (the species feeding upon the other). Let us indicate by β_1 the increase of individuals of the first species and by β_2 the increase of individuals of the second species due to a certain number of encounters, for example n . In the preceding case β_1 would have to be taken negative and β_2 positive. In the time dt the increases of the two species will be respectively

$$dN_1 = \lambda_1 N_1 dt + \frac{\beta_1}{n} \alpha N_2 N_1 dt,$$

$$dN_2 = \lambda_2 N_2 dt + \frac{\beta_2}{n} \alpha N_1 N_2 dt.$$

Using

$$\frac{\beta_1}{n} \alpha = \mu_1, \quad \frac{\beta_2}{n} \alpha = \mu_2$$

the preceding equations will become

$$[19] \quad \begin{cases} \frac{dN_1}{dt} = N_1 (\lambda_1 + \mu_1 N_2) \\ \frac{dN_2}{dt} = N_2 (\lambda_2 + \mu_2 N_1) \end{cases}$$

and if we make evident the signs which are given in the preceding case, writing

min were destroyed, there would, in all probability, be less game than at present, although hundreds of thousands of game animals are now annually shot."

CHARLES DARWIN, *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Sixth edition, with corrections to 1871. London, JOHN MURRAY, 1882 (pp. 53—54).

$$\begin{array}{ll} \lambda_1 = \varepsilon_1 & \lambda_2 = -\varepsilon_2 \\ \mu_1 = -\gamma_1 & \mu_2 = \gamma_2 \end{array}$$

we arrive again at the equations (A_1) and (A_2) of section 3, namely

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (\varepsilon_1 - \gamma_1 N_2) \\ \frac{dN_2}{dt} &= N_2 (-\varepsilon_2 + \gamma_2 N_1). \end{aligned}$$

Thus appears a justification (as mentioned in N. 1 of § 3) of the assumption that the coefficients of increase are linear with respect to N_2 and N_1 .

2. Let us now take equations [19] without concerning ourselves with the signs of the coefficients, that is admitting that they may be positive or negative; we may assume that they represent the laws of increase of two species living together for which λ_1 and λ_2 are the coefficients of increase, while μ_1 and μ_2 are the coefficients of increase depending on encounters. The signs of λ_1 and λ_2 tell us if the species are increasing or decreasing by themselves, while the signs of the coefficients μ_1 and μ_2 indicate whether the encounters are favorable or unfavorable to one species and to the other respectively. For example if λ_1 and λ_2 are positive and μ_1, μ_2 are negative this will show that the species are increasing by themselves, and that the encounters are unfavorable to both species. We shall consider all possible cases, making all possible combinations of these coefficients taking them positive or negative. According to the signs of $\lambda_1, \mu_1, \lambda_2, \mu_2$ the different cases relating to equations [19] are represented in the following figures:

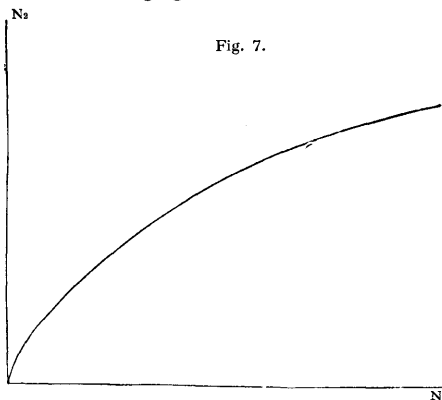


Fig. 7.

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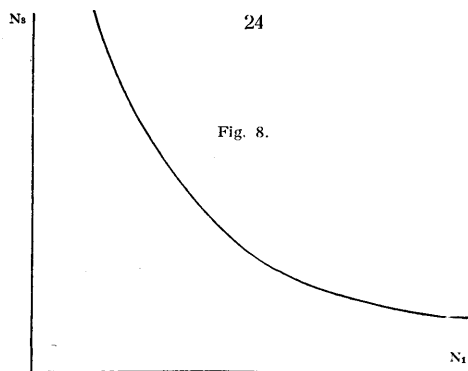


Fig. 8.

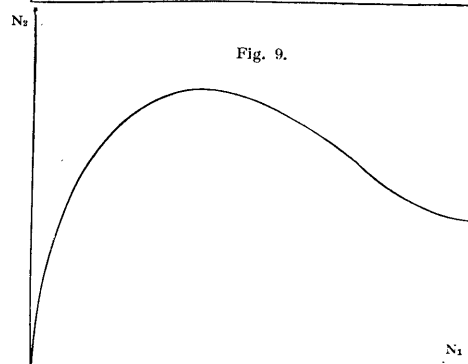


Fig. 9.

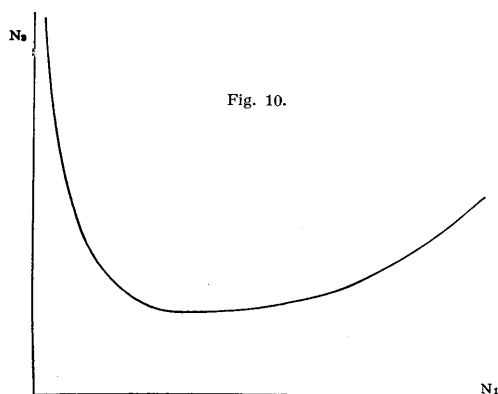


Fig. 10.

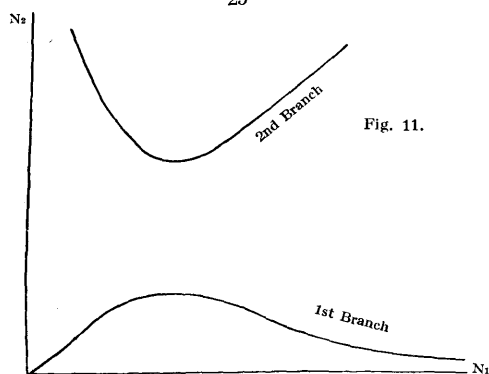


Fig. 11.

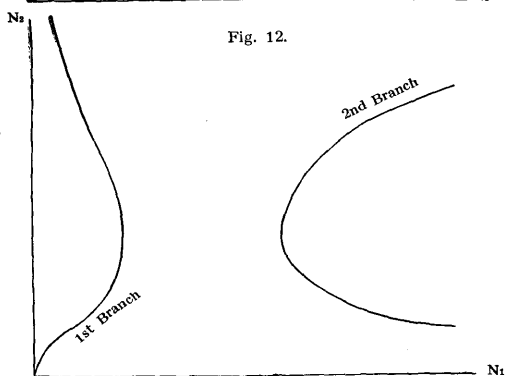


Fig. 12.

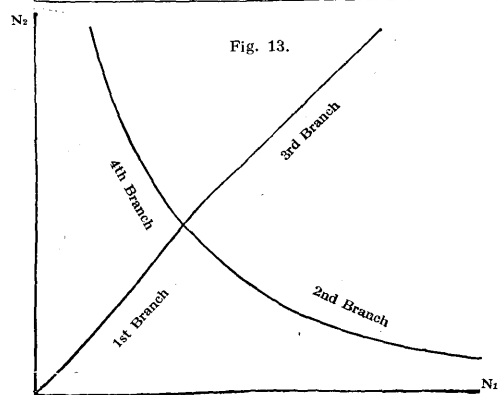


Fig. 13.

The following table indicates which cases correspond to the preceding figures.

$\lambda_1 > 0, \mu_1 > 0, \lambda_2 > 0, \mu_2 > 0, \left. \begin{array}{l} \lambda_1 < 0, \mu_1 < 0, \lambda_2 < 0, \mu_2 < 0, \end{array} \right\}$	fig. 7	$\left\{ \begin{array}{l} \text{l. r.} \\ \text{r. l.} \end{array} \right.$
$\lambda_1 < 0, \mu_1 < 0, \lambda_2 > 0, \mu_2 > 0, \left. \begin{array}{l} \lambda_1 > 0, \mu_1 > 0, \lambda_2 < 0, \mu_2 < 0, \end{array} \right\}$	fig. 8	$\left\{ \begin{array}{l} \text{r. l.} \\ \text{l. r.} \end{array} \right.$
$\lambda_1 > 0, \mu_1 > 0, \lambda_2 > 0, \mu_2 < 0, \left. \begin{array}{l} \lambda_1 < 0, \mu_1 < 0, \lambda_2 < 0, \mu_2 > 0, \end{array} \right\}$	fig. 9	$\left\{ \begin{array}{l} \text{l. r.} \\ \text{r. l.} \end{array} \right.$
$\lambda_1 < 0, \mu_1 < 0, \lambda_2 > 0, \mu_2 < 0, \left. \begin{array}{l} \lambda_1 > 0, \mu_1 > 0, \lambda_2 < 0, \mu_2 > 0, \end{array} \right\}$	fig. 10	$\left\{ \begin{array}{l} \text{r. l.} \\ \text{l. r.} \end{array} \right.$
$\lambda_1 > 0, \mu_1 < 0, \lambda_2 > 0, \mu_2 < 0, \left. \begin{array}{l} \lambda_1 < 0, \mu_1 > 0, \lambda_2 < 0, \mu_2 > 0, \end{array} \right\}$	fig. 11	$\left\{ \begin{array}{l} \text{l. r. 1st branch} \\ \text{r. l. 2nd branch} \\ \text{r. l. 1st branch} \\ \text{l. r. 2nd branch} \end{array} \right.$
$\lambda_1 > 0, \mu_1 < 0, \lambda_2 > 0, \mu_2 < 0, \left. \begin{array}{l} \lambda_1 < 0, \mu_1 > 0, \lambda_2 < 0, \mu_2 > 0, \end{array} \right\}$	fig. 12	$\left\{ \begin{array}{l} \text{u. 1st branch} \\ \text{d. 2nd branch} \\ \text{d. 1st branch} \\ \text{u. 2nd branch} \end{array} \right.$
$\lambda_1 > 0, \mu_1 < 0, \lambda_2 > 0, \mu_2 < 0, \left. \begin{array}{l} \lambda_1 < 0, \mu_1 > 0, \lambda_2 < 0, \mu_2 > 0, \end{array} \right\}$	fig. 13	$\left\{ \begin{array}{l} \text{l. r. 1st branch, 2nd branch} \\ \text{r. l. 3rd branch, 4th branch} \\ \text{r. l. 1st branch, 2nd branch} \\ \text{l. r. 3rd branch, 4th branch} \end{array} \right.$

In the preceding table *l. r.* signifies that with increase in time the curve is traced from left to right, *r. l.* from right to left, *d.* downward and *u.* upward.

§ 5. Limits within which a Cause destructive of two Species favors the Species fed upon.

1. We have shown (§ 3, N. 7) that decreasing ε_1 , namely the coefficient of increase of the species fed upon, and increasing ε_2 , or the coefficient of decrease of the species feeding upon the other, causes an increase in the average of the individuals of the first species and diminishes that of the second species, from which we have enunciated in N. 8 the law: If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the

average of the number of individuals of the species that is eaten increases, and that of the individuals of the species feeding upon the other diminishes.

But we have added that this law is valid within certain limits, that is as long as ϵ_1 stays positive.

2. We shall now conduct a study of the behavior of the phenomenon in detail. Let us denote by $\alpha\lambda$ the ratio between the number n_1 of individuals of the first species which are consumed, that is which are subtracted from the biological association, in the unit of time, and the total number of individuals in it, and by $\beta\lambda$ the analogous ratio for the second species. During the time dt there are lost from the biological association respectively

$$n_1 dt = \alpha\lambda N_1 dt \quad \text{and} \quad n_2 dt = \beta\lambda N_2 dt$$

individuals of the two species, wherefore the equations (A_1) , (A_2) must be modified by substituting in them for ϵ_1 and ϵ_2 respectively

$$\epsilon_1 - \alpha\lambda, \quad \epsilon_2 - \beta\lambda.$$

The anharmonic ratio of the four numbers n_2 , N_2 , n_1 , N_1 , that is

$$(n_2 : N_2) : (n_1 : N_1) = \frac{\beta}{\alpha} = \delta,$$

gives the ratio of the percentages of destruction or subtraction for the two species, which can be supposed to depend solely upon the way in which this destruction or subtraction occurs, while the intensity of the destruction or subtraction can be made to depend upon λ . Increasing λ then, while α and β remain constant, will have the significance of intensifying the subtraction if the same means of carrying

it out is always used, while changing the ratio $\delta = \frac{\beta}{\alpha}$ means altering the mode of procedure through which the destruction or subtraction occurs.

To refer to a concrete example, let us consider two species of fish living together, the second of which feeds on the first. Increasing λ without varying either α or β means intensifying the fishing, always employing the same method of fishing, while changing $\delta = \frac{\beta}{\alpha}$ means changing the method of fishing.

3. The equations (A_1) and (A_2) will become then

$$[20] \quad \frac{dN_1}{dt} = (\epsilon_1 - \alpha\lambda - \gamma_1 N_2) N_1$$

$$[20'] \quad \frac{dN_2}{dt} = (-\epsilon_2 - \beta\lambda + \gamma_2 N_1) N_2.$$

If $\epsilon'_1 = \epsilon_1 - \alpha\lambda > 0$ the fluctuation will occur with a period T (§ 3, N. 4). The number of individuals of the first species subtracted in the time dt will be

$$\alpha\lambda N_1 dt,$$

and during the period T

$$\int_0^T \alpha\lambda N_1 dt,$$

whence the average of individuals subtracted in the unit of time will be

$$P = \frac{1}{T} \int_0^T \alpha\lambda N_1 dt = \frac{\alpha\lambda}{T} \int_0^T N_1 dt.$$

But since from § 3, N. 7

$$\frac{1}{T} \int_0^T N_1 dt = \frac{\epsilon_2 + \beta\lambda}{\gamma_2} = \frac{\epsilon'_2}{\gamma_2},$$

we have

$$P = \frac{\alpha\lambda (\epsilon_2 + \beta\lambda)}{\gamma_2}.$$

As $\epsilon_1 - \alpha\lambda > 0$, the upper limit of λ will be $\frac{\epsilon_1}{\alpha}$ and consequently the upper limit of P will be

$$P_m = \frac{\epsilon_1 (\epsilon_2 + \delta\epsilon_1)}{\gamma_2}.$$

If we refer to the concrete example of fishing, we may conclude that, if the same method of fishing is maintained (that is if δ is constant), the average quantity of the first species, caught in the unit of time, during a cycle of fluctuation, can not exceed P_m , though it may approach this number as closely as we please.

Also we may say that P_m will be greater according as the harmonic ratio δ is greater.

4. If λ exceeds the value $\frac{\epsilon_1}{\alpha}$ so that

$$\epsilon_1 - \alpha\lambda < 0,$$

then the fluctuation will cease to exist, both the species will tend to disappear (see § 4) and we shall have the case denoted in § 4 with the type represented in figure 9 in which the curve is to be read from right to left.

It is interesting to examine the boundary case in which λ attains the value $\frac{\epsilon_1}{\alpha}$. We arrive then at the point of transition from the type represented in fig. 2 to the type represented in fig. 9. As indicated in § 4, we have not considered the several cases of transition among the various types; but we shall examine this now because the subject which we are now treating requires it. It can serve as an example of the treatment of the various cases of transition from one type to another.

If $\lambda = \frac{\epsilon_1}{\alpha}$ the equations [20], [20'] become

$$[21] \quad \frac{dN_1}{dt} = -\gamma_1 N_1 N_2,$$

$$[21'] \quad \frac{dN_2}{dt} = (-\epsilon_2'' + \gamma_2 N_1) N_2,$$

where

$$\epsilon_2'' = \epsilon_2 + \epsilon_1 \delta.$$

These equations have the integral

$$[22] \quad N_1 \epsilon_2'' e^{-\gamma_2 N_1} = C e^{\gamma_1 N_2},$$

where C is a positive constant.

Letting

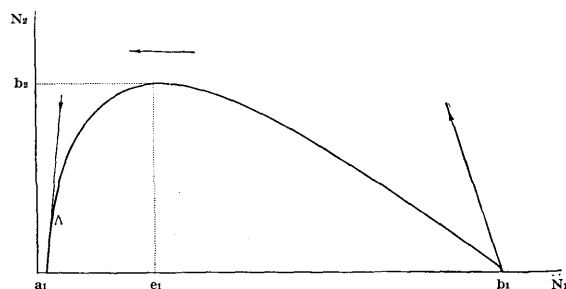
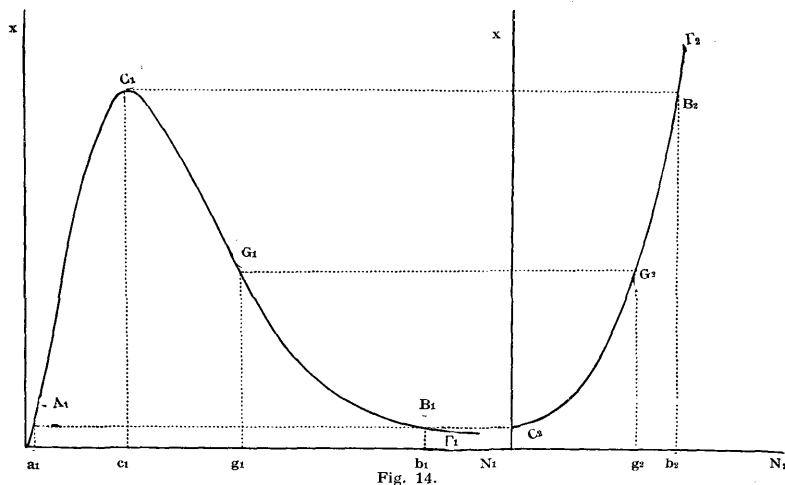
$$x = N_1 \epsilon_2'' e^{-\gamma_2 N_1} = C e^{\gamma_1 N_2}$$

the two curves Γ_1 and Γ_2 which have (N_1, x) and (N_2, x) respectively for abscissa and ordinate are represented in figure 14, whence employing the same mode of procedure which was followed in § 3, N. 3, (cf. fig. 1 and fig. 2) we can draw the curve which has [22] for its equation. (See fig. 15.)

The minimum and maximum values a_1 , b_1 of N_1 will give the two real roots of the equation

$$[22'] \quad N_1 \epsilon_2'' e^{-\gamma_2 N_1} = C.$$

When $\epsilon_1' = \epsilon_1 - \alpha\lambda$ becomes 0, the cyclical curves of fig. 3 assume, at the limit, the form of the curve of fig. 15. The lower part of the former



curves approaches the straight line segment $a_1 b_1$ of fig. 15. But while the curves of fig. 3 are traced clear around periodically, which constitutes the phenomenon of fluctuation, the line segment $a_1 b_1$ can never be traced because an infinite period of time is necessary for reaching the point a_1 . Then any point whatever on the straight line $a_1 b_1$ corresponds to N_1 constant and $N_2 = 0$.

In fig. 16 three curves are represented, I, II, III, which issue from the same point P . Their respective equations are

- I. $N_1^{\epsilon'_2} e^{-\gamma_2 N_1} = C' N_2^{-\epsilon'_1} e^{\gamma_1 N_2}$
 II. $N_1^{\epsilon''_2} e^{-\gamma_2 N_1} = C'' e^{\gamma_1 N_2}$
 III. $N_1^{\epsilon'''_2} e^{-\gamma_2 N_1} = C''' N_2^h e^{\gamma_1 N_2}.$

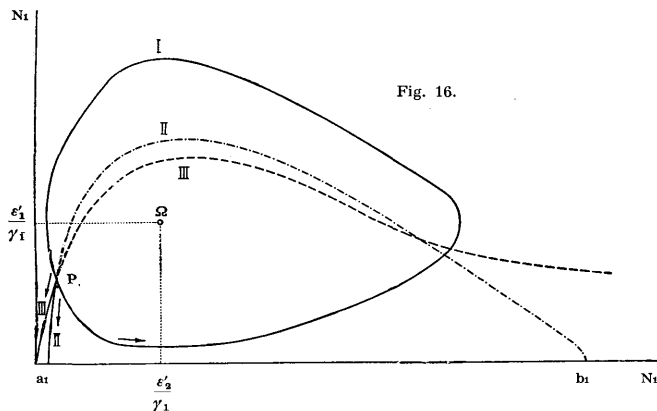


Fig. 16.

No. I is a curve of fluctuation which therefore corresponds to $\epsilon'_1 > 0$ (for this reason it is of the type of those in fig. 2), No. II is a curve of the type of those in fig. 15 (curve of transition from the type in fig. 2 to the type of fig. 9), No. III is a curve of the type of those in fig. 9 and corresponds to $\epsilon_1 - \alpha\lambda$ negative and equal to $-h$. We have besides

$$0 < \epsilon'_2 < \epsilon''_2 < \epsilon'''_2.$$

The curves mentioned refer respectively to the three cases in which the intensity of destruction of the species does not attain the limit $\frac{\epsilon_1}{\alpha}$, or is equal to it, or exceeds it.

§ 6. The Case of any Number whatever of Species which contend for the same Food.

1. It is easy to extend what has been done in the case of two species living together, which contend for the same food, to the case of any number of species.

Let us take the number of species to be n and let us assume $\epsilon_1, \epsilon_2, \dots, \epsilon_n$ to be the coefficients of increase which each species would have if alone.

Let us denote by $F(N_1, N_2, \dots, N_n) dt$ the diminution in the quantity of food in the time dt , when the numbers of individuals of the different species are respectively N_1, N_2, \dots, N_n . This function will be zero for $N_1 = N_2 = \dots = N_n = 0$; it will be positive and increasing and will increase indefinitely with an indefinite increase in each N_r . For simplicity we could take F linear, that is

$$F(N_1, N_2, \dots, N_n) = \alpha_1 N_1 + \alpha_2 N_2 + \dots + \alpha_n N_n$$

where the coefficients α_r are positive. But we shall leave F general.

The presence of N_1 individuals of the first species, of N_2 of the second, etc. will influence the coefficients of increase reducing ϵ_r to $\epsilon_r - \gamma_r F(N_1, \dots, N_n)$ where the positive coefficient γ_r measures the influence which the diminution of the food has upon the increase of the species.

We shall have then the differential equations

$$[23] \quad \frac{dN_r}{dt} = N_r (\epsilon_r - \gamma_r F(N_1, \dots, N_n)), \quad (r = 1, 2, \dots, n)$$

from which follows

$$\frac{1}{\gamma_r N_r} \frac{dN_r}{dt} - \frac{1}{\gamma_s N_s} \frac{dN_s}{dt} = \frac{\epsilon_r}{\gamma_r} - \frac{\epsilon_s}{\gamma_s}$$

and integrating and passing from logarithms to numbers

$$\frac{N_r \frac{1}{\gamma_r}}{\frac{1}{N_s \gamma_s}} = C e^{\left(\frac{\epsilon_r}{\gamma_r} - \frac{\epsilon_s}{\gamma_s} \right) t}$$

where C is a positive constant.

2. Let us arrange the ratios $\frac{\epsilon_r}{\gamma_r}$ in order of size, that is let us suppose¹⁾

$$\frac{\epsilon_1}{\gamma_1} > \frac{\epsilon_2}{\gamma_2} > \frac{\epsilon_3}{\gamma_3} > \dots > \frac{\epsilon_n}{\gamma_n},$$

then we shall have, if $r < s$

¹⁾ Let us exclude the cases of equality as of infinitesimally small probability.

$$\lim_{t=\infty} \frac{N_r \gamma_r}{N_s \gamma_s} = \infty.$$

As a consequence of this result either N_r can, with increase of time, take values as large as we please, or

$$\lim_{t=\infty} N_s = 0.$$

But the first case is to be excluded, because F increases indefinitely with indefinite increase of N_r , therefore in [23] the second member becomes negative when N_r exceeds a certain limit; whence the upper limit of N_r is finite. Then the second case must hold. From this it follows that all the species tend to disappear except the first.

To have the asymptotic variation of N_1 it will suffice to repeat what has been done in the case of two species alone.

§ 7. Case of any Number whatever of Species some of which feed upon others.

1. Let us consider the case of n species and let us suppose that the encounter of two individuals of different species always carries a result favorable to the species to which one belongs, and unfavorable to that to which the other belongs, or else a zero result for both. If N_r is the number of individuals of the species r and N_s the number of individuals of the species s the probability of an encounter of an individual of one with an individual of the other will be proportional to $N_r N_s$ whence we can assume that the number of encounters which take place in the unit of time is equal to $m_{rs} N_r N_s$. Let us suppose that at each encounter there are destroyed p_{rs} individuals (p_{rs} will evidently be a fraction) of one of the two species, for example of the species r , then in the unit of time $m_{rs} p_{rs} N_r N_s$ individuals of this species will be destroyed. Let us see how the influence that this has on the number of individuals of the other species can be calculated.

A rough calculation can be made in this way: Let us denote by $\beta_1, \beta_2, \dots, \beta_n$ the average weights of all the individuals of the n species and by P_1, P_2, \dots, P_n the total weights of all the individuals belonging to each species. To get the number of individuals of each species it will suffice to take

$$N_1 = \frac{P_1}{\beta_1}, \dots, N_r = \frac{P_r}{\beta_r}, \dots, N_n = \frac{P_n}{\beta_n}.$$

Now if an individual of the species r is eaten by individuals of the species s the weight P_r will become $P_r - \beta_r$ while the weight P_s will become $P_s + \beta_r$ and for this reason the respective numbers of individuals of the two species will become roughly

$$\frac{P_r - \beta_r}{\beta_r} = N_r - 1, \quad \frac{P_s + \beta_r}{\beta_s} = N_s + \frac{\beta_r}{\beta_s}.$$

Then in a very rough way we can say that in the unit of time, by virtue of the encounters of individuals of the species r with individuals of the species s , the diminution of individuals of species r will be given by

$$m_{rs} p_{rs} N_r N_s$$

and the increase of individuals of species s , also in the unit of time, will be given by

$$m_{rs} p_{rs} N_r N_s \frac{\beta_r}{\beta_s}.$$

Letting $m_{rs} p_{rs} \beta_r = a_{rs}$ the diminution of individuals of the species r will be

$$\frac{1}{\beta_r} a_{rs} N_r N_s$$

and the increase of individuals of the species s will be

$$\frac{1}{\beta_s} a_{rs} N_r N_s$$

or also letting $a_{rs} = -a_{sr}$ (supposing a_{sr} to be negative) we can say that in the unit of time, by virtue of their encounters, the numbers of individuals of the species r and of the species s increase respectively by

$$\frac{1}{\beta_r} a_{sr} N_r N_s, \quad \frac{1}{\beta_s} a_{rs} N_r N_s,$$

and hence in the time dt , through their encounters, they increase respectively by

$$\frac{1}{\beta_r} a_{sr} N_r N_s dt, \quad \frac{1}{\beta_s} a_{rs} N_r N_s dt.$$

The same can be said of each other pair of species. In other words the numbers $\frac{1}{\beta_1}, \frac{1}{\beta_2}, \dots, \frac{1}{\beta_n}$ have been assumed as the equivalents of the individuals of the various species. In fact to grant that $\frac{1}{\beta_r}$ individuals of the species r can be transformed into $\frac{1}{\beta_s}$ individuals of the species s means that $\frac{1}{\beta_r}$ individuals of the species r are equivalent to $\frac{1}{\beta_s}$ individuals of the species s . Thus, taken in a very rough first approximation, we have as equivalent the reciprocals of the average weights, but it will suffice for us to take as hypothesis the existence of equivalent numbers, even if these do not coincide with the reciprocals of the average weights, in order to obtain the same results which we have now secured.

2. Let us call ϵ_r the coefficient of increase of the species r while that is alone, then if all the n species live together we shall have for the increase of the individuals N_r in the time dt

$$dN_r = \epsilon_r N_r dt + \frac{1}{\beta_r} \sum_s^n a_{sr} N_r N_s dt,$$

whence we shall have the differential equations:

$$\frac{dN_r}{dt} = \left(\epsilon_r + \frac{1}{\beta_r} \sum_s^n a_{sr} N_s \right) N_r, \quad (r = 1, 2, \dots, n)$$

or likewise

$$[B] \quad \beta_r \frac{dN_r}{dt} = \left(\epsilon_r \beta_r + \sum_s^n a_{sr} N_s \right) N_r, \quad (r = 1, 2, \dots, n)$$

in which

$$a_{rs} = -a_{sr}, \quad a_{rr} = 0, \quad \beta_1, \beta_2, \dots, \beta_n > 0.$$

In the case of two species only, one of which feeds upon the other, we have considered the equations (§ 3, N. 1)

$$\frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2) N_1, \quad \frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1) N_2.$$

If we put

$$-\gamma_1 = \frac{a_{21}}{\beta_1}, \quad \gamma_2 = \frac{a_{12}}{\beta_2}$$

these equations assume the form [B], with the need only of writing ϵ_2 instead of $-\epsilon_2$ and understanding that ϵ_2 is negative. We see therefore that in this case there is no need of a special hypothesis.

For an association of n species we must distinguish the case in which the number of the species is even from that in which the number is odd.

In the first case the following statement can be proved: If there exists a stationary state¹⁾, placing the species in any state whatever different from the stationary state, the number of individuals of each species will remain limited between two positive numbers.

3. We must now establish some definitions in order to enunciate certain propositions without ambiguity.

If $N(t)$ indicates the number of individuals of a species and always remains included between two positive numbers, the species will be said to have limited variation between positive numbers.

If $N(t)$ approaches zero this signifies that the species is exhausting itself or also that the variation consists in a depletion.

If $N(t)$ is limited between two positive numbers, $N(t)$ will be said to have fluctuations if for $t > t_0$ (for t_0 however large) N has maximum and minimum values.

The fluctuations will be said to be damped if the oscillation (the difference between the upper and the lower limit) of $N(t)$ for $t > t_0$ can be made as small as we please by sufficiently increasing t_0 . In this case and in this case only the fluctuations permit that N approach a fixed and finite limit for $t = \infty$.

$N(t)$ will be said to vary asymptotically and to approach asymptotically the limit q , if $N(t)$ has no fluctuations and approaches the fixed and finite limit q for $t = \infty$.

The limits for $t = \infty$ of the averages of N_1, N_2, \dots, N_n in the time $t_0 t$, will be called the asymptotic averages.

4. For an association of an even number of species we now express the following general propositions, omitting the demonstrations:

1) If there exists a stationary state for the biological association, the numbers of individuals of each species are limited between positive numbers, fluctuations always existing which are not damped, and the asymptotic aver-

¹⁾ That is a system of positive values of N_1, N_2, \dots, N_n satisfying the equations

$$0 = \epsilon_r \beta_r + \sum_s^n a_{sr} N_s \quad (r = 1, 2, \dots, n).$$

ages of the numbers of individuals of all the separate species are the values corresponding to the stationary state.

II) The deviations from the stationary state can be made as small as we please, provided the initial state is sufficiently near to the stationary state.

In other words:

The stationary state is always a stable state¹⁾.

III) The small fluctuations of n species living together can be obtained by means of the superposition of $\frac{n}{2}$ fluctuations not damped and each having a period of its own.

As in general the periods $T^{(h)}$ will be incommensurable with each other, so the resulting fluctuation will not be periodic. Let it be observed that the number of the periods $T^{(h)}$ is equal to half the number of the species living together, but let it be called to mind that the laws of fluctuation now obtained hold in the case in which the number of species living together is even.

To summarize, the three theorems which we have designated by I, II, III, can be considered as three general laws of variation of an even number of species living together.

We can also enunciate the proposition: in order that there may exist a stationary state and ensuing fluctuations, some of the coefficients ϵ_r of increase must be positive and others negative, that is to say:

If by themselves all the species increase or all decrease, neither a stationary state nor ensuing fluctuations can exist.

If the number of species is odd it is not possible that the number of individuals of each species should stay limited between two positive numbers.

To thoroughly understand the significance of this theorem it is necessary to consider it as a purely theoretical result. Let us observe in the meantime that if one of the species should tend toward depletion, the number of the species will tend to become even and we shall return to the case considered previously.

But if the number of individuals of one of the species should increase indefinitely, it can be recognized that equations $[B]$ will no longer be valid. In fact we have supposed the ϵ_r constants, that is to say independent of

¹⁾ The stability here is thought of in the sense analogous to the stability of equilibrium in mechanics.

the number of individuals present, which can be allowed if this number does not exceed a certain limit, but beyond this it can not be true any longer, whence the equations will be modified, at least for the changed value which will have to be attributed to the constants ϵ_r , in order to arrest the increase of that species which would increase indefinitely.

§ 8. Extension of the three fundamental Laws on Fluctuations to the Case of Associations of any Number whatever of Species.

1. In § 3 three fundamental laws on the fluctuations of two species living together have been stated. What is the extension of these to the general case of n species?

In § 7 it has been stated that in the case of an even number of species, if the fundamental determinant (the determinant of the system of equations B) is different from zero and if there exists a stationary state of the species without depletion, the variations of the numbers of individuals of the several species are limited between positive numbers and some fluctuations always exist which are not damped. Thus is enunciated the extension of the first law relative to two species. Evidently with this extension the property of periodicity is lost while that of fluctuation remains.

2. Let us admit as verified the aforementioned hypotheses and let us begin with an observation with regard to the extension of the second law (that is to say that of the invariability of the averages of the number of individuals) which, lacking periodicity, can not specify the duration of the time in which the averages must be taken. But we know that, taking the averages for infinitely long durations of time, these approach the roots of the equations of equilibrium. Now these roots are independent of the initial conditions, whence the second law remains unaltered if we take as averages (cf. § 7) of the numbers of individuals of separate species, the limits of the same averages for infinitely long durations of time (asymptotic averages).

3. The question now is to see what form the third law will assume in general, namely the law of disturbance of the averages, always granting as verified the aforesaid hypotheses. For the averages of the numbers of individuals of the several species we shall always assume the asymptotic averages.

In the third law (§ 3, N. 8) a distinction is made between the species

that is eaten and the species feeding upon the other. When we pass to more than two species, it may be that the individuals of one species are eaten by those of another and themselves feed upon the individuals of a third species. Wishing to keep the distinction between species that are eaten and those feeding upon others it is necessary to admit that if a species A feeds upon another there is not any species that eats A and hence that if a species B is eaten by another, it does not feed upon any other species of the biological association.

4. Now we can state the theorem that if we keep the preceding hypotheses the numbers of the species eating others must be equal to the number of the species fed upon.

Whence we can suppose that $n = 2p$ and that the species $1, 2, \dots, p$ are feeding upon others and the species $(p+1), (p+2), \dots, 2p$ are fed upon. Then for the existence of a stationary state $\epsilon_1, \epsilon_2, \dots, \epsilon_p$ must be negative and $\epsilon_{p+1}, \epsilon_{p+2}, \dots, \epsilon_{2p}$ must be positive.

Now let us increase

$$|\epsilon_1|, \quad |\epsilon_2|, \dots, |\epsilon_p|$$

and let us diminish

$$|\epsilon_{p+1}|, \quad |\epsilon_{p+2}|, \dots, |\epsilon_{2p}|$$

namely let us destroy one set of species as much as the other in proportion to the number of individuals which they have respectively. Some one of the

$$N_{p+1}, N_{p+2}, \dots, N_{2p}$$

satisfying the equations of equilibrium will have to increase and some one of the

$$N_1, N_2, \dots, N_p$$

satisfying the same equations must diminish. Reciprocally if none of the N_{p+1}, \dots, N_{2p} decreases, but all or some increase, if none of the N_1, \dots, N_p increases, but all or some diminish, then $|\epsilon_{p+1}|, |\epsilon_{p+2}|, \dots, |\epsilon_{2p}|$ must diminish and $|\epsilon_1|, |\epsilon_2|, \dots, |\epsilon_p|$ must increase, that is to say individuals of the species feeding upon others must be destroyed, as well as of the species eaten, in proportion to their number.

It is in this that the extension of the third law consists, which (recalling the significance of the roots of the equations of equilibrium) can be enunciated as follows:

In a conservative association of even order, with determinant different from zero, for which a stationary state exists and the species feeding upon others can be distinguished from those eaten, if all the species are destroyed uniformly and in proportion to the number of their individuals, the asymptotic averages of the number of individuals of some of the species eaten (if not of all) will increase, and the asymptotic averages of the numbers of individuals of some of the species feeding upon others (if not of all) will diminish.

Naturally this proposition holds up to a certain limit of destruction (cf. §§ 4, 5), and if the roots of the equations of equilibrium are positive.

§ 9. Case in which the Coefficient of increase of each separate Species depends on the Number of Individuals of that same Species.

1. Various times in preceding sections we have had occasion to consider cases in which the calculation would lead to an indefinite increase of the number of individuals of one or more species. Such a result must be considered theoretical and we have not failed to give explicit warning on this as in N. 1 of § 4, observing that with the increase of the number of individuals the equations must become invalid, and in particular that the coefficients of increase must be modified because of the indefinite increase in the number of individuals.

This necessitates a consideration of the influence which the number of individuals of one species has upon its coefficient of increase. It is evident that this effect can be neglected as long as the number of individuals does not exceed certain limits, but it is necessary to take it into account when the calculation leads to an infinite increase of individuals. Let us see how this can be done.

In the case in which only one species exists, and if we admit the coefficient of increase as constant and equal to ϵ , we shall have

$$\frac{dN}{dt} = \epsilon N$$

where N denotes the number of individuals, whence

$$N = N_0 e^{\epsilon t}$$

where N_0 is the initial number of individuals. If ϵ is positive N will increase indefinitely.

Now let us suppose that the coefficient of increase is not constant, but is given by $\epsilon - \lambda N$ where ϵ and λ are positive constants. We shall have

$$N = \frac{C\epsilon e^{\epsilon t}}{1 + C\lambda e^{\epsilon t}}$$

and hence

$$\lim_{t \rightarrow \infty} N = \frac{\epsilon}{\lambda}.$$

Corresponding changes can be made in equations [B], and from a study of them we may state the theorem:

If a stationary state exists and if the coefficients of increase of one or more species decrease linearly with the increase of the number of the respective individuals, while the coefficients of increase of the other species are constants, starting out from any initial state whatever different from the stationary state, we shall have for the first species either asymptotic variations or fluctuations which will be damped. If all the coefficients decrease in the afore-said manner the system will tend toward the stationary state¹).

In certain ways the actions which tend to damp the increase of each species with the increase of the number of individuals belonging to it produce an effect analogous to that of internal attritions in a material system, that is they damp the fluctuations.

§ 10. Conservative and dissipative Biological Associations.

1. The considerations of the last section can be notably extended; we shall thus be led to a fundamental classification of biological associations.

To this end let us suppose that the coefficients of increase depend linearly in any way upon the number of individuals, not only of each species, but of the various species and let the effects of the encounters of individuals of different species be felt in any way whatever, but constant, by the species themselves, proportional to the number of encounters, without further concern over the satisfaction of the hypothesis of § 7, N. 1.

¹) Also if some coefficients λ_r are zero, the state of the system can approach the stationary state. (Cf. § 8, N. 4.)

It is easy to be convinced with particular examples that according to different cases there may be asymptotic variation and damped fluctuations.

Equations [B] then assume the general form

$$[C] \quad \frac{dN_r}{dt} = \left(\epsilon_r - \sum_s^n p_{rs} N_s \right) N_r$$

where the coefficients ϵ_r and p_{rs} are any constants whatever.

We can consider the ϵ_r as dependent on the constant causes of increase or decrease of the species, and the other terms as dependent upon the reciprocal actions of the individuals. Evidently with this there is shown an extension of the concept of reciprocal action among the various individuals much greater than has been done previously.

If each species were alone the ϵ_r would be their coefficients of increase, while

$$\epsilon_r - \sum_s^n p_{rs} N_s$$

are the coefficients of increase of the same species as a result of their living together. We shall call these last the true coefficients of increase and ϵ_r the rough coefficients of increase or also we shall call them simply coefficients of increase when confusion can not arise between the two sets.

2. First of all we can say that it is sufficient that one of the coefficients be positive, in order that all the species should not be exhausted.

Let the quantities $\alpha_1, \alpha_2, \dots, \alpha_n$ be positive and let us place

$$F(N_1, N_2, \dots, N_n) = \sum_r^n \sum_s^n \alpha_r p_{rs} N_s N_r.$$

We shall have the theorem:

If the form F is positive definite, there will exist a number N such that none of the numbers N_1, N_2, \dots, N_n can remain larger than N , starting from a certain instant.

In fact from [C] it follows that

$$\sum_r^n \alpha_r \frac{dN_r}{dt} = \sum_r^n \alpha_r \epsilon_r N_r - F(N_1, N_2, \dots, N_n).$$

Letting $N_r = 1$, let us denote by m_r the lower limit of the values of F for all possible values of $N_1, N_2, \dots, N_{r-1}, N_{r+1}, \dots, N_n$. m_r will be > 0 . Let m be the smallest of the numbers m_1, m_2, \dots, m_n . Besides let

$$\sum_{r=1}^n |\alpha_r \epsilon_r| < E.$$

Let us suppose that N_r after a certain instant t_1 stays greater than

$$\frac{E+1}{m} = N.$$

Let us denote by $M(t_2)$ the greatest of the numbers $N_1(t_2)$, $N_2(t_2)$, \dots , $N_n(t_2)$ where $t_2 > t_1$.

Then we shall have

$$F(N_1, N_2, \dots, N_n)_{t=t_2} > mM^2(t_2)$$

$$\sum_{r=1}^n \alpha_r \epsilon_r N_r(t_2) < EM(t_2)$$

whence it follows that

$$\left(\sum_{r=1}^n \alpha_r \frac{dN_r}{dt} \right)_{t=t_2} > (E - mM(t_2)) M(t_2).$$

Now

$$M(t_2) > \frac{E+1}{m}$$

hence

$$\left(\sum_{r=1}^n \alpha_r \frac{dN_r}{dt} \right)_{t=t_2} < -\frac{E+1}{m}, \quad (t_2 > t_1),$$

a consequence of which would be that starting from a certain moment, some one of N_1, N_2, \dots, N_n would have to become negative which is absurd, since N_r can be only positive as follows also from [C]. In fact from these equations is derived

$$N_r = N_r^0 e^{\int_0^t (\epsilon_r - \sum_s p_{rs} N_s) dt}$$

where N_r^0 is the value of N_r for $t = 0$, whence as N_r^0 is positive so will N_r remain. Therefore there exists the number $N = \frac{E+1}{m}$ such that each N_r after a certain instant t_1 can not remain greater than that number.

Combining the last two theorems now we can state the proposition: If at least one of the coefficients of increase is positive and

if the form E is positive definite the biological association will be stable.

The stability consists in the fact that the whole association does not tend toward depletion, and no one species can increase indefinitely.

As the N_i are all positive so the preceding theorem can be extended to the case in which the form F is not zero except when every $N_i = 0$ and is positive for all positive values of the N_i .

3. We can easily see that if the form F is positive definite the determinant formed with the p_{rs} can not be zero. Let us suppose that it is zero. Then there would exist some numbers N_1, N_2, \dots, N_n (positive, negative, or zero, but not all zero) which would satisfy the equation

$$\sum_s^n p_{rs} N_s = 0$$

and hence

$$0 = \sum_r^n \sum_s^n \alpha_r p_{rs} N_s N_r = F(N_1, N_2, \dots, N_n)$$

which contradicts the hypothesis that the form F is positive definite.

Having made this premise, let us suppose that the equations

$$[C] \quad \epsilon_r - \sum_s^n p_{rs} N_s = 0$$

when solved with respect to N_s give the solutions $q_s \neq 0$. We shall have then the identities

$$\epsilon_r = \sum_s^n p_{rs} q_s$$

whence equations $[C]$ will become

$$\frac{dN_r}{dt} = - \sum_s^n p_{rs} (N_s - q_s) N_r$$

that is by letting

$$\frac{N_r}{q_r} = n_r$$

we shall have

$$[24] \quad \frac{dn_r}{dt} = - \sum_s^n p_{rs} q_s (n_s - 1) n_r.$$

From these equations it follows that

$$\frac{1}{n_r} \frac{dn_r}{dt} = - \sum_s^n p_{rs} q_s (n_s - 1).$$

Let α_r represent positive constant quantities; then we shall have

$$\sum_r \alpha_r q_r \frac{n_r - 1}{n_r} \frac{dn_r}{dt} = - \sum_r^n \sum_s^n p_{rs} \alpha_r q_r q_s (n_s - 1) (n_r - 1).$$

Let us place

$$[25] \quad \frac{1}{2} (p_{rs} \alpha_r + p_{sr} \alpha_s) = m_{rs} = m_{sr},$$

$$[26] \quad F(x_1, x_2, \dots, x_n) = - \sum_r \sum_s m_{rs} x_r x_s,$$

then the preceding equation can be written

$$\frac{d}{dt} \sum_r \alpha_r q_r (n_r - \log n_r) = -F(x_1, x_2, \dots, x_n)$$

where

$$x_r = (n_r - 1) q_r.$$

Integrating and passing from logarithms to numbers, we shall have

$$\left(\frac{e^{n_1}}{n_1} \right)^{\alpha_1 q_1} \left(\frac{e^{n_2}}{n_2} \right)^{\alpha_2 q_2} \dots \left(\frac{e^{n_n}}{n_n} \right)^{\alpha_n q_n} = C e^{-\int_0^t F dt}$$

where C is a positive constant.

If q_1, q_2, \dots, q_n are positive, namely if there exists a stationary state and if $\alpha_1, \alpha_2, \dots, \alpha_n$ can be so chosen that the quadratic form [26]¹⁾ is identically zero, the numbers of individuals of the separate species will be limited between positive numbers and fluctuations must exist which are not damped. If a stationary state exists and if the positive constants $\alpha_1, \alpha_2, \dots, \alpha_n$ can take such values as to make the form [26] positive we can say that the variation of the numbers of individuals of the separate species is confined between two positive numbers²⁾; but if the form is

¹⁾ In this case, in order that the determinant of the p_{rs} be different from zero, n will have to be even.

²⁾ This property leads at once to the recognition that the limits of the averages of N_1, N_2, \dots, N_n in intervals of time increasing infinitely are q_1, q_2, \dots, q_n .

positive definite besides this it will follow that all the variations of the separate species will be asymptotic or there will be damped fluctuations which make the biological association tend toward the stationary state.

The proof of this proposition is analogous to the proof of the proposition of § 9.

Besides we find that every time the form [26] is positive the limits of the average of N_1, N_2, \dots, N_n in intervals of time increasing indefinitely will be q_1, q_2, \dots, q_n .

The expression F can be written

$$[27] \quad F = \sum_r^n \sum_s^n \alpha_r p_{rs} (N_r - q_r) (N_s - q_s).$$

In § 9 the action damping the fluctuations has been compared to an internal attrition. The preceding form F can be taken as a measure of this damping action, which characterizes the tendency toward the stationary state of the group of all the species, and in fact, if F is zero the biological association will not tend toward a limit state, while if it is positive definite the association will tend toward the stationary state.

We shall call the form $F(x_1, x_2, \dots, x_n)$ the fundamental form and the equations [C] the equations of equilibrium. We exclude the case in which these equations have zero roots, that is we exclude the possibility that the stationary state can coincide with the exhaustion of any one of the species.

4. Now we can review the hypothesis of § 7, N. 1, and get a deeper insight into its significance.

Let us suppose we give to each individual of the species r a positive value α_r . The value of the whole biological association will be $V = \sum_r^n \alpha_r N_r$ whence, from the equations [C] will follow

$$dV = \sum_r^n \alpha_r \epsilon_r N_r dt - \sum_r^n \sum_s^n p_{rs} \alpha_r N_r N_s dt.$$

The increase of value of the biological association in the time dt consists then of two parts

$$dV_1 = \sum_r^n \alpha_r \epsilon_r N_r dt$$

$$dV_2 = \sum_r^n \sum_s^n p_{rs} \alpha_r N_r N_s dt.$$

The first is due to the constant causes of increase and decrease of each species (particularized by ϵ_r), and the second is due to the reciprocal actions of the various individuals in the general sense understood before.

If the α_r can be chosen in such a way that dV_2 be zero whatever may be N_1, N_2, \dots, N_n , the value of the biological association will not change in consequence of the reciprocal actions of the individuals. A biological association of this nature, namely in which it is possible to assign to the separate individuals such values that their reciprocal actions keep the value of the entire association constant will be said to be conservative. Evidently for a conservative system the hypothesis of § 7, N. 1 is satisfied. Reciprocally, if that hypothesis is holding and the reciprocal actions between individuals of the same species are negligible, the biological association will be conservative.

Absolutely conservative biological associations are probably ideals which can only approximate the conditions effective in nature. But a special example of conservative systems is considered in § 7, N. 2.

When to separate individuals there can be assigned values (equal for those of the same species) such that the fundamental form F be positive definite the reciprocal actions between individuals will tend to diminish the value of the entire association which can therefore be called dissipative. It seems that in many real cases biological associations must approximate dissipative associations.

§ 11. General Theorems on conservative and dissipative Biological Associations.

1. A proposition can be stated which says the value of a conservative biological association: 1) approaches zero if all the coefficients of increase are negative and only when all are negative; 2) approaches infinity if all are positive¹⁾.

The first part of this proposition can be extended to dissipative systems.

In fact from [C], using [25], it follows that

$$\sum_r^n \alpha_r \frac{dN_r}{dt} = \sum_r^n \alpha_r \epsilon_r N_r - \sum_r^n \sum_s^n m_{rs} N_r N_s.$$

¹⁾ In this statement we have excluded the case of zero coefficients of increase as we shall also exclude it in the extension of the proposition.

If the form

$$\sum_r^n \sum_s^n m_{rs} N_r N_s$$

is positive definite or semi positive definite then

$$\sum_r^n \alpha_r \frac{dN}{dt} \leq \sum_r^n \alpha_r \epsilon_r N_r$$

and if

$$\epsilon_r < -\epsilon, \quad (r = 1, 2, \dots, n)$$

ϵ being a positive quantity, we shall have

$$\sum_r^n \alpha_r N_r < \sum_r^n \alpha_r N_r^0 e^{-\epsilon t}$$

which proves that the value of the biological association approaches zero if all the coefficients of increase are negative; then in order that the biological association should not exhaust itself it is sufficient that one only of these coefficients should be positive (cf. § 10 N. 2).

As for the second part of the preceding proposition, by virtue of what is shown in § 10, N. 2 it must be replaced by: the value of a dissipative biological association stays limited.

For a conservative association it is possible to prove the following theorem: None of the several species can either exhaust itself or increase indefinitely in a finite time.

2. Let us pass to the case of dissipative associations: For these we know that the number of individuals of each species is limited, but it can be proved that the number can not however become zero in a finite time.

The conclusion will be: In a dissipative association no species can exhaust itself in a finite time, whereas the number of individuals of each species is limited.

3. Then we can state the theorem: In order that in a dissipative association or in a conservative association of even order (with determinant different from zero) the number of individuals of each species should remain between positive numbers, a necessary and sufficient condition is that the roots of the equations of equilibrium be positive.

§ 12. Fluctuations Peculiar to the System, forced Fluctuations, and the Principle of their Superposition.

1. In equations [C] of § 10, which can be considered as the most general and as summing up all those preceding, we have supposed that the coefficients of increase ϵ_r be constants; but really these change and in general their changes are periodic or due to the addition of more periodic terms. Certainly in all practical cases we shall have to consider an annual period in connection with the changes of seasons and meteorological conditions. But nothing precludes the existence of other periods.

Let us try to take account of these periodic disturbances of the coefficients of increase, for which let us substitute

$$\epsilon_r + g'_r \cos kt + g''_r \sin kt$$

for ϵ_r where g'_r , g''_r and k are constant quantities.

Equations [C] will become

$$[D] \quad \frac{dN_r}{dt} = (\epsilon_r + g'_r \cos kt + g''_r \sin kt - \sum_s^n p_{rs} N_s) N_r$$

and [24]

$$\frac{dn_r}{dt} = (g'_r \cos kt + g''_r \sin kt - \sum_s^n p_{rs} q_s (n_s - 1)) n_r$$

in which we shall suppose each q_s positive.

Let us observe that ϵ_r are the average values of the coefficients of increase during the period $\frac{2\pi}{k}$; we can then state the theorem: If the coefficients of increase are periodic and their average values differ little from the changeable values, and if taking these average values as the coefficients of increase, there result asymptotic variations or damped fluctuations or fluctuations not damped near to a stationary state (variations peculiar to the system), then for small fluctuations corresponding to periodic coefficients of increase the principle of superposing on the forced fluctuations the variations peculiar to the system will be applicable, that is to say small fluctuations will be obtained, superposing on the variations peculiar to the system those which are forced having the period of the coefficients of increase, when that period does not coincide with any of the periods of the casual fluctuations peculiar to the system.

§ 13. Disturbance Produced in a Biological Association having a stationary State by the Addition of a new Species.

1. By using results of preceding sections we can state the following theorem: If a stationary state exists for a certain biological association, but by adding a new species to it the possibility of the stationary state is lost because the equations of equilibrium have a negative root for the number of individuals of the species added, the small variations of the whole association (supposed dissipative) will consist of a variation of the original association near to its stationary state superimposed on a depletion of the new species¹).

For this reason the species added will tend to a depletion and the others will approach a variation near to the stationary state, whence the addition of the new species will produce a disturbance which will tend to disappear.

§ 14. Study of a particular Biological Association of three Species.

1. As an example of the treatment developed previously let us examine a particular case which, because of the theory shown above, can be treated mathematically in full.

Let us suppose three species living together in a limited environment, for example on an island. Of these three species let the first eat the second and this the third and not vice versa. For example we can take a species of carnivorous animals that feed upon an herbivorous species and this in turn feeds upon a vegetable species, admitting that for this last the same treatment holds as that used for the animals. Another example is furnished by plants their parasites and parasites of these parasites.

2. Let us admit the biological association to be conservative (cf. § 10).

If we indicate the number of individuals of the three species by N_1 , N_2 , N_3 we shall have equations (see [B], § 7, N. 2)

$$\begin{aligned}\beta_1 \frac{dN_1}{dt} &= (\beta_1 \epsilon_1 + a_{21} N_2 + a_{31} N_3) N_1 \\ \beta_2 \frac{dN_2}{dt} &= (\beta_2 \epsilon_2 + a_{12} N_1 + a_{32} N_3) N_2\end{aligned}$$

¹) It is opportune to compare this theorem with that of § 11.

$$\beta_3 \frac{dN_3}{dt} = (\beta_3 \epsilon_3 + a_{13} N_1 + a_{23} N_2) N_3$$

where $\beta_1, \beta_2, \beta_3$ are constant quantities.

In our case we must take

$$\begin{array}{lll} \epsilon_1 = -l < 0, & a_{21} = a > 0, & a_{31} = 0, \\ \epsilon_2 = -m < 0, & a_{12} = -a < 0, & a_{32} = b > 0, \\ \epsilon_3 = k > 0, & a_{13} = 0, & a_{23} = -b < 0, \end{array}$$

where a, b, l, m, k are constant quantities.

According to values of these coefficients of increase and of voracity and values of $\beta_1, \beta_2, \beta_3$, the following cases and subcases can be presented:

1st Case.— $\beta_3 ka - \beta_1 lb < 0$

The food furnished to the carnivori by the herbivori is not sufficient to maintain the carnivorous species and this is depleted, while the herbivori and the plants tend toward a periodic fluctuation not damped. (We can suppose the coefficient of increase of the plants, k , to be constant because in this case the vegetable species can not increase indefinitely.)

2nd Case.— $\beta_3 ka - \beta_1 lb > 0$

If the coefficient of increase of the vegetable species were constant, the number of individuals in it would grow indefinitely, hence it is proper to suppose that this coefficient decreases proportionally to the number of individuals.

2nd Case, subcase a). — The food provided by the plants is not sufficient to maintain the herbivori, hence the herbivorous species and the carnivorous species die out, while the vegetable species tends toward a constant value.

2nd Case, subcase b). — The plants are sufficient to maintain the herbivori, but there is not sufficient food for the carnivori through the herbivori, hence the carnivorous species is depleted, while the herbivori and plants tend toward a damped fluctuation, and finally to a stationary state.

2nd Case, subcase c). — The food is sufficient so that all the species live, and through asymptotic and damped variations they all tend toward a stationary state.