that they may be alarmed at extremely dilute emanations (Schreckstoff) from injured fish skin. It would seem too that the acuity of the sense of smell in fishes is of similar sensitivity as that of dogs and insects where but a few molecules stimulate the end organ. In contrast, the common chemical sense and the ability to discriminate temperature differences are crude senses when compared with the olfactory system.

Techniques have been developed whereby it is now possible to hatch and maintain salmon through the fingerling stage in aquaria at Madison. Preliminary results from a set of experiments currently in progress indicate that the olfactory system of salmon is very acute, and that they can discriminate between stream odors.

A set of field experiments must also be undertaken to furnish final proof of the hypothesis herein contained. Of a number of possible methods of solution, one promises to be of some practical value. The hypothesis could be tested by exposing salmon to a constant, artificial odor through the fingerling stage and then determining if the fish conditioned in a hatchery could be decoyed to a neighboring stream upon return from the sea. Should this be the case, it would aid in salvaging the declining salmon runs where new dams may obstruct passage to their parent streams. . . .

Kormondy, E.J. 1965. Readings in Ecology.
Prentice-Hall, Inc. NJ. 219 pp.

THE STUDY OF POPULATIONS

Discrete populations of a species are sufficiently unit-like in their characteristics and responses to permit their being objectified. Among the many facets of a population, ecologists are concerned with aspects of their growth (natality, mortality, growth form, etc.), regulation (fluctuations, oscillations, dispersal, etc.), and inter- and intraspecific interactions (cooperation, competition, etc.).

Since its inception, this field has had a strong mathematical orientation in formulating and testing descriptive and predictive models. Much of its empirical and theoretical development has had an animal focus based on data derived largely from laboratory populations of relatively few diverse kinds of organisms. The original anthropocentric orientation given the field continues, for in spite of the more esoteric and academic aspects of population ecology, the implications regarding the human population are not easily avoided.

AN ESSAY ON THE PRINCIPLE OF POPULATION AS IT AFFECTS THE FUTURE IMPROVEMENT OF SOCIETY

Thomas Robert Malthus—1798

Reprint of the first and second chapters of the first edition. *London, Johnson*, 1798.

This is the most significant essay on population ever written and perhaps one of the most influential essays in all literature. Malthus' practical and realistic analysis demonstrated the principle that a population will outstrip its means of subsistence owing to inherent differences in their rates of increase and that under such stress vice and misery will operate to restrain population growth. This principle shattered a prevalent utopian aura in which man was to enjoy unlimited progress and infinite perfectibility. The second, and subsequent, editions of the essay lacked the forcefulness of the first, being mitigated in the proposing of "moral restraint," i.e., chastity, as a preventive check on population growth.

. . . In entering upon the argument I must premise that I put out of the question, at present, all mere conjectures, that is, all suppositions, the probable realization of which cannot be inferred upon any just philosophical grounds. A writer may tell me that he thinks man will ultimately become an ostrich. I cannot properly contradict him. But before he can expect to bring any reasonable person over to his opinion, he ought to shew, that the necks of mankind have been gradually elongating, that the lips have grown harder and more prominent, that the legs and feet are daily altering their shape, and that the hair is beginning to change into stubs of feathers. And till the probability of so wonderful a conversion can be shewn, it is surely lost time and lost eloquence to expatiate on the happiness of man in such a state; to describe his powers, both of running and flying, to paint him in a condition where all narrow luxuries would be condemned, where he would be employed only in collecting the necessaries of life, and where, consequently, each man's share of labour would be light, and his portion of leisure ample.

I think I may fairly make two postulata.

First, That food is necessary to the existence of man.

Secondly, That the passion between the sexes is necessary and will remain nearly in its present state.

These two laws, ever since we have had any knowledge of mankind, appear to have been fixed laws of our nature, and, as we have not hitherto seen any alteration in them, we have no right to conclude that they will ever cease to be what they now are, without an immediate act of power in that Being who first arranged the system of the universe, and for the advantage of his creatures, still executes, according to fixed laws, all its various operations.

I do not know that any writer has supposed that on this earth man will ultimately be able to live without food. But Mr. Godwin has conjectured that the passion between the sexes may in time be extinguished. As, however, he calls this part of his work a deviation into the land of conjecture, I will not dwell longer upon it at present than to say that the best arguments for the perfectibility of man are drawn from a contemplation of the great progress that he has already made from the savage state and the difficulty of saying where he is to stop. But towards the extinction of the passion between the sexes, no progress whatever has hitherto been made. It appears to exist in as much force at present as it did two thousand or four thousand years ago. There are individual exceptions now as there always have been. But, as these exceptions do not appear to increase in number, it would surely be a very unphilosophical mode of arguing, to infer merely from the existence of an exception, that the exception would, in time, become the rule, and the rule the exception.

Assuming then, my postulata as granted, I say, that the power of population is indefinitely greater than the power in the earth to produce subsistence for man.

Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will shew the immensity of the first power in comparison of the second.

By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal.

This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty must fall some where and must necessarily be severely felt by a large portion of mankind.

Through the animal and vegetable kingdoms, nature has scattered the seeds of life abroad with the most profuse and liberal hand. She has been comparatively sparing in the room and the nourishment necessary to rear them. The germs of existence contained in this spot of earth, with ample food, and ample room to expand in, would fill millions of worlds in the course of a few thousand years. Necessity, that imperious all pervading law of nature, restrains them within the prescribed bounds. The race of plants, and the race of animals shrink under this great restrictive law. And the race of man cannot, by any efforts of reason, escape from it. Among plants and animals its effects are waste of seed, sickness, and premature death. Among mankind, misery and vice. The former, misery, is an absolutely necessary consequence of it. Vice is a highly probable consequence, and we therefore see it abundantly prevail, but it ought not, perhaps, to be called an absolutely necessary consequence. The ordeal of virtue is to resist all temptation to evil.

This natural inequality of the two powers of population and of production in the earth and that great law of our nature which must constantly keep their effects equal form the great difficulty that to me appears insurmountable in the way to the perfectibility of society. All other arguments are of slight and subordinate consideration in comparison of this. I see no way by which man can escape from the weight of this law which pervades all animated nature. No fancied equality, no agrarian regulations in their utmost extent, could remove the pressure of it even for a single century. And it appears, therefore, to be decisive against the possible existence of a society, all the members of which should live in ease, happiness, and comparative leisure; and feel no anxiety about providing the means of subsistence for themselves and families.

Consequently, if the premises are just, the argument is conclusive against the perfectibility of the mass of mankind.

I have thus sketched the general outline of the argument, but I will examine it more particularly, and I think it will be found that experience, the true source and foundation of all knowledge, invariably confirms its truth. . . .

NOTICE SUR LA LOI QUE LA POPULATION SUIT DANS SON ACCROISSEMENT

P. F. Verhulst—1838

Reprinted from Correspondence mathematique et physique **10**: 113–121, 1838. Translated by Lawrence Wilson, 1964.

The first mathematical formulation of population growth was made in this essay. The logistic equation which Verhulst derived describes the nature of population increase as it occurs under limiting conditions. A plot of the equation is the familiar S-shaped population curve. Not unlike other discoveries in science, Verhulst's contribution was not widely recognized until some time after Pearl and Reed (see p. 66) independently derived the same equation in 1920.

It is generally known that Malthus established as his first principle that the human population tends to grow in geometrical progression according to which it will double after a certain period of time, for example, every twenty-five years. This proposition is incontrovertible if the continually increasing difficulty of guaranteeing subsistence once the population has reached a certain density or the resources upon which the population draws in growing, even when the society is still nascent (e.g., the greater division of labor, the existence of a stable government and means of defense assuring public order, etc.) are kept in mind.

Indeed, *all things being equal*, if one thousand individuals have become two thousand after twenty-five years, these two thousand will become four thousand after the same lapse of time.

In our old European societies where the fertile land had been cultivated for a very long time, the labor expended in improving acreage already under cultivation can result only in a constantly decreasing amount compared to what it originally produced. Assuming that the production of the soil has been doubled, it is not very likely that one will succeed in making it produce a third more in the second period. The virtual increase in population thus finds a limit in the area and fertility of the country, and the population tends, consequently, to become stationary.

The same is not true in certain truly exceptional cases—for example, when a civilized people cultivate a fertile territory, previously uninhabited, or when it expends an industriousness which results in great temporary benefits. A numerous family then becomes an asset and the second generation finds it easier to establish itself since it does not have to struggle like the first generation against the odds with which the native state of the land confronted the first settlers.

To judge the rapidity with which the population grows in a given country, the yearly increase in population must be divided by the figure of the original population. This relationship being independent of the absolute size of the population, it can be regarded as the measure of this rapidity. If it is constant, the population increases geometrically; if it is growing, the progression is more than geometrical, and less than geometrical if it is decreasing.

Various hypotheses concerning the resistance or the sum of the obstacles put in the way of the indefinite development of the population can be made.

Mr. Quetelet suggests that it is proportional to *the square of the rapidity with which the population tends to grow.*

This amounts to making the change in the population that of a moving body which falls in going through a resistant milieu. The results of this comparison agree in a satisfactory manner with the statistical data and the results I have obtained with my own formulae, when an indefinitely increasing density is granted in passing through the strata of the milieu.

Population growth has, of necessity, a limit if only in the area of land indispensable for accommodating that population. When a nation has consumed all the fruits of its fields, it can indeed obtain foodstuffs from outside through the exchange of its other products, and can thus support a new increase of population. But it is obvious that these imports must be limited and be halted even long before the surface of the entire country is taken up with cities. All the formulae by which an attempt will be made to represent the law of population must therefore satisfy the condition of admitting a *maximum* which will be attained only at an infinitely remote time. This *maximum* will be the figure of the population when it has become stationary.

I have long tried to determine by analysis what the probable law of population is; but I have abandoned this kind of research because the data provided by observation are too few to permit verification of the formulae in such a way as to leave no doubt as to their exactness. However, since the path I have followed seems to me to lead to the discovery of the true law, once there is sufficient data, and since the results I have obtained may be of interest, at least as a matter for speculation, I felt myself obliged to accept Mr. Quetelet's invitation to make them public.

Let p be the population and let us represent by dp the infinitely small increase it makes within the infinitely short time dt. If the population grew geometrically, we would have the equation $dp/dt = mp$. But since the rate of growth is retarded by the increase in the number of inhabitants itself, we shall have to remove from mp an unknown function of p, so the formula to be integrated will become

$$\frac{dp}{dt} = mp - \varphi(p).$$

The simplest hypothesis that one could make on the nature of the function φ, is to assume $\varphi(p) = np^2$. The integral of the above equation then becomes

$$t = \frac{1}{m}[\log. p - \log. (m - np)] + \text{constant.}$$

and it will require three observations to determine the two coefficients m and n and the arbitrary constant.

In solving the last equation for p, it becomes

$$p = \frac{mp'e^{mt}}{np'e^{mt} + m - np'} \qquad (1)$$

in designating by p' the population which exists at $t = 0$, and by e the base of the Napierian logarithm. If $t = \infty$, then the corresponding value of p is $p = m/n$. Such is therefore the upper limit of the population.

Instead of assuming $\varphi p = np^2$, one can make $\varphi p = np^\alpha$, α being any number, or $\varphi p = n \log. p$. Each of these hypotheses equally well satisfies the observed facts, but by the same token they yield very different values for the upper limit of the population.

I have assumed successively

$$\varphi p = np^2, \quad \varphi p = np^3, \quad \varphi p = np^4, \quad \varphi p = n \log. p;$$

and the differences between the calculated population and those which provide the observation are found to be essentially the same.

When the population increases more or less in geometrical progression, the term $-\varphi p$ becomes $+\varphi p$; the differential equation is then integrated as in the preceding case but one imagines that it can no longer be the maximum population. . . .

ON THE RATE OF GROWTH OF THE POPULATION OF THE UNITED STATES SINCE 1790 AND ITS MATHEMATICAL REPRESENTATION

Raymond Pearl and Lowell J. Reed—1920

Reprinted by permission of the publisher from Proceedings of the National Academy of Sciences 6:275–288, 1920.

In this paper the logistic curve of population growth under limiting conditions is derived and applied to the population of the United States. The paper is of interest not alone for the independent discovery of a mathematical formulation described a century earlier by Verhulst (see p. 64) but also because of the influence the senior author had in promoting the use of statistical analysis in ecology. The limitations of the sigmoid growth model have been increasingly recognized; L. B. Slobodkin discusses this point (1961. Growth and regulation of populations. New York, Holt, Rinehart and Winston).

It is obviously possible in any country or community of reasonable size to determine an empirical equation by ordinary methods of curve fitting, which will describe the normal rate of population growth. Such a determination will not necessarily give any inkling whatever as to the underlying organic laws of population growth in a particular community. It will simply give a rather exact empirical statement of the nature of the changes which have occurred in the past. No process of empirically graduating raw data with a curve can in and of itself demonstrate the fundamental law which causes the occurring change. In spite of the fact that such mathematical expressions of population growth are purely empirical, they have a distinct and considerable usefulness. This usefulness arises out of the fact that actual counts of population by census methods are made at only relatively infrequent intervals, usually 10 years and practically never oftener than 5 years. For many statistical purposes, it is necessary to have as accurate an estimate as possible of the population in inter-censal years. . . .

The usual method followed by census offices in determining the population in inter-censal years is of one or the other of two sorts, namely, by arithmetic progression or geometric progression. These methods assume that for any given short period of time the population is increasing either in arithmetic or geometric ratio. Neither of these assumptions is ever absolutely accurate even for short intervals of time, and both are grossly inaccurate

for the United States, at least, for any considerable period of time. . . .

Obviously the best general method of estimating population in inter-censal years is that of fitting an appropriate curve to *all* the available data, and extrapolating for years beyond the last census, and reading off from the curve values for inter-censal years falling between earlier censuses. The methods of arithmetic or geometric progression use only two census counts at the most. Fitting a curve to all the known data regarding population by the method of least squares must obviously give a much sounder and more accurate result. In making this statement, one realizes perfectly, of course, the dangers of extrapolation. . . . In keeping sharply before our minds the dangers of extrapolation from a curve, we are apt to forget that the methods of extrapolation by arithmetic or geometric progression have much less general validity than from a curve, and the inaccuracies are found in practice, except by the rarest of accidents, to be actually greater.

The first one to attempt an adequate mathematical representation of the normal rate of growth of the population of the United States was Pritchett. Taking the census data from 1790 to 1880, inclusive, Pritchett fitted by the method of least squares the following equation:

$$P = A + Bt + Ct^2 + Dt^3 \qquad \text{(i)}$$

where P represents the population and t the time from some assumed epoch. As a matter of fact, Pritchett took the origin of the curve at 1840, practically the center of the series. With this third-order parabola Pritchett got a very accurate representation of the population between the dates covered. As will presently appear this curve did not give, even within the period covered, as accurate results as a more adequate curve would have done, and it overestimated the population after a very short interval beyond the last observed ordinate. . . .

Some 13 years ago one of the writers demonstrated the applicability of a logarithmic curve of the form

$$y = a + bx + cx^2 + d\log x \qquad \text{(ii)}$$

to the representation of growth changes, using the aquatic plant *Ceratophyllum* as material. Following the application of this curve to growth of this plant it was found equally useful in representing a wide range of other growth and related changes. . . .

While the increase in size of a population cannot on *a priori* grounds be regarded, except by rather loose analogy, as the same thing as the growth of an organism in size, nevertheless it is essentially a growth phenomenon. It, therefore, seems entirely reasonable that this type of curve should give a more adequate representation of population increase than a simple third-order parabola. The actual event justifies this assumption, as will presently appear. . . .

To the data of . . . [recorded population from 1790–1910] the following equation was fitted by the method of least squares, taking origin at 1780, and making due allowance in the abscissal intervals for the actual dates of the several censuses:

$$y = a + bx + cx^2 + d\log x$$

where y denotes population and x time. The actual equation deduced was

$$y = 9{,}064{,}900 - 6{,}281{,}430x + 842{,}377x^2 + 19{,}829{,}500\log x. \qquad \text{(iii)}$$

The results [indicate] . . . that as a purely empirical representation of population growth in the United States equation (iii) gives results of a very high degree of accuracy. Indeed, interpolation on this curve for inter-censal years may obviously be relied upon with a greater probability that the estimated figures approximate the unknown true facts than is afforded by any other estimating expedient hitherto applied to the known data. . . .

It is quite clear on *a priori* grounds, as was first pointed out by Malthus in non-mathematical terms, that in any restricted area, such as the United States, a time must eventually come when population will press so closely upon subsistence that its rate of increase per unit of time must be reduced to the vanishing point. In other words, a population curve may start. . . with a convex face to the base, but presently it must develop a point of inflection, and from that point on present a concave face to the x axis, and finally become asymptotic, the asymptote representing the maximum number of people which can be supported on the given fixed area. Now, while an equation like (ii) can, and will in due time, develop a point of inflection and become concave to the base it never can become asymptotic. It, therefore, cannot be regarded as a hopeful line of approach to a true law of population growth. . . .

It has seemed worth while to attempt to develop such a law, first by formulating a hypothesis which rigorously meets the logical requirements, and then by seeing whether in fact the hypothesis fits the known facts. The general biological hypothesis which we shall here test embodies as an essential feature the idea that the rate of population increase in a limited area at any instant of time is proportional (a) to the magnitude of the population existing at that instant (amount of increase already attained) and (b) to the still unutilized potentialities of population support existing in the limited area.

The following conditions should be fulfilled by any equation which is to describe adequately the growth of population in an area of fixed limits. (1). Asymptotic to a line $y = k$ when $x = +\infty$. (2). Asymptotic to a line $y = 0$ when $x = -\infty$. (3). A point of inflection at some point $x = \alpha$ and $y = \beta$. (4). Concave upwards to left of $x = \alpha$ and concave downward to right of $x = \alpha$. (5). No horizontal slope except at $x = \pm\infty$. (6). Values of y varying continuously from 0 to k as x varies from $-\infty$ to $+\infty$.

In these expressions y denotes population, and x denotes time. An equation which fulfils these requirements is

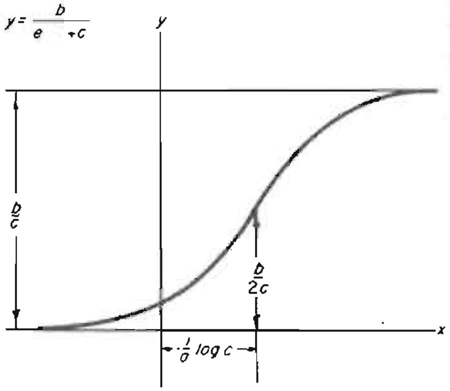

FIG. 2. *General form of curve given by equation (ix).*

$$y = \frac{be^{ax}}{1 + ce^{ax}} \qquad \text{(ix)}$$

when a, b and c have positive values.

In this equation the following relations hold:

$$x = +\infty \qquad y = \frac{b}{c} \qquad \text{(x)}$$

$$x = -\infty \qquad y = 0 \qquad \text{(xi)}$$

Relations (x) and (xi) define the asymptotes. The point of inflection is given by $1 - ce^{ax} = 0$, or

$$x = -\frac{1}{a} \log c \qquad y = \frac{b}{2c} \qquad \text{(xii)}$$

The slope at the point of inflection is $ab/4c$. Expressing the first derivative of (xi) in terms of y, we have

$$\frac{dy}{dx} = \frac{ay(b - cy)}{b} \qquad \text{(xiii)}$$

Putting the equation in this form shows at once that it is identical with that describing an autocatalyzed chemical reaction, a point to which we shall return later.

The general form of the curve is shown in figure 2.

The question now is how well does (ix) represent the known historical facts as to the growth in population of the United States, and to what legitimate deductions as to the future course of population in this country does it lead ? . . .

. . . The most that can be asserted is that equation (xviii) gives nearly or quite as good a fit to the observations as does the logarithmic parabola. If we properly graduated the data, by the method of moments, we should probably get a result measurably better than that from equation (iii).

The significance of the result lies in this consideration. A curve which on *a priori* grounds meets the conditions which must be satisfied by a true law of population growth, actually describes with a substantial degree of accuracy what is now known of the population history of this country. . . .

THE QUANTITATIVE ANALYSIS OF ENVIRONMENTAL FACTORS

Royal N. Chapman—1928

Reprinted by permission of the publisher from Ecology **9**:111–122, 1928.

The much used terms "biotic potential" and "environmental resistance" had their origin and empirical verification in this paper. But, perhaps Chapman's greater contribution to ecology was the direction he gave to laboratory population studies. In particular, his population research on the flour beetle was continued and very considerably expanded by Thomas Park and his students. Park reviewed much of this work in 1962 (Science **138**: *1369–1375).*

. . . It was once believed that mathematical expressions must be confined to the description of surfaces and solids just as we now have a feeling that they must be confined to phenomena in the field of physics. It was once considered that heat conduction was subject to too many factors to permit itself to be handled by mathematical calculations, just as we now have a feeling that ecological phenomena are subject to so many factors that they do not lend themselves to mathematical methods. Those of us who are engaged in the study of animal ecology may do well to pause and consider the future of our branch of science in the light of the work of Fourier, who more than a century ago, began to apply mathematical methods to the study of the transmission of heat through solids. In this day when it is possible for physicists and engineers to calculate so exactly the amount of heat required to warm a given space surrounded by walls with given coefficients of conduction and subject to known external conditions, it is hard to realize that there was once a day when it seemed to be impossible to apply quantitative calculations to the transmission of heat. All of the objections which now stand in the way of the use of these methods in ecology then stood in the way of the use of these methods in connection with thermodynamics. . . .

The animal ecologists find themselves handicapped in the use of quantitative methods because of the difficulty in obtaining quantitative samples, the lack of a method of expressing the abundance of organisms, and of expressing the effect of the environment in terms of the quantity of organisms. As a result of the consideration of some of these handicaps, it has seemed that it might be possible to find some characteristics, essentially biotic, which could be used as a measure of the organisms and the environment, and which might be subject to experimental verification.

It has long been known that the possibilities of reproduction of the various species of organisms are enormous, and that they far exceed the realization which the species ever has in numbers of individuals. The fact that eventually but two out of an enormous number of progeny would survive to replace the parents, was an essential part of Darwin's theory of the survival of the fittest and the action of natural selection. Many calculations have been made to show the possibilities of the various organisms to reproduce. . . .

. . . The variations in the abundance of insects, in so far as we have data to represent them, indicate a remarkable constance in numbers when compared with the potential number which might exist at any one time. Thus it seems that whatever the potential rate of development of an organism may be, its environment offers sufficient resistance to multiplication to cause its numbers to tend to remain constant. It is this fact, obvious though it may be, that will now be considered.

In drawing analogies from the works of Fourier and Ohm it is recognized that the cases may not be strictly comparable to animal abundance. Yet it seems evident that we have in nature a system in which the potential rate of reproduction of the animal is pitted against the resistance of the environment, and that the quantity of organisms which may be found is a result of the balance between the biotic potential, or the potential rate of reproduction, and the environmental resistance.

For this purpose, therefore, biotic potential may be defined as the mean maximum rate of reproduction in a given period of time under given conditions. The action of the environment, then, must necessarily be expressed in terms of resistance to this maximum rate of reproduction. An empirical formula similar to Ohm's formula, representing the concentration of organisms, or abundance of organisms, as equal to the biotic potential divided by the environmental resistance, may aid in making the complex factors of the organism and the environment appear as unity to us. At least, it is possible to conceive of everything as having a place in this formula. The environmental resistance will include the physical factors of the environment, temperature, humidity, etc. and also the biotic factors of the environment, parasites, competitors, etc. The advantage of the formula will be practically the same as those which Ohm realized. When concentration and biotic potential are known, a value may be ascribed to environmental resistance. A knowledge of any two of the three variables will make it possible to calculate the value of the third. . . .

The hypothesis needs the support of experimental data based upon controlled conditions. Such data have been obtained from a study of the confused flour beetle, *Tribolium confusum*. . . .

The conditions of the experiments were made as simple as possible. The object was to determine, first, whether a condition of equilibrium would be reached in which the population, as expressed in the number of individuals per gram of flour, would remain constant regardless of the size of the environment. Under such conditions the environmental resistance would be equal to the biotic potential and the conditions of the hypothetical formula would be satisfied. Secondly it was sought to determine whether the effective rate of reproduction of single pairs of beetles was inversely proportional to the environmental resistance, which, in this case, is a function of the total size of the environment.

To determine the first point, a series of environments was set up in which the depth of the pure whole wheat flour was constant at two centimeters, but the quantities of flour in the different environments formed a geometric series, containing 4, 8, 16, 32, 64 and 128 grams each. The populations of adult beetles which were introduced at the start also formed a geometric series such that there was one pair of bettles to each four grams of flour in each environment. The sexes of the beetles were determined but the ages were at random. The moisture was kept constant and the temperature was maintained at 27°C.

The eggs, larvae and pupae were counted and the flour renewed at each observation. The various stages of beetles were separated from the flour by means of standard silk bolting cloth. . . . there was a rapid increase in numbers, which was followed by a condition of relative stability with practically no larvae or pupae. The number of eggs present at each observation is an indication of the total biotic potential of the population. In spite of the large number of eggs which were always present, there were no appreciable changes in the number of adult beetles. When eggs were removed from the culture they hatched on schedule time, and an equal number of new eggs appeared in the original culture. This demonstrates the fertility of the eggs. The fact that the lack of increase in the population was due to the eggs being eaten by the adults was demonstrated by placing eggs in cultures which contained only male beetles. The per cent of eggs eaten varied directly with the population of adults per gram of flour. Pupae, and to some extent larvae, were also eaten in environments which contained high concentration of beetles. Thus we have an environmental resistance which is a function of the size of the environment. . . .

TABLE II. *Beetles (Tribolium confusum) per gram of flour*

Days	4 G.	8 G.	16 G.	32 G.	64 G.	128 G.
	.5	.5	.5	.5	.5	.5
15	15	17	20	17	21	19
30	30	25	26	22	24	23
50	35	33	32	35	32	34
64	39	39	34	39	40	37
78	35	41	39	36	37	39
101	40	46	38	44	49	39
114	48	45	36	43	40	40
134	37	50	41	41	48	45
156	38	49	46	44	45	47
171	46	49	46	43	42	40

The first point, therefore, seems well demonstrated. A condition of equilibrium is attained in which the biotic potential is equaled by the environmental resistance and the population remains relatively constant.

For the second point, namely the relation between the increase of a population and the size of the environment, attention is called to . . . [the] series of experiments [in which] a single pair of newly emerged adult beetles was placed in each of the environments which formed the same geometric series of sizes as in Table [II]. In this case, in the same period of time, one pair of beetles gave rise to 178 individuals in an environment of 4 grams and another gave rise to over 4,500 in 128 grams. The intermediate environments had populations of intermediate sizes. . . .

It is rather obvious that the formula $C = Bp/R$ must hold when C is the concentration of insects, Bp the biotic potential, and R the resistance. When we substitute the known values and solve for the value of resistance we get

$$43.97 = \frac{(43.97 \times 8.4)\ .25}{R}$$

or

$$R = \frac{(43.97 \times 8.4)\ .25}{43.97}.$$

The average number of eggs laid per female per day is 8.4 for these experiments, and 25 per cent of the population are females. The obvious solution is that $R = 2.1$. This is naturally the formula expressing the state of equilibrium and not the original increase of the population. Time does not enter into the formula in this case because population does not change with time.

The mere substantiation of the hypothesis would be of little consequence if it were not that by means of the method the quantitative analysis of environmental relationship is made possible. The valuation of each factor becomes subject to experimental verification. It is only necessary to vary one factor at a time and determine its effect upon the potential and actual populations. . . .

Thus, in the study of this particular species, the way seems open for the logical and methodical analysis of the environmental relationships. In the course of such an investigation certain fundamental principles are to be demonstrated which apply to animals in general, many of which do not lend themselves to such close analysis.

The next logical step is the consideration of the potential and resistance represented in each species of a natural community of organisms which are interdependent and self supporting. The analysis of such a system is complex but the analysis of the tensions and phases of a physical system is also complex but nevertheless possible. . . .

PERIODIC FLUCTUATIONS IN THE NUMBERS OF ANIMALS: THEIR CAUSES AND EFFECTS

Charles S. Elton—1924

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Charles Elton's concern with conceptualizing ecology into basic principles was developed in his text (1927. Animal ecology, London, Sidgwick and Jackson) and gave new direction, impetus and stature to ecology. Among the many principles he developed was that of periodic fluctuations as characteristic of natural populations. The first scientific report on this phenomenon was the one that follows.

Professor Elton, Director of the Bureau of Animal Population, Oxford University since its founding in 1932, was honored as Eminent Ecologist by the Ecological Society of America in 1961. In our correspondence concerning the use of the following article he provided interesting commentary on the nature of scientific investigation and integrity. He wrote that the paper was the "honest effort of an enthusiastic 24-year old, working without a statistical environment. . . [that] the correlation between Norwegian and Canadian lemming-fox cycles may *actually exist . . . and* could *be synchronized through climate . . . [and] that the sunspot theory for the ten-year cycle was a dead duck even by 1930; but when I wrote the 1924 paper it was at any rate possible."*

The significance and reality of cycles is examined critically by L. C. Cole (1954. Some features of random population cycles. Journal of Wildlife Management **18**: *2–24).*

3. PERIODIC FLUCTUATIONS IN ANIMAL NUMBERS.

Lemmings. The lemmings are a group of rodents, resembling in appearance small guinea-pigs, which live in arctic and sub-arctic countries, where they occupy the ecological niche of the mice and rabbits of lower latitudes. Evidence is given below that the numbers of lemmings fluctuate periodically all over the arctic regions.

1. *Southern Norway.* The Norwegian Lemming (*Lemmus lemmus*) inhabits the arctic regions of Norway down to sea-level, and occurs further south in the mountains. It follows the zone of arctic-alpine tundra, above the tree limit, which in the mountains of South Norway is about 3000 to 4000 feet above sea-level. The data about the lemming are taken from Collett.

For many years the lemmings have periodically forced themselves upon public attention in Southern Norway by migrating down in swarms into the lowland in autumn, and in many cases marching with great speed and determination into the sea, in attempting to swim across which they perish. The details of the fate of the migrants do not concern us here and are fully described by Collett. The main point is that all these lemmings die, and none return to the mountains, the chief cause of death being an epidemic bacterial disease. It seems pretty certain that the immediate cause of the migration is overpopulation in the usual habitat. Lemming pairs usually have their own territory, nearly all the migrants are young animals of that year, and while large numbers are concerned in migrating, each individual still remains solitary and pursues its own independent course. These facts, taken with the stupendous numbers of migrants, and the fact that a certain number of lemmings stay behind and do not migrate, show that the phenomenon is analogous to infanticide among human beings as a method of preventing overpopulation. As a matter of fact the epidemic also attacks the stay-at-home animals, and thus the population is still further reduced. The lemming-years are such conspicuous phenomena that it is safe to assume that all which have occurred (since about 1860) have been recorded. Lemming-years in Norway have the status of great floods or terrible winters.

It should be remembered that lemming migration is only an indicator of overpopulation which passes a certain point, and therefore lemmings might have a small maximum which did not lead to migration. A study of the lemming-years of South Norway leads to the following results:

(*a*) Lemming overproduction occurs periodically every few years and culminates in an autumn migration. It is usually found either that some of the migrants of that year survive the first winter and carry on the invasion of the lowland in the next summer, or else overproduction in one district is followed in the next year by overproduction in a neighbouring one; so a lemming maximum may cover one or two years. For this reason, owing to the difficulty of knowing when the maximum has ended, in the following treatment, the first year of onset of migration is taken as the maximum, except in 1890 and 1894, when the migration was very small compared to that of the next year.

(*b*) The area of great over-increase varies in size and position, but often includes several distinct, and for lemmings isolated, mountain blocks.

(*c*) With one exception, a lemming maximum has occurred every three or four years (occasionally two or five). See diagram C, fig. 2.

(*d*) The exception noted above is the year 1898. It is probable, in view of the evidence to follow that there was a maximum of lemmings in the mountains, but not sufficient to cause a migration, especially as there was one in North Finland in 1897.

(*e*) If we assume a maximum in 1898, the mean period between maxima is 3.6 years (1862–1909).

I have not been able to obtain full information of lemming-years since 1910, but Dr. Grieg informs me that there was one in the Hardanger region in 1922–1923. It is highly probable that records will be found for 1914 and 1918.

The Wood Lemming (*Lemmus* (*Myopus*) *schisticolor*) which lives lower down on the mountains than its ally, is also subject to "good years" followed by migration. So far as the data go, over-increase is found to take place in the same years as the common lemming (1883, 1888, 1891–92, 1894–95, 1902, 1906). . . .

3. *Canada.* The Barren Grounds of Canada are inhabited by lemmings of several species, chiefly the Hudson Bay Lemming (*Lemmus* (*Dicrostonyx*) *richardsoni*), and the Tawny Lemming (*L. trimucronatus*). There is practically no direct evidence as to the periodicity of their fluctuations, or details about them. But they are well known to fluctuate, and according to Rae the North American species migrate in certain years after the manner of the Norwegian species. There was a big migration of Lemmus at Point Barrow, Alaska, in 1888. However, we can attack the question from another angle. The lemming is the main source of food of the arctic fox; there is not the smallest doubt that the latter depends very largely on the lemming, just as its allies further south depend on hares, rabbits, and mice. As will be shown later, the number of red foxes fluctuates with the number of rabbits (and probably mice), so we should expect the number of arctic fox to give a good indication of the number of lemmings. This is in fact so. The curve A in fig. 2 shows the variation from year to year of the number of arctic fox skins taken by the Hudson Bay Company. If we plot the year before each fox maximum as in diagram B, we obtain the years when there was presumably a maximum of lemmings. The agreement with lemming-years in Norway is seen to be remarkable. In three cases the maximum in Canada occurs a year before, and in three cases a year after that in South Norway, so that the variations cancel out and leave us with the same mean period: 3.6 years. The reason why the maximum of fox skins occurs in the year after that of the lemmings is clearly shown by Manniche's study of a lemming-year in Greenland. In the autumn of 1906 there were colossal numbers of lemmings, but these mostly disappeared before the winter was far advanced. He attributed this death to the cold early winter with little snow to protect the animals, but it is highly probable that disease was an important cause. The foxes swarmed in autumn, partly owing to immigration, but also presumably more young grew up successfully. They fed entirely on lemmings. But in the winter the lemmings had died or were inaccessible under the snow. Foxes make caches of lemmings for the winter, but by the spring these must have been used up, for Manniche was able to trap large numbers of foxes owing to their hunger. Now the Hudson Bay Company fur returns for any year include the catch of the winter before; in fact this is the main item, *i.e.* a maximum of skins in 1907 means many foxes caught in the winter 1906–1907, and in the spring. Such abundance will, of course, be the result of the year 1906, since arctic foxes mate in the spring and the young do not grow up until the autumn. So any abundance in fur returns for one year necessarily implies abundant food supply in the preceding year. . . .

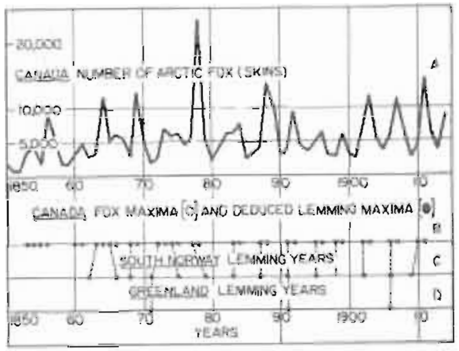

FIG. 2. *Years of lemming maxima in Canada, the mountains of South Norway, and Greenland. The years for Canada are deduced from the curve (A) of arctic fox skins taken annually by the Hudson Bay Company. (Data for Canada from Hewitt, 1921; for Norway from Collett, 1911; for Greenland from Winge, 1902, and Manniche, 1910).*

Effect of lemming fluctuations. The lemming fluctuations have very powerful effects on the animals associated with them. This has already been shown for the arctic fox. In Norwegian lemming-years vast crowds of birds (owls, hawks, ravens, etc.), and mammals (stoats, foxes, etc.), are attracted to the mountains, and their numbers increase not only by their immigration but probably by their larger and more successful broods, due to the abundance of food. Similarly the arctic carnivores are profoundly affected. It is probable that many skuas and snowy owls only breed at all in lemming-years. There is not space here to follow out the readjustments of the food-cycle which result from the lemming-years. Two examples must suffice. The Short-eared Owl (*Asio flammeus*) collects in numbers and battens upon lemmings in South Norway lemming-years, and the Peregrine Falcon (*Falco peregrinus*), which hardly ever visits that country in normal years, comes and eats the owls. Again, in Greenland, an abundance of lemmings causes the arctic foxes to neglect other sources of food such as Ptarmigan and other birds. The latter accordingly increase. But in the next spring and summer, when there are few lemmings, these birds fare badly.

The causes of lemming fluctuations. It is clear that the causes of these fluctuations might lie either with the lemmings themselves or with their environment. It is possible to conceive that there might be some rough natural period in the increase of lemmings' numbers (in the sense of having an increase in their "bank balance" of numbers every year), which was terminated after a few years by migration and disease following upon overpopulation, and that the population was thus reduced and the process started all over again. A little consideration will show that such an explanation of lemming periodicity is quite untenable. It is inconceivable that such a process could cause synchronised maxima on the various mountain blocks of southern Norway, which as far as lemmings are concerned, are isolated from one another, or again in the different districts of Scandinavia. When we find further that the lemming maxima are practically synchronous all over the arctic regions and the mountains of southern Scandinavia, any such "natural rhythm" becomes out of the question. Of course the natural rate of increase is a very fundamental factor in determining the size of periodicity into which the fluctuations will fit. The cause of the periodicity must therefore lie with the environment, and here the only possible factor which is acting in a similar way all over these regions is climate. We do not know how this climatic factor acts, whether directly, or indirectly through plants, or other animals, but there can hardly be any doubt that we have here to look for a periodic climatic effect whose period is about 3.6 years on the average, and which acts over the whole of the arctic regions and in the Norwegian mountains. It will be shown later that it probably occurs in temperate regions also. . . .

I shall attempt to show that the 10- to 11-year period of the rabbit may be due primarily to the 11-year period in the sun. If this is so, the fox curve indicates that the solar period is having a slight effect in the arctic regions. This agrees with the conclusion reached from other evidence, that the effect of the solar variation is greatest in the tropics and gets fainter farther from the equator. It will be seen that there is no known cause for this well-marked 3 1/2-year period in the arctic climate. It might be caused by some short period in the sun, or by some unknown terrestrial factor, or the complicated interaction of several such factors.

Since the curve for the arctic fox shows a well-marked 3.6-year periodicity with a less distinct 10- or 11-year period underlying it, it might be thought probable that the curve for the numbers of the southern red fox, which shows a definite periodicity of about ten years, would have a concealed short period. This is found to be the case. . . . Now the southern fox feeds both on rabbits and mice. The rabbits cause the 10-year period in the fox, and it is shown later that there is a short period of 3½ years in Norwegian mice. It is very probable that the short period in the red fox curve is caused by variations in the supply of mice in Canada. It might also be caused by climate acting directly; but the absence of any such period in the lynx curve goes against this idea, since the lynx eats rabbits only. In any case the ultimate cause must be climate.

It appears then that there are two periods in the numbers of foxes and their food, and that the effects of the shorter one are more marked in the arctic, while those of the longer one are more marked in the temperate regions. This difference must be to a large extent due to the difference in prey, *i.e.* lemmings in the one place and mice and rabbits in the other, but the climatic difference may also be of the same nature.

Finally, it should be noted that the lemming differs from most of the other fluctuating rodents in that it does not have more young in a brood in good years; it probably has more broods in a given time, and the young grow up more successfully under the good conditions. . . .

COOPERATION AND CONFLICT AMONG PRIMITIVE ORGANISMS

Paul R. Burkholder—1952

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The numerous potential interactions between species populations, and the wide diversity in which such relationships are expressed, can be meaningfully considered in terms of coaction theory. Although this is one of the salient concepts developed in this essay, two other major ideas are evident—that there is considerable cooperation among organisms, here evidenced at the microbial level, and that microbes have a little-explored ecology.

. . . In the complex struggle for survival, preservation of the individual and the perpetuation of its kind are of primary importance to all forms of life. In mixed natural populations of organisms, such main goals are attained by numerous kinds of coactions, both harmful and beneficial. Thus, organisms may be forced to compete for food and shelter, or they may have to devise special ways of protecting themselves against harm, while others come to depend upon associates for their own good or for mutual welfare. All organisms are dependent upon the varied activities of other organisms for the supplies of essential stuffs carrying elementary components which can be used and reused many times in the cycles of the elements which are part of the balance of nature. Countless hordes of microorganisms decompose the metabolic products formed by other organisms, processes which are continued in stepwise fashion until the complex organic compounds of worn out or dead protoplasm become disintegrated into simple molecules, once again available for the feeding habits of plant and animal life in forest, field, or fishery.

TYPES OF COACTION

. . . The relationships among various plant and animal organisms, including man and the causative agents of his diseases, can be analyzed profitably in terms of coaction theory. According to Edward Haskell, the physical and chemical activities of organisms involve two main categories of relationship which are associated with different degrees of power or influence upon the fundamental processes of growth, maintenance, reproduction, and other activities of individuals or classes. The power relationship has often been stated in terms of *the weak* and *the strong*, but any differences may be expressed simply as symbols a and α representing distinguishing characters in two systems. If 0 be taken to mean the rate of an activity, such as, for example, a process of metabolite utilization, carried on by each class in the absence of others, + for all accelerations of this activity in either class by some other, and — for decelerations, then the cross tabulation of +, 0, and — simply yields the possible main types of coactions as shown in Table I.

TABLE I. *The nine possible coactions between weak and strong organisms*

(*a*)	*weak*	−	0	+
(*α*) *s*	+	— + predation	0 + allotrophy	+ + symbiosis
t r	0	— 0 amensalism	0 0 neutrality	+ 0 commensalism
o n g	—	— — synnecrosis	0 — allolimy	+ — parasitism

In regard to any metabolic activity then, a and α individuals or classes can exhibit nine qualitatively different relations toward each other. It can be shown that certain major properties of group relationships and social organization are regulated by numerous coactions of many types and with varying intensity of expression. The terms which Haskell applied to nutritional coactions were invented *de novo* or were taken from the literature of microbiology and ecology. In the table, the left-hand sign refers to the effect of coaction upon the weak and the right-hand sign signifies the effect upon the strong. In the case of neutrality (0 0), neither type is helped or hindered. Many saprophytic microbes appear to live together without appreciable influence on each other. In predation, the weak prey are damaged by the strong predators which benefit by the minus-plus relationship (— +). Parasitism, a plus-minus relationship (+ —) signifies that the weak parasite is benefited at the expense of the strong host. Commensalism generally connotes coactions in which the weak benefit and the strong are unaffected (+ 0). Some harmless bacteria living in the intestines of animals receive the benefits of shelter and food and are said to be commensals because, while bacteria profit greatly, the animal is supposed to lose or gain practically nothing from the relationship. A familiar example of commensalism in the bacteriological laboratory is found in the cultivation of facultative aerobic and obligate anaerobic bacteria near each other in nutrient media contained in sealed Petri dishes. The aerobe grows first and consumes the free oxygen with liberation of carbon dioxide; the anaerobe then is able to grow without accumulating hydrogen peroxide and other products of metabolism which would poison it. Thus the anaerobe is definitely benefited, whereas the aerobe is neither helped nor harmed. The opposite of commensalism is called amensalism (— 0). The relationship of allotrophy means feeding the other (0 +); and the opposite relationship, that is, starving the other, is termed allolimy (0 —). In the relationship of antibiosis, where one organism produces a substance which is harmful to another, the coaction might be of the parasitic, amensal or some other type, depending upon whether the organism producing the inhibitory substance derives benefit, harm, or nothing out of the relationship. Symbiosis signifies mutual aid (+ +); and finally, mutual depression or death together (— —) has been given the name synnecrosis. The broad nutritive relationships classified under the term metabiosis are concerned with the cycles of elements and are more general in effect than the specific relations between organisms as listed in the table of coactions.

The exploitation of various hosts by parasitic lower forms of life constitutes one of the most important types of coaction. . . . Most parasites occasion some damage to their host, and in this respect they are inept at their ungrateful mode of existence, for excessive injury to the host will result unfavorably to the parasite. Some main considerations in the parasite's struggle for existence are a good source of food, easy living, protection from enemies, and avoidance of competition. The wholly effective parasite must be adapted to live in or on its host without causing unfavorable reactions. The process of adaptation between parasite and host is probably mutual, and requires numerous generations of selection of the fittest individuals. Bacterial generations are a matter of thirty minutes, human generations thirty years. Assuming the same mutation frequency and similar adaptation rates, microbes have a fine chance to become adapted to human tissues before man becomes tolerant to parasites. Neophytic pathogens, like gonococcus and the whooping cough bacilli, cause violent reactions every time they multiply in a host. Other chronic pathogens and their host are better adapted; the host becomes accustomed to having the highly adapted etiological agents growing within its tissues. Syphilis, tuberculosis, and leprosy are important examples. In still other instances, the process of adaptation may progress to the level of commensalism, as is exemplified by harmless organisms of the human throat and intestine. In view of the extensive production of B vitamins by the intestinal microflora in animals and man, it may be that one stage in the evolution of parasitism to saprophytism is represented in true symbiosis. Plants apparently lack the ability to produce immune substances, and sometimes the plant host species succumbs to new parasites before adaptive mechanisms are given an opportunity to come into operation. Thus, the chestnut blight fungus *Endothia parasitica* all but wiped out the American chestnut tree two decades ago.

Coaction analysis has great significance for all who desire a broad understanding of life on the earth and who wish to do something constructive about it for mankind through the avenues of medicine and agriculture. In the field of human interests, undesirable activities of many parasites can be alleviated or avoided by the scientific application of chemical agents possessing selective and powerful inhibitory action against the causative agents of plant, animal, and human diseases. . . .

COOPERATION AND CONFLICT IN ECOLOGY

Metabiosis. . . . The production and exchange of water-soluble B vitamins among organisms living together or developing in sequence is of great significance in ecology. Beneficial exchange of growth factors among microbes, resulting in the formation of satellite colonies on agar plates, has become a familiar phenomenon to all bacteriologists. Microbes having deficient inheritance with regard to their ability to synthesize essential metabolites are enabled to grow near colonies of other microorganisms which produce enough vitamins and amino acids for themselves and also for their neighbors. . . . Thus, Robbins found that a fungus requiring thiamine could live in association with another mold which synthesizes this vitamin, and so flourish in an environment where otherwise it could not have survived owing to B_1 avitaminosis. Such exchanges may be nonspecific with regard to the kinds of organisms which are present, and it may be said that, in metabiosis, no constant biotic association is necessary as in the species-specific symbiotic relations which occur in lichens or legume nodules.

Symbiosis. Examples of cooperative association where two or more species live together in symbiosis with mutual benefit are abundantly present in nature. . . .

One of the finest examples of symbiosis in all of biology is found in the way of living shown by lichens. The lichen *Cladonia cristatella* is a beautiful green and red organism, composed of an alga and a fungus living together in a mutual welfare association. The alga reduces carbon dioxide to form carbohydrates for itself and for the fungus which cannot make such foodstuffs, and the fungus holds the partnership together while conserving moisture and making minerals available for both members of the household. When the two symbionts are divorced by suitable laboratory techniques, as Castle has recently done, then the alga and fungus cells may be grown separately on appropriate media. When attempts are made later to unite them by bringing the growing cultures of alga and fungus together, they fail to make a lichen, probably because of the imbalanced nutritive conditions in artificial media and unusual circumstances of the laboratory environment. So it must be admitted that the conditions necessary to make symbiosis function smoothly are not completely known. . . .

Antibiosis. . . . Frequently the struggle for "a place in the sun" is exhibited through negative coactions among primitive organisms, both in pure cultures as well as in mixed populations. Under crowded conditions lack of available food may limit growth and lead to selective elimination of weaker components. Bacteria, yeasts, molds, and protozoa may compete with each other for food and a place to live. Elaboration of waste products and formation of "staling" substances which are inimical to many organisms represent one aspect of microbial antagonism. Organic acids, alcohols, and specific toxic substances synthesized by some organisms often interfere with the metabolism of others so as to cause temporary cessation of growth or even to kill them outright. In other instances, metabolic products of one type of organism may be the essential basis of a food chain for many other types in series.

Antibiosis is a special case of antagonism in which an organism produces an injurious compound which may inhibit growth or destroy another organism. The word "antibiotic" was coined by Vuillemin in 1889, and ten years later extended by Ward to include the antagonistic relations among microbes. As long ago as 1889, the phenomenon of bacterial antibiosis in a Petri plate culture was demonstrated by Doehle and photographed by Hoppe-Seyler, so this kind of biotic relationship is not a new discovery of the 20th century. . . .

The interdependence of organisms for preservation of natural ecological equilibria is frequently not appreciated until some unusual event disturbs the balance. The main point is well illustrated by reference to the behavior of intestinal flora. For a long time the common bacteria harbored in the intestines of mammals were generally regarded as commensals with no great significance. Recent studies indicate the importance of the cellulose-decomposing bacteria in helping cattle to digest coarse feedstuffs in the rumen, and, in addition, demonstrate how very dependent the dairy industry is upon B vitamin synthesis by other members of the flora in the alimentary tract of *Bos*. Thus with the help of the intestinal flora, the cow supplies more vitamins in her milk than are contained in the feeds taken into her body. In a similar way, man also depends upon intestinal flora for help in the maintenance of normal conditions. Some individuals who lack the capacity to secrete a protein material called "intrinsic factor," in their stomachs become ill with pernicious anemia. It now appears as if bacteria in the stomach and intestines continually produce and absorb vitamin B_{12}, but in the absence of intrinsic factor the essential vitamin is not available for absorption into the human blood stream. . . .

Throughout the discussion of coactions among primitive organisms, the benefits derived out of cooperative relationships have been emphasized at the molecular, cellular, organismal, and societal levels of biological integration. A proper understanding of the ecology of microbes and man often provides means for improving the human welfare, as for example, when antibiotics are developed to relieve the ills of mankind or when harmful coactions are neutralized and converted into beneficial relationships.

During three thousand millions of years, progressive evolution from minerals to man has achieved for us an awareness of the cosmos and the imagination and ability to explore the universe with telescopes, test tubes and microscopes. Yet it is clear that we have much further to go than we have come, for we are only now at the beginning of understanding relationships among races and nations and our ultimate destiny. Those who believe that negative coactions must of necessity be expressed in the repeated uprising of weak against strong, leading to final synnecrosis, may do well to consider the possibility of embracing an ideology which seeks adequate knowledge and means for systematic conversion of negative relationships into positive coactions, so that human culture shall survive and man continue to expand his comprehension and enjoyment of the universe.

COMPETITION FOR COMMON FOOD IN PROTOZOA

G. F. Gause—1934

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Gause's Rule is essentially that two species cannot occupy the same niche at the same time. Although never formally stated by Gause, it is implicit in this discussion. The Gausian exclusion principle has been especially well studied by Peter Frank in Daphnia *(1957. Ecology* **38***: 510–519) and Thomas Park in* Tribolium *(1948. Ecological Monographs* **18***: 265–308). Slobodkin (1961. Growth and regulation of populations. New York, Holt, Rinehart and Winston) gives an excellent critique of Gause's studies and on the function of competition in population regulation. At the time of this study, Gause was associated with the Zoological Museum of the University of Moscow.*

Figure 18 represents the growth of the number of individuals in pure lines of *Paramecium caudatum* and *Stylonychia mytilus* cultivated separately and in a mixed population. These data are founded on two experiments which gave similar results. At the beginning of the experiment into each tube were placed five *Paramecium*, or five *Stylonychia*, or five *Paramecium* plus five *Stylonychia* in the case of a mixed population. *Stylonychia* for inoculation must be taken from young cultures to avoid an inoculation of degenerating individuals.

(5) The growth curves of the number of individuals in Figure 18 are S-shaped and resemble our well known yeast curves. After growth has ceased the level of the saturating population is maintained for a short time, and then begins the dying off of the population which is particularly distinct in *Stylonychia*. It is evident that this dying off is regulated by factors quite different from those which regulate growth, and that a new system of relations comes into play here. Therefore there is no reason to look for rational equations expressing both the growth and dying off of the populations.

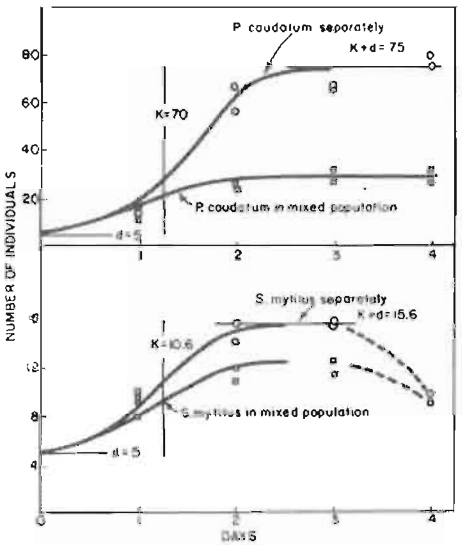

FIG. 18. *The growth in number of individuals of* Paramecium caudatum *and* Stylonychia mytilus *cultivated separately and in the mixed population.* d *denotes lower asymptote.*

Figure 18 shows that *Stylonychia*, and especially *Paramecium*, in a mixed culture attain lower levels than separately. The calculated coefficients of the struggle for existence have the following values: α (influence of *Stylonychia* on *Paramecium*) = 5.5 and β (influence of *Paramecium* on *Stylonychia*) = 0.12. This means that *Stylonychia* influences *Paramecium* very strongly, and that every individual of the former occupies a place available for 5.5 Paramecia. With our technique of cultivation it is difficult to decide on what causes this depends. As a supposition only one can point to food consumption.

(6) We have but to change slightly the conditions of cultivation and we shall obtain entirely different results. [Let us consider]. . . the growth of populations of the same species on a dense "oaten medium with sediment" sown with various wild bacteria. Here owing to an increase in the density of food the absolute values of the maximal population in both species have considerably increased. The character of growth of the mixed population now essentially differs from the former one: *Paramecium* strongly influences *Stylonychia*, while *Stylonychia* has almost no influence upon *Paramecium*. . . .

(3) In an experiment of such a type all the properties of the medium are brought to a certain invariable "standard state" at the end of every 24 hours. Hence, we acquire the possibility of investigating the following problem: can two species exist together for a long time in such a microcosm, or will one species be displaced by the other entirely? This question has already been investigated theoretically by Haldane, Volterra and Lotka. It appears that the properties of the corresponding equation of the struggle for existence are such that if one species has any advantage over the other it will inevitably drive it out completely. It must be noted here that it is very difficult to verify these conclusions under natural conditions. For example, in the case of competition between two species of crayfish a complete supplanting of one species by another actually takes place. However, there is in nature a great diversity of "niches" with different conditions, and in one niche the first competitor possessing advantages over the second will displace him, but in another niche with different conditions the advantages will belong to the second species which will completely displace the first. Therefore side by side in one community, but occupying somewhat different niches, two or more nearly related species. . . will continue to live in a certain state of equilibrium. There being but a single niche in the conditions of the experiment it is very easy to investigate the course of the displacement of one species by another. . . .

. . . The curves of growth of pure populations of *P. caudatum* and *P. aurelia* with different concentrations of the bacterial food show that the lack of food is actually a factor limiting growth in these experiments. With the double concentration of food the volumes of the populations of the separately growing species also increase about twice (from 64 up to 137 in *P. caudatum;* 64 × 2 = 128; from 105 up to 195 in *P. aurelia*; 105 × 2 = 210). Under these conditions the differences in the growth of populations of *P. aurelia* and *P. caudatum* are quite distinctly pronounced: the growth of the biomass of the former species proceeds with *greater rapidity*, and it accumulates a *greater biomass than P. caudatum at the expense of the same level of food resources*. . . .

(3) We will now pass on to the growth of a mixed population of *P. caudatum* and *P. aurelia*. . . . For a detailed acquaintance with the properties of a mixed population we will consider the growth with a half-loop concentration of bacteria (Fig. 24). First of all we see that as in the case examined before the competition between our species can be divided into two separate stages: up to the fifth day there is a competition between

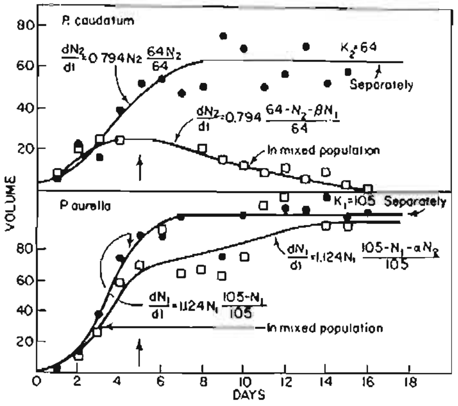

FIG. 24. *The growth of the "volume" in* Paramecium caudatum *and* Paramecium aurelia *cultivated separately and in the mixed population on the buffered medium with the "half-loop" concentration of bacteria.*

the species for seizing the so far unutilized food energy; then after the fifth day of growth begins the redistribution of the completely seized resources of energy between the two components, which leads to a complete displacement of one of them by another. The following simple calculations can convince one that on the fifth day all the energy is already seized upon. At the expense of a certain level of food resources which is a constant one in all "half-loop" experiments and may be taken as unity, *P. aurelia* growing separately produces a biomass equal to 105 volume units, and *P. caudatum* 64 such units. Therefore, one unit of volume of *P. caudatum* consumes $\frac{1}{64} = 0.01562$ of food, and one unit of volume of *P. aurelia* $\frac{1}{105} = 0.00952$. In other words, one unit of volume of *P. caudatum* consumes 1.64 times as much food as *P. aurelia*, and the food consumption of one unit of volume in the latter species constitutes but 0.61 of that of *P. caudatum*. These coefficients enable us to recalculate the volume of one species into an equivalent in respect to the food consumption volume of another species.

On the fifth day of growth of a mixed population the biomass of *P. caudatum* (in volume units) is equal to about 25, and of *P. aurelia* to about 65. If we calculate the total of these biomasses in equivalents of *P. aurelia*, we shall have: $(25 \times 1.64) + 65 = 106$ (maximal free growth of *P. aurelia* is equal to 105). The total of the biomasses expressed in equivalents of *P. caudatum* will be $(65 \times 0.61) + 25 = 65$ (with the free growth 64). This means that on the fifth day of growth of the mixed population the food resources of the microcosm are indeed completely taken hold of.

(4) The first period of competition up to the fifth day is not all so simple as we considered it in the theoretical discussion of the third chapter, or when examining the population of yeast cells. The nature of the influence of one species on the growth of another does not remain invariable in the course of the entire first stage of competition, and in its turn may be divided into two periods. At the very beginning *P. caudatum* grows even somewhat better in a mixed population than separately. . . apparently in connection with more nearly optimal relations between the density of Paramecia and that of the bacteria in accordance with the already mentioned data of Johnson. At the same time *P. aurelia* is but very slightly oppressed by *P. caudatum*. As the food resources are used up, the Johnson effect disappears, and the species begin to depress each other as a result of competition for common food.

It is easy to see that all this does not alter in the least the essence of the mathematical theory of the struggle for existence, but only introduces into it a certain natural complication: the coefficients of the struggle for existence, which characterize the influence of one species on the growth of another, do not remain constant but in their turn undergo regular alterations as the culture grows. . . .

(5) It remains to examine the second stage of the competition, i.e., the direct displacement of one species by another. An analysis of this phenomenon can no longer be reduced to the examination of the coefficients of multiplication and of the coefficients of the struggle for existence, and we have to do in the process of displacement with a quite new qualitative factor: the rate of the stream which is represented by population having completely seized the food resources. As we have already mentioned in Chapter III, after the cessation of growth a population does not remain motionless and in every unit of time a definite number of newly formed individuals fills the place of those which have disappeared during the same time. Among different animals this can take place in various ways, and a careful biological analysis of every separate case is here absolutely necessary. In our experiments the principal factor regulating the rapidity of this movement of the population that had ceased growing was the following technical measure: a sample equal to $\frac{1}{10}$ of the population was taken every day and then destroyed. In this way a regular decrease in the density of the population was produced and followed by the subsequent growth up to the saturating level to fill in the loss.

During these elementary movements of thinning the population and filling the loss, the displacement of one species by another took place. The biomass of every species was decreased by $\frac{1}{10}$ daily. Were the species similar in their properties, each one of them would again increase by $\frac{1}{10}$, and there would not be any alteration in the relative quantities of the two species. However, as one species grows quicker than another, it succeeds not only in regaining what it has lost but also in seizing part of the food resources of the other species. Therefore, every elementary movement of the population leads to a diminution in the biomass of the slowly growing species, and produces its entire disappearance after a certain time. . . .

In summing up we can say that in spite of the complexity of the process of competition between two species of infusoria, and as one may think a complete change of conditions in passing from one period of growth to another, a certain law of the struggle for existence which may be expressed by a system of differential equations of competition remains invariable all the time. The law is that the species possess definite potential coefficients of multiplication, which are realized at every moment of time according to the unutilized opportunity for growth. We have only had to change the interpretation of this unutilized opportunity. . . .

THE INFLUENCE OF INTERSPECIFIC COMPETITION AND OTHER FACTORS ON THE DISTRIBUTION OF THE BARNACLE *CHTHAMALUS STELLATUS*

Joseph H. Connell—1961

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Laboratory studies have the advantage of manipulating and controlling the environment in the analysis of population growth; such studies may lead to models restricted in application to the general situation, and thereby over- or underestimate the role of given phenomena. The lead paragraph of this article indicates such an instance. Fraught with the problem of vagaries of the environment and the resultant more difficult analysis of cousative relationships, this study does demonstrate the need for and feasibility of studying population interactions under natural conditions. Connell's study was conducted at the Isle of Cumbrae, Scotland and received the 1963 Mercer Award of the Ecological Society of America as an outstanding contribution by a young ecologist during the preceding two years.

Most of the evidence for the occurrence of interspecific competition in animals has been gained from laboratory populations. Because of the small amount of direct evidence for its occurrence in nature, competition has sometimes been assigned a minor role in determining the composition of animal communities. . . .

In the course of an investigation of the animals of an intertidal rocky shore I noticed that the adults of 2 species of barnacles occupied 2 separate horizontal zones with a small area of overlap, whereas the young of the species from the upper zone were found in much of the lower zone. The upper species, *Chthamalus stellatus* (Poli) thus settled but did not survive in the lower zone. It seemed probable that this species was eliminated by the lower one, *Balanus balanoides* (L), in a struggle for a common requisite which was in short supply. In the rocky intertidal region, space for attachment and growth is often extremely limited. This paper is an account of some observations and experiments designed to test the hypothesis that the absence in the lower zone of adults of *Chthamalus* was due to interspecific competition with *Balanus* for space. . . .

METHODS

Intertidal barnacles are very nearly ideal for the study of survival under natural conditions. Their sessile habit allows direct observation of the survival of individuals in a group whose positions have been mapped. Their small size and dense concentrations on rocks exposed at intervals make experimentation feasible. In addition, they may be handled and transplanted without injury on pieces of rock, since their opercular plates remain closed when exposed to air. . . .

To measure the survival of *Chthamalus*, the positions of all individuals in a patch were mapped. Any barnacles which were empty or missing at the next examination of this patch must have died in the interval, since emigration is impossible. The mapping was done by placing thin glass plates (lantern slide cover glasses, 10.7 × 8.2 cm, area 87.7 cm^2) over a patch of barnacles and marking the position of each *Chthamalus* on it with glass-marking ink. The positions of the corners of the plate were marked by drilling small holes in the rock. Observations made in subsequent censuses were noted on a paper copy of the glass map. . . .

For censusing, the stones were removed during a low tide period, brought to the laboratory for examination, and returned before the tide rose again. . . .

The effect of competition for space on the survival of *Chthamalus* was studied in the following manner: After the settlement of *Balanus* had stopped in early June, having reached densities of 49/cm^2 on the experimental areas . . . a census of the surviving *Chthamalus* was made on each area. . . . Each map was then divided so that about half of the number of *Chthamalus* were in each portion. One portion was chosen (by flipping a coin), and those *Balanus* which were touching or immediately surrounding each *Chthamalus* were carefully removed with a needle; the other portion was left untouched. In this way it was possible to measure the effect on the survival of *Chthamalus* both of intraspecific competition alone and of competition with *Balanus*. . . .

RESULTS

The effects of physical factors. . . . In the absence of *Balanus* and *Thais*, and protected by the cages from damage by water-borne objects, the survival of *Chthamalus* was good at all levels. For those which had settled normally on the shore. . . . the poorest survival was on the lowest area. . . . On the transplanted stones. . . constant immersion in a tide pool resulted in the poorest survival. The reasons for the trend toward slightly greater mortality as the degree of immersion increased are unknown. . . .

Chthamalus is tolerant of a much greater degree of immersion than it normally encounters. This is shown by the survival for a year on area 12 in a tide pool, together with the findings of Fischer and Barnes, who found that *Chthamalus* withstood submersion for 12 and 22 months, respectively. Its absence below M.T.L. [mean tide level] can probably be ascribed either to a lack of initial settlement or to poor survival of newly settled larvae. . . .

At the upper shore margins of distribution *Chthamalus* evidently can exist higher than *Balanus* mainly as a result of its greater tolerance to heat and/or desiccation. . . . Records from a tide and wave guage operating. . . about one-half mile north of the study area showed that a period of neap tides had coincided with an unusual period of warm calm weather in April so that for several days no water, not even waves, reached the level of Area 1. In the period between the censuses of February and May, *Balanus* aged one year suffered a mortality of 92%, those 2 years and older, 51%. Over the same period the mortality of *Chthamalus* aged 7 months was 62%, those 1½ years and older, 2%. Records of the survival of *Balanus* at several levels below this showed that only those *Balanus* in the top quarter of the intertidal region suffered high mortality during this time.

Competition for space. . . . Intraspecific competition leading to mortality in *Chthamalus* was a rare event. For areas 2 to 7, on the portions from which *Balanus* had been removed, 167 deaths were recorded in a year. Of these, only 6 could be ascribed to crowding between individuals of *Chthamalus*. On the undisturbed portions no such crowding was observed. This accords with Hatton's observation that he never saw crowding between individuals of *Chthamalus* as contrasted to its frequent occurrence between individuals of *Balanus*.

Interspecific competition between *Balanus* and *Chthamalus* was, on the other hand, a most important cause of death of *Chthamalus*. This is shown both by the direct observations of the process of crowding at each census and by the differences between the survival curves of *Chthamalus* with and without *Balanus*. From the periodic observations it was noted that after the first month on the undisturbed portions of areas 3 to 7 about 10% of the *Chthamalus* were being covered as *Balanus* grew over them; about 3% were being undercut and lifted by growing *Balanus*; a few had died without crowding. By the end of the 2nd month about 20% of the *Chthamalus* were either wholly or partly covered by *Balanus*; about 4% had been undercut; others were surrounded by tall *Balanus*. These processes continued at a lower rate in the autumn and almost ceased during the later winter. In the spring *Balanus* resumed growth and more crowding was observed. . . . Above M.T.L., the *Balanus* tended to overgrow the *Chthamalus*, whereas at the lower levels, undercutting was more common. This same trend was evident within each group of areas, undercutting being more prevalent on area 7 than on area 3, for example. The faster growth of *Balanus* at lower levels (Hatton; Barnes and Powell) may have resulted in more undercutting. . . .

. . . *Chthamalus* kept free of *Balanus* survived better than those in the adjacent undisturbed areas on all but areas 2 and 14a. Area 2 was in the zone where adults of *Balanus* and *Chthamalus* were normally mixed; at this high level *Balanus* evidently has no influence on the survival of *Chthamalus*. On Stone 14a, the survival of *Chthamalus* without *Balanus* was much better until January when a starfish, *Asterias rubens* L., entered the cage and ate the barnacles. . . .

. . . crowding of newly settled *Chthamalus* by older *Balanus* in the autumn mainly takes the form of undercutting, rather than of smothering as was the case in the spring. The reason for this difference is probably that the *Chthamalus* are more firmly attached in the spring so that the fast growing young *Balanus* grow up over them when they make contact. In the autumn the reverse is the case, the *Balanus* being firmly attached, the *Chthamalus* weakly so.

Although the settlement of *Chthamalus* on Stone 15 in the autumn of 1954 was very dense, $32/\mathrm{cm}^2$, so that most of them were touching another, only 2 of the 41 deaths were caused by intraspecific crowding among the *Chthamalus*. This is in accord with the findings from the 1953 settlement of *Chthamalus*. . . .

. . . The mortality rates of *Balanus* were about the same as those of *Chthamalus* in similar situations except at the highest level, area 1, where *Balanus* suffered much greater mortality than *Chthamalus*. Much of this mortality was caused by intraspecific crowding at all levels below area 1. . . .

After a year of crowding the average population densities of *Balanus* and *Chthamalus* remained in the same relative proportion as they had been at the start, since the mortality rates were about the same. However, because of its faster growth, *Balanus* occupied a relatively greater area and, presumably, possessed a greater biomass relative to that of *Chthamalus* after a year.

The faster growth of *Balanus* probably accounts for the manner in which *Chthamalus* were crowded by *Balanus*. It also accounts for the sinuosity of the survival curves of *Chthamalus* growing in contact with *Balanus*.

The mortality rate of these *Chthamalus*. . . was greatest in summer, decreased in winter and increased again in spring. The survival curves of *Chthamalus* growing without contact with *Balanus* do not show these seasonal variations which, therefore, cannot be the result of the direct action of physical factors such as temperature, wave action or rain. . . .

From all these observations it appears that the poor survival of *Chthamalus* below M.H.W.N. [mean high water, neap tide] is a result mainly of crowding by dense populations of faster growing *Balanus*.

At the end of the experiment in June, 1955, the surviving *Chthamalus* were collected from 5 of the areas. . . the average size was greater in the *Chthamalus* which had grown free of contact with *Balanus*; in every case the difference was significant ($P < .01$, Mann-Whitney U. test. . . .)

These *Chthamalus* were examined for the presence of developing larvae in their mantle cavities. . . . in every area the proportion of the uncrowded *Chthamalus* with larvae was equal to or more often slightly greater than on the crowded areas. The reason for this may be related to the smaller size of the crowded *Chthamalus*. It is not due to separation, since *Chthamalus* can self-fertilize. Moore and Barnes have shown that the number of larvae in an individual of *Balanus balanoides* increases with increase in volume of the parent. Comparison of the cube of the diameter, which is proportional to the volume, of *Chthamalus* with and without *Balanus* shows that the volume may be decreased to $\frac{1}{4}$ normal size when crowding occurs. Assuming that the relation between larval numbers and volume in *Chthamalus* is similar to that of *Balanus*, a decrease in both frequency of occurrence and abundance of larvae in *Chthamalus* results from competition with *Balanus*. Thus the process described in this paper satisfies both aspects of interspecific competition as defined by Elton and Miller: "in which one species affects the population of another by a process of interference, i.e., by reducing the reproductive efficiency or increasing the mortality of its competitor. . . ."

DISCUSSION

"Although animal communities appear qualitatively to be constructed as if competition were regulating their structure, even in the best studied cases there are nearly always difficulties and unexplored possibilities" (Hutchinson).

In the present study direct observations at intervals showed that competition was occurring under natural conditions. In addition, the evidence is strong that the observed competition with *Balanus* was the principal factor determining the local distribution of *Chthamalus*. *Chthamalus* thrived at lower levels when it was not growing in contact with *Balanus*. . . .

The causes of zonation. The evidence presented in this paper indicates that the lower limit of the intertidal zone of *Chthamalus stellatus* at Millport was determined by interspecific competition for space with *Balanus balanoides*. *Balanus*, by virtue of its greater population density and faster growth, eliminated most of the *Chthamalus* by directing crowding.

At the upper limits of the zones of these species no interaction was observed. *Chthamalus* evidently can exist higher on the shore than *Balanus* mainly as a result of its greater tolerance to heat and/or desiccation.

The upper limits of most intertidal animals are probably determined by physical factors, such as these. Since growth rates usually decrease with increasing height on the shore, it would be less likely that a sessile species occupying a higher zone could, by competition for space, prevent a lower one from extending upwards. . . .

In regard to the lower limits of an animal's zone, it is evident that physical factors may act directly to determine this boundary. For example, some active amphipods from the upper levels of sandy beaches die if kept submerged. However, evidence is accumulating that the lower limits of distribution of intertidal animals are determined mainly by biotic factors. . .

TERRITORY IN BIRD LIFE

H. Eliot Howard—1920

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Territoriality is a means by which a population can regulate the limited physical and nutritive resources available to it. First described in a conceptual framework by Howard, the various modes of its expression and the range of vertebrate and invertebrate animals exhibiting such behavior has been increasingly recognized. The complexities of the phenomenon are discussed by C. R. Carpenter (1958. A. Roe and G. G. Simpson, eds. Territoriality: a review of concepts and problems. Behavior and evolution. New Haven, Yale University Press).

In his *Manual of Psychology* Dr. Stout reminds us that "Human language is especially constructed to describe the mental states of human beings, and this means that it is especially constructed so as to mislead us when we attempt to describe the working of minds that differ in a great degree from the human."

The use of the word "territory" in connection with the sexual life of birds is open to the danger which we are here asked to guard against, and I propose, therefore, before attempting to establish the theory on general grounds, to give some explanation of what the word is intended to represent and some account of the exact position that representation is supposed to occupy in the drama of bird life.

The word is capable of much expansion. There cannot be territories without boundaries of some description; there cannot well be boundaries without disputes arising as to those boundaries; nor, one would imagine, can there be disputes without consciousness as a factor entering into the situation; and so on, until by a simple mental process we conceive of a state in bird life analogous to that which we know to be customary amongst ourselves. Now, although the term "breeding territory," when applied to the sexual life of birds, is not altogether a happy one, it is difficult to know how otherwise to give expression to the facts observed. Let it then be clearly understood that the expression "securing a territory" is used to denote a process, or rather part of a process, which, in order to insure success to the

individual in the attainment of reproduction, has been gradually evolved to meet the exigencies of diverse circumstances. Regarded thus, we avoid the risk of conceiving of the act of securing a territory as a detached event in the life of a bird, and avoid, I hope, the risk of a conception based upon the meaning of the word when used to describe human as opposed to animal procedure.

Success in the attainment of reproduction is rightly considered to be the goal towards which many processes in nature are tending. But what is meant by success? Is it determined by the actual discharge of the sexual function? So many and so wonderful are the contrivances which have slowly been evolved to insure this discharge, that it is scarcely surprising to find attention focused upon this one aspect of the problem. Yet a moment's reflection will show that so limited a definition of the term "success" can only be held to apply to certain forms of life; for where the young have to be cared for, fostered, and protected from molestation for periods of varying lengths, the actual discharge of the sexual function marks but one stage in a process which can only succeed if all the contributory factors adequately meet the essential conditions of the continuance of the species.

Securing a territory is then part of a process which has for its goal the successful rearing of offspring. In this process the functioning of the primary impulse, the acquirement of a place suitable for breeding purposes, the advent of a female, the discharge of the sexual function, the construction of the nest, and the rearing of offspring follow one another in orderly sequence. But since we know so little of the organic changes which determine sexual behaviour, and have no means of ascertaining the nature of the impulse which is first aroused, we can only deal with the situation from the point at which the internal organic changes reflect themselves in the behaviour to a degree which is visible to an external observer. That point is reached when large numbers of species, forsaking the normal routine of existence to which they have been accustomed for some months, suddenly adopt a radical change in their mode of behaviour. How is this change made known to us?. . . by all those movements. . . which the term migration, widely applied, is held to denote. Now the impulse which prompts these travelling hosts must be similar in kind whether the journey be long or short; and it were better, one would think, to regard such movements as a whole than to fix the attention on some one particular journey which fills us with amazement on account of the magnitude of the distance traversed or the nature of the difficulties overcome. For, after all, what does each individual seek?. . . the majority seek neither continent nor country, neither district nor locality is their aim, but a place wherein the rearing of offspring can be safely accomplished; and the search for this place is the earliest visible manifestation in many species of the reawakening of the sexual instinct.

The movements of each individual are then directed towards a similar goal, namely, the occupation of a definite station; and this involves for many species a distinct change in the routine of behaviour to which previously they had been accustomed. Observe, for example, one of the numerous flocks of Finches that roam about the fields throughout the winter. Though it may be composed of large numbers of individuals of different kinds, yet the various units form an amicable society actuated by one motive—the procuring of food. And since it is to the advantage of all that the individual should be subordinated to the welfare of the community as a whole there is no dissension, apart from an occasional quarrel here and there.

In response, however, to some internal organic change, which occurs early in the season, individuality emerges as a factor in the developing situation, and one by one the males betake themselves to secluded positions, where each one, occupying a limited area, isolates itself from companions. Thereafter we no longer find that certain fields are tenanted by flocks of greater or less dimensions, while acres of land are uninhabited, but we observe that the hedgerows and thickets are divided up into so many territories, each one of which contains its owner. This procedure, with of course varying detail, is typical of that of many species that breed in Western Europe. . . . Whilst for the purpose of the theory I shall give expression to this behaviour in terms of that theory, and speak of it as a disposition to secure a territory, using the word disposition, which has been rendered current in recent discussion, for that part of the inherited nature which has been organised to subserve a specific biological purpose—strict compliance with the rules of psychological analysis requires a simpler definition; let us therefore say "disposition to remain in a particular place in a particular environment."

But even granting that this disposition forms part of the hereditary equipment of the bird, how is the process of reproduction furthered? The mere fact of remaining in or about a particular spot cannot render the attainment of reproduction any less arduous, and may indeed add to the difficulties, for any number of individuals might congregate together and mutually affect one another's interests. A second disposition comes, however, into functional activity at much the same stage of sexual development, and manifests itself in the male's intolerance of other individuals. And the two combined open up an avenue through which the individual can approach the goal of reproduction. In terms of the theory I shall refer to this second disposition as the one which is concerned with the defence of the territory. . . .

Now the male inherits a disposition which leads it to remain in a restricted area, but the disposition cannot determine the extent of that area. How then are the boundaries fixed? That they are sometimes adhered to with remarkable precision, that they can only be encroached upon at the risk of a conflict—all of this can be observed with little difficulty. But if we regard them as so many lines definitely delimiting an area of which the bird is cognisant, we place the whole behaviour on a different level of mental development, and incidentally alter the complexion of the whole process. It would be a mistake, I think, to do this. Though conscious intention as a factor may enter the situation, there is no necessity for it to do so; there is no necessity, that is to say, for the bird to form a mental image of the area to be occupied and shape its course accordingly. The same result can be obtained without our having recourse to so complex a principle of explanation, and that by the law of habit formation. In common with other animals, birds are subject to this law in a marked degree. An acquired mode of activity becomes by repetition ingrained in the life of the individual, so that an action performed to-day is liable to be repeated tomorrow so long as it does not prejudice the existence or annul the fertility of the individual. . . .

The intolerance that the male displays towards other individuals, usually of the same sex, leads to a vast amount of strife. Nowhere in the animal world are conflicts more frequent, more prolonged, and more determined than in the sexual life of birds; and though they are acknowledged to be an important factor in the life of the individual, yet there is much difference of opinion as to the exact position they occupy in the drama of bird life. Partly because they frequently happen to be in evidence, partly because they are numerically inferior, and partly, I suppose, because the competition thus created would be a means of maintaining efficiency, the females, by common consent, are supposed to supply the condition under which the pugnacious nature of the male is rendered susceptible to appropriate stimulation. And so long as the evidence seemed to show that battles were confined to the male sex, so long were there grounds for hoping that their origin might be traced to such competition. But female fights with female, pair with pair, and, which is still more remarkable, a pair will attack a single male or a single female; moreover, males that reach their destination in advance of their prospective mates engage in serious warfare. How then is it possible to look upon the individuals of one sex as directly responsible for the strife amongst those of the other, or how can the female supply the necessary condition? As long as an attempt is made to explain it in terms of the female, the fighting will appear to be of a confused order; regard it, however, as part of a larger process which demands, amongst other essential conditions of the breeding situation, the occupation of a definite territory, and order will reign in place of confusion.

But even supposing that the male inherits a disposition to acquire a suitable area, even supposing that it inherits a disposition which results indirectly in the defence of that area, how does it obtain a mate?. . .

. . . Here the song, or the mechanically produced sound, comes into play, and assists in the attainment of this end. Nevertheless if every male were to make use of its powers whether it were in occupation of a territory or not, if the wandering individual had an equal chance of attracting a mate, then it would be idle to attempt to establish any relation between "song" on the one hand, and "territory" on the other, and impossible to regard the voice as the medium through which an effectual union of the sexes is procured. But there is reason to believe that the males utilise their powers of producing sound only under certain well-defined conditions. For instance, when they are on their way to the breeding grounds, or moving from locality to locality in search of isolation, or when they desert their territories temporarily, as certain of the residents often do, they are generally silent; but when they are in occupation of their territories they become vociferous—and this is notoriously the case during the early hours of the day, which is the period of maximum activity so far as sexual behaviour is concerned. So that just at the moment when the sexual impulse of the female is most susceptible to stimulation, the males are betraying their positions and are thus a guide to her movements. Nevertheless, even though she may have discovered a male ready to breed, success is not necessarily assured to her; for with multitudes of individuals striving to procreate their kind, it would be surprising if there were no clashing of interests, if no two females were ever to meet in the same occupied territory. Competition of this kind is not uncommon, and the final appeal is to the law of battle, just as an appeal to physical strength sometimes decides the question of the initial ownership of a territory. . . .

A STUDY OF SOME ANT LARVAE WITH A CONSIDERATION OF THE ORIGIN AND MEANING OF THE SOCIAL HABIT AMONG INSECTS

William Morton Wheeler—1918

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Communication among organisms assumes many diverse behavioral expressions and utilizes various physical and chemical media. In this selection, Wheeler introduces the term trophallaxis and discusses its significance in the establishment and maintenance of ant societies. Wheeler's work on the behavior of social insects, notably ants, not only stimulated considerable work but also considerable discussion of his analogy of the insect society and the individual organism. (*See also Allee, p. 98.*)

The facts collated in the foregoing paragraphs relate to the exudate organs, but we had previously seen that the salivary glands of larval ants probably subserve a similar function in the life of the colony in addition to digesting proteid foods extraintestinally and producing silk at the time of pupation. The question arises as to whether there is any evidence that in other groups of social insects the salivary glands of the larva produce substances which are consumed by the worker nurses. Fortunately there are some very pertinent observations at hand in the French literature which is so rich in splendidly original works on the habits and taxonomy of insects. The observations to which I refer relate to the social wasps. Du Buysson observed that the larvæ of *Vespa* "secrete from the mouth an abundant liquid. When they are touched the liquid is seen to trickle out. The queen, the workers and the males are very eager for this secretion. They know how to excite the offspring in such a way as to make them furnish the beverage." And Janet was able to prove that the secretion is a product of the salivary, or spinning glands and that it flows from an opening at the base of the labium. "This product," he says, "is often imbibed by the imagines, especially by the just emerged workers and by the males, which in order to obtain it, gently bite the head of the larva."

The most illuminating study of this matter, however, is found in a fine paper by Roubaud on the wasps of Africa. His account of the primitive wasps of the genus *Belonogaster* presents a striking picture of one of the earliest stages in the social life of wasps. . . .

Roubaud summarizes the general bearing of his observations in the following paragraph:

> The reciprocal exchange of nutriment between the adult females and the larvæ, the direct exploitation of the larval secretion without alimentary compensation by the males and just emerged females are trophobiotic phenomena the elucidation of which is of great importance to an understanding of the origin of the social tendencies in the Vespidæ, as we shall show in the sequel. The retention of the young females in the nest, the associations between isolated females, and the coöperative rearing of a great number of larvae are all rationally explained, in our opinion, by the attachment of the wasps to the larval secretion. The name *œcotrophobiosis* (from οἶκος, family) may be given to this peculiar family symbiosis which is characterized by reciprocal exchanges of nutriment between larvæ and parents, and is the *raison d'être* of the colonies of the social wasps. The associations of the higher Vespids has, in our opinion, as its first cause the trophic exploitation of the larvæ by the adults. This is, however, merely a particular case of the *trophobiosis* of which the social insects, particularly the ants that cultivate aphids and coccids, furnish so many examples.

It does not seem to me that the term "œcotrophobiosis" is aptly chosen. Apart from its length, it implies, as Roubaud states, a relationship between adult and larval members of the same colony or family, comparable with that existing between ants on the one hand and Aphids, Coccids, Membracids and Lycænid larvæ on the other. This relationship, however, is, so far as nutrition is concerned, one-sided since the ants exploit the aphids, etc., and may defend or even transport them, but do not feed them. Moreover, even in *Belonogaster* the feeding of adults and larvæ is reciprocal, and the latter could not be reared if they were actually exploited to such an extent as to interfere with their growth. As the relationship is clearly coöperative or mutualistic, I suggest the term *trophallaxis* (from τροφή, nourishment and ἀλλάττειν, to exchange) as less awkward and more appropriate than "œcotrophobiosis.". . .

Although considerable evidence thus points to trophallaxis as the source of the social habit in wasps, ants and termites, it must be admitted that the phenomenon has not been observed in the social bees. That the latter may have passed through a phylogenetic stage like that of *Synagris* seems to be indicated by the solitary bees of the genus *Allodape* to which I have already referred. Brauns' observations, though meager, show nevertheless that *Allodape* has reached Roubaud's fourth stage, that of direct feeding of the larvæ from day to day, and if I am right in supposing that the peculiar appendages of the larvæ are exudate organs, there would be grounds for assuming that trophallaxis occurs in this case. On the other hand, it has often been suggested (*e. g.*, by von Buttel-Reepen) that the three social subfamilies, the stingless bees (Meliponinæ), bumble-bees (Bombinæ) and honey bees (Apinæ) have developed from the solitary bees by another and more direct path, for the Meliponinæ, though living in populous societies, still bring up their brood in essentially the same way as the solitary bees, *i, e.*, by sealing up the eggs in cells provisioned with honey-soaked pollen. The Bombinæ, however, keep opening the cells from time to time and giving the larvæ a little food at a time, and in the honey bee the cells are left open till pupation and the larvæ fed more coninuously. Numerous facts indicate that the Bombinæ are the most primitive, the Apinæ the most specialized of existing social bees, and that the Meliponinæ, though closely resembling the solitary bees in the care of the young, are nevertheless in other respects very highly specialized (vestigial sting, elaborate nest architecture, etc.). It is therefore not improbable that these bees, after passing through a stage more like that of the Bombinæ, have reverted secondarily to a more ancient method of caring for their brood. . . .

Another objection that may be urged against the view that trophallaxis is so fundamental as I contend, is the behavior of the ants towards their inert pupæ, which though transported and defended as assiduously as the larvæ, yield neither liquid exudates nor secretions. This does not seem to me to be a serious objection, because the pupæ evidently have an attractive odor and may therefore be said to produce volatile exudates like certain myrmecophiles. Both the larvæ and pupæ, moreover, evidently represent so much potential or stored nutriment available for the adult ants when the food-supply in the environment of the colony runs very low or ceases entirely. Infanticide and cannibalism then set in with the result that the devouring of the young of all stages may keep the adult personnel of the colony alive till the trophic conditions of the environment improve. Certain predatory tropical species (Dorylinæ, Cerapachyini) regularly raid the colonies of other ants and carry home and devour their brood. . . .

If we confine our attention largely to the ants, I believe it can be shown that trophallaxis, originally developed as a mutual trophic relation between the mother insect and her larval brood, has expanded with the growth of the colony like an ever-widening vortex till it involves, first, all the adults as well as the brood and therefore the entire colony; second, a great number of species of alien insects that have managed to get a foothold in the nest as scavengers, prædators or parasites (symphily); third, alien social insects, *i.e.*, other species of ants (social parasitism); fourth, alien insects that live outside the nest and are "milked" by the ants (trophobiosis), and, fifth, certain plants which are visited or sometimes partly inhabited by the ants (phytophily). In other words the ants, have drawn their living environment, so far as this was possible, into a trophic relationship, which, though imperfect or one-sided in the cases of trophobiosis and photophily, has nevertheless some of the peculiarities of trophallaxis. A brief sketch of each of these five expansions, indicated as annular areas in the accompanying diagram (Fig. 12), may not be out of place.

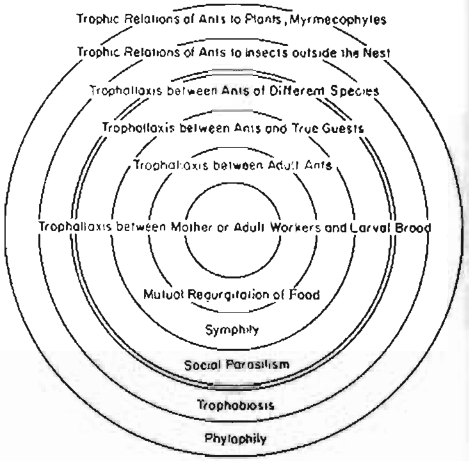

FIG. 12. *Diagram to illustrate the expansions of the trophallactic and trophic relationships within and outside the ant colony. The confines of the nest are indicated by the double line.*

1. There is a very close resemblance between the behavior of adult ants towards one another and their behavior towards their young. The adults feed one another with regurgitated food or even with secretions as is the case with *Crematogaster* (*Physocrema*) *inflata*, an Indomalayan species, the workers of which have great sugar-glands in the back of the thorax. Many ants transport each other, and the transported ant assumes a quiescent, larval or pupal attitude. This is best seen in certain Ponerinæ, *e.g.*, in the species of *Lobopelta*, which carry their males under the body as if they were larvæ or pupæ. On such occasions the males keep their legs and antennæ in the pupal position. Moreover, when the food-supply of the colony is cut off ants often devour other ants of the colony as if they were larvæ or pupæ. The largest workers (soldiers) are eliminated first, either because they represent more stored food or because their continued life in the colony constitutes a greater drain on the food resources, or for both reasons. . . .

2. Among myrmecophiles and termitophiles Wasmann has shown that there are certain species (symphiles) that have trophallactic relations

with their hosts. Among ants especially these relations are so intimate that the symphiles may be regarded as integral members of the colony. The adult Lomeschusine beetles, *e.g.*, are not only fed and licked, but their young are treated as if they were ant larvæ, owing to the presence of trichome glands ("external exudate organs" of Wasmann) in the former and fatty, or internal exudatoria in the latter.

3. The various parasitic ants, of which a number of species have come to light within recent years and have been described by Wasmann, Donisthorpe, Emery, myself and others, can be shown to have established trophallactic relations with their host species. One of the most instructive is *Leptothorax emersoni* which lives with *Myrmica canadensis*. I have described its habits and those of one of its subspecies in three of my former papers.

4. The relations of ants to plant-lice and other Homoptera and to the larvæ of Lepidoptera outside the nest are, as I have said, incompletely trophallactic, since these insects are not fed, though they may be defended by the ants. The Homoptera are not fed probably for the simple reason that their mouthparts are so peculiarly specialized for piercing plant-tissues and sucking their juices, and the Lepidopteron larvæ have, as a rule, no occasion to abandon their leaf diet. There are, however, several cases in which both caterpillars and Homoptera have entered into more intimate association with the ants. Many of the root aphids and coccids and their eggs are collected and kept by the ants in their nests, at least during certain seasons of the year. . . .

5. The fifth expansion of trophallaxis, namely the acquisition of trophic relations with the myrmecophytes, or plants possessing extra-floral nectaries or food-bodies, is also imperfect like ordinary trophobiosis, since the ants merely obtain nutriment from the plants and possibly afford them some protection. The nectar and other plant-foods are for the purposes of the ants merely so many exudates like the excrement of the Homoptera (honey-dew) and the sweet secretions of the Lycænid caterpillars which feed on the foliage. . .

STUDIES IN ANIMAL AGGREGATIONS: CAUSES AND EFFECTS OF BUNCHING IN LAND ISOPODS

W. C. Allee—1926

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The phenomenon of animal aggregations received its major exploitation by Allee at the University of Chicago and Wheeler (see p. 94) at Harvard University, the two foremost students of animal sociology during the first half of the twentieth century. This is Allee's first paper dealing with the topic; it indicates the analytic, interpretive and conceptual framework in which his subsequent research was conducted.

STATEMENT OF THE GENERAL PROBLEM

Many animals ordinarily living without physical contact with their fellows in nature at times come together to form more or less dense clusters or aggregations. Classic examples of this are furnished by the swarms of the honey-bee and of Eciton, the army ant, or by the hibernating aggregations of the coccinellid beetles. Deegener has devoted an extensive monograph to cataloging and naming the different types of such aggregations as well as others in which physical contact is not necessarily established.

Other species that are not known to form such aggregations in nature do so readily enough when brought into artificial conditions in the laboratory. The formation of such bunches by controlled stimulation, the effects of various environmental conditions upon their formation, and particularly the analysis of movements which result in aggregations were a favorite study some years ago during the height of the 'tropism' and 'trial and error' controversy. . . .

In addition to the large literature dealing with the formation of aggregations under laboratory conditions, there are many descriptions of aggregations more or less incidentally discovered in nature. Such groupings have excited particular attention when they have shown some signs of integration in behavior.

There is, however, a lack of information of the physiological effect of such congregations upon the animals forming them. The present report is largely concerned with this aspect of the general aggregations problem, although attention must necessarily be paid to the conditions under which aggregations occur. . . .

FACTORS CONTROLLING BUNCHING IN LAND ISOPODS

1. Moisture. These isopods may be found aggregated in damp places during dry periods or at least in situations where they are protected from the evaporating power of the air. This suggested the possibility that their bunching reaction might be controlled in part by controlling the moisture present. . . . When land isopods (Cylisticus convexus DeG., Porcellio scaber Latr., Oniscus asellus L., Tracheoniscus rathkei Brandt, or Armadillidium vulgare Latr.) are placed on air-dry filter-paper they tend to collect in bunches within a few

minutes unless the paper and the atmosphere are too dry, in which case they remain scattered and frantically active until death. . . .

2. Temperature. In experiments on the effect of temperature on bunching, fifteen isopods of either Porcellio or Cylisticus or both were placed in crystallization dishes on slightly moistened filterpaper making conditions favorable for bunching. . . .

These observations indicate that while temperature affects the bunching reaction of land isopods, it does not control the reaction so markedly or completely as does the moisture content of the substratum.

3. Light. When these isopods were exposed to light there was a differential effect depending on the amount of moisture present in the substratum. The isopods are strongly photonegative, and bunching occurred even on a moist background when the animals were illuminated, but these bunches broke up when the light was removed. On the other hand, the bunches on a dry substratum were more dense in the darkness than in the light, since the latter stimulated those on the upper layer to move about while in darkness they heaped into one large compact bunch. In all cases there was more bunching on the dry substratum than on the moist. . . .

4. Contact. Land isopods are strongly positive in their thigmotropic reaction; this combined with their reactions to moisture and to light sends them under boards and in crevices. When such places are not available, there is a tendency to form aggregations with each other which will satisfy the same tactile reaction. Bunches are more likely to be found near the angle or corner of a container than out in the open and all possible use is made of available surfaces. As in the other elements making for aggregation, reaction to contact is less strong than the effect of moisture. . . .

METHOD OF FORMING AGGREGATIONS

The aggregations so far described were formed by what has been called the 'selection of random movement' type of reaction. Usually the animals wandered over the surface of their container, preferably around the margin, and came to rest in the position in which they were apparently least stimulated. In order to find how the aggregations were formed when the conditions were as nearly uniform in all parts of the container as they could be made, Mr. Vernon S. Downs conducted a long series of observations. Under uniform conditions, the isopods usually wandered about until one came to rest for some reason or other. Sometimes inequalities developed in an environment at first uniform and at other times the isopod apparently stopped for internal reasons. After one stopped there was a distinct tendency for the others to come to rest near by. They might or might not be in physical contact with the first, although they had frequently just crawled over it before stopping. In their incipient stages these bunches were frequently rather loose. The isopods would then alternate periods of rest and of motion. During some of the latter many or even all might start up again. Often a nucleus remained consisting of the original isopod and one or more others. Around such a nucleus the isopods would again gather. The bunch would become consolidated by slight movements toward the more stationary individuals on the part of those on the periphery. Partially successful attempts were made to control the place of bunch formation on a uniform field by gluing a recently killed isopod to the substratum.

When a drop of water was introduced on a dry background the isopods tended to occupy all of that favorable location regardless of whether or not they were in contact. The bunching in physical contact came later and might take place as a thigmotropic reaction, perhaps modified by chemical stimuli. . . .

PHYSIOLOGICAL EFFECT OF AGGREGATING

1. On water content. Experiments were run on Oniscus asellus and Cylisticus convexus to determine the effect upon body weight of exposure to increased or to decreased water content in their environment. . . .

Summary of experiment

1. Six bunched O. asellus, average weight 82.3 mg.; one isolated isopod, weight 85.5 mg. After eighteen hours on moist filter-paper, showed a gain of 12 and 21 per cent, respectively.
2. Ten bunched O. asellus, average weight 115 mg.; two isolated isopods weighed 138 and 124, respectively. After eighteen hours under less moist conditions, showed gains of 0.3, 0.9, and 1 per cent, respectively.
3. Ten bunched C. convexus, average weight 36.7 mg., gained 2.3 per cent in twenty-four hours, while five isolated animals weighing from 30 to 32 mg. gained 9, 12.6, 11, 12.2, and 10 per cent respectively.

These three bunches gained an average of 3.8 per cent under conditions which caused eight similar isolated animals to gain 9.7 per cent. The rate of gain was two to four times as fast when the isopods were isolated as when they were bunched.

Similar experiments when bunches and single individuals were allowed to dry showed that the aggregated isopods lose water less rapidly than isolated ones and that the lag is at about the same ratio as in the preceding case. . . .

These observations show that the formation of aggregations tends to render the isopods less easily affected by the water content of their environment and markedly decreases the rapidity of change of body moisture when this is not in equilibrium with the surroundings.

2. Effect of bunching on respiration. . . .Large Armadillidium vulgare. . . isolated for one hour had a respiratory rate equivalent to a movement of mercury 85.5 mm. per second and kilogram in one set and 79.6 in another as compared with 61.1 and 54, respectively, for those bunched the same length of time. The difference is about of the same order as for Tracheoniscus. In exact ratios, the rate of oxygen consumption with bunched and isolated Armadillidium was 1:1.486 and 1:1.368, while with the Tracheoniscus this ratio was 1:1.214 and 1:1.344.

The Armadillidium tests allow other comparisons. Since groups of isolated or bunched individuals were set away in the dark for approximately twenty-four hours, one can compare their physiological condition near the beginning of this period with that at the end and also make cross comparisons.

In general, the determinations show that, under the conditions of the experiment, there is a very marked decrease in oxygen consumption after twenty-four hours' isolation (and starvation); 70 and 65 per cent, respectively, in two sets of experiments. There is a similar, but less pronounced, reduction when the animals are bunched (and starved); 31 and 29 per cent, respectively. At the end of twenty-four hours, the bunched isopods were uniformly using more oxygen per unit weight than were the isolated individuals. The observed ratios were: 1:1.64 and 1:1.48. All the differences mentioned are statistically significant, since the least difference in means is still over 11.5 times their combined probable error. . . .

SIGNIFICANCE OF THE BUNCHING HABIT IN LAND ISOPODS

. . .Under ordinary conditions, aggregations of these land isopods are formed as a result of individual reactions and occur as follows: There is first a period of random movement which is more rapid at high temperatures and is slowed down by cold. During this period movement is stimulated by light and by evaporation. There is a tendency for individuals to stop in conditions that least stimulate them, such as a more moist place on the paper, a region satisfying thigmotropic reactions, or in least illumination. When a number of isopods stop in the same general region there is a tendency for them to move together even if not quite touching—a reaction probably caused by chemical stimulation and later by responses to both tactile and chemical stimuli.

During their wandering the isopods may stop near a quiet individual apparently as they would stop near any other object which gave them the same tactile satisfaction.

Considering all the evidence at hand, it seems that these isopods aggregate primarily through a tolerance of other individuals in a restricted favorable region which may lead to a use of other individuals in satisfying thigmotropic tendencies or in avoiding light. There is, however, an element of mutual attraction which Deegener calls 'social instinct' and Wallin regards as 'prototaxis' shown by the fact that the isopods will occupy less than the whole available and apparently equally desirable space. The question not settled is whether to the isopod the vacated space is as near isopod optimum as the space taken, regardless of the presence of other isopods.

One hesitates to ascribe a positive primitive social impulse to the reactions of these animals so long as it is possible to explain the observed phenomena on other grounds. We know that what were formerly regarded as 'social instincts' in the breeding season have been further analyzed in large part into chemotropism, thigmotropism, etc. Wallin's 'prototaxis' seems to belong to the same type of reactions as those usually described as social instincts so far as it applies to the relations between animals, since it is admittedly built of other recognizable components, such as chemotropism. Certainly, only the elements of a reaction that cannot be explained otherwise should be ascribed to 'prototaxis.' . . .

If the foregoing analysis be sound, as it appears to be, then the first step toward social life in lower animals is the appearance of tolerance for other animals in a limited space where they have collected as a result of tropistic reactions to environmental stimuli. Such collections frequently occur in connection with some phase of breeding activity or of reproduction, but in the land isopods it is well exhibited without sexual significance.

A first advance in social life is made when these groupings serve to promote the welfare of the individuals forming them. This is accomplished in the land isopods by keeping the animals more quiet and so preserving their vitality, by conserving their water content and probably by lessening the rate of change of temperature. Robertson's infusoria and most of the animals tested by Drzewina and Bohn appear to so react on their environment as to render it more favorable.

The land isopods have gone little beyond such a stage in their social development. There is some slight evidence of mutual attraction, but the experiments to date do not reveal how much of this would be exhibited toward similar inanimate objects. There is also evidence of integrated group behavior in that the bunch shows occasional periods of activity apparently originating in one individual and passed mechanically through the group. Such activity may be the beginning of disintegration of the bunch, but it frequently results in a closer aggregation because the animals tend to move together as a result of their brief period of mild activity. Such group behavior is much more simple than that which Newman and Allee observed for aggregated phalangids, or Blair, Hess, and others have found in fireflies, and is far removed from the complex group behavior of the social insects or mammals.

NATURAL SELECTION AND FAMILY SIZE IN THE STARLING

David Lack—1948

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Lack's major premise of population regulation is that it is determined by natural selection acting through various processes. In the case in point, clutch-size in birds is determined by natural selection acting through survival of the young. The comprehensive statement of his viewpoint was elaborated in Natural regulation of animal numbers (1954. Oxford, Clarendon Press). Professor Lack has been Director of the Edward Gray Institute of Field Ornithology at Oxford University for many years.

. . . the limitation of clutch-size to a comparatively small number of eggs cannot be adequately explained on purely physiological grounds. The view that it is adjusted to the mortality of the species is also untenable. The alternative hypothesis was put forward that it is ultimately selected by the number of young which the parents can raise, the latter being determined by the available food supply. This view, so acceptable *a priori* to the population-geneticist and so difficult, apparently, for the traditional ecologist, was supported by much circumstantial evidence, chiefly relating to seasonal and regional trends of variation in clutch-size.

In the present paper, an attempt is made to provide direct evidence, to test whether, in fact, the young from broods of large size are at a disadvantage compared with those from broods of small size. It might be expected that, for broods above the average size, proportionate mortality among the young would rise as brood-size increased. When this is so, a point is quickly reached where an increase in the number of eggs is offset by the increased mortality, so that there is no increase in the number of young raised. One might reasonably hope to find evidence for this turning point in nature. . . .

CLUTCH-SIZE

In Britain, Holland and Switzerland, the Starling lays its first clutch in April or early May. A smaller number of layings occur in late May and in June, these being due partly to one-year-old birds breeding for the first time, partly to older birds whose first layings were destroyed, and partly to older birds which have already raised one brood in the season. In this paper, all clutches laid in April, and all broods with young old enough to band in May, have been classified as "early" broods, and they have been separated from later layings, which are on the average somewhat smaller in size. . . . In general, 5 is the commonest size of an early laying, and 4 of a late clutch.

The Starling also shows a regional variation in clutch-size. As in many other passerine species, average clutch-size is somewhat smaller in England than in central Europe at the same latitude. . . .

PARENTAL FEEDING RATE

The hypothesis of this paper rests on the assumption that the parent Starlings bring less food to each nestling in a large than a small brood. This was found by Kluijver to hold in the Starling, . . . but further data on this point are desirable. However, a similar result was obtained for most other species in which this problem has been investigated by Moreau. To summarise these data: with a brood of larger size, the parents increase the number of their feeding visits, but the increase is not sufficient to offset the larger number of young, so that each nestling is fed less often in a large than in a small brood.

MORTALITY IN THE NEST

Owing to the above fact, it was expected that the young would show, on the average, a proportionately higher mortality in large than small broods. The nesting data for the Starling in Britain did not suggest this, but were too few for analysis. Fortunately, extensive nest records are available from Holland since 1922, in the form of the number of eggs laid and the number of young alive on the observer's last visit. These. . . show decisively that the above expectation is not realized.

. . .in early layings, the proportion of eggs which give rise to fledged young is approximately the same for clutches of 3, 4, 5, 6, 7 and 8 eggs. For late layings, the answer is similar; (except for an apparent lower success for clutches of 6, which is attributable merely to random sampling, as a similar drop is not found for clutches of 7). When the losses of entire broods are included in the analysis. . .the results for early layings again show no variation with clutch-size, and the apparent variation in late layings is doubtless due to random sampling, the losses of entire broods being very erratic in their incidence from place to place and year to year. Nestling mortality was found to be independent of brood-size in the four other small passerine species in which this point has been studied. . . .

NESTLING WEIGHT

The fact that nestling mortality is similar for broods of different sizes was first discovered for the Robin (*Erithacus rubecula*). To investigate the problem further, nestling Robins were weighed daily from hatching to flying. This unexpectedly revealed that there were extremely marked individual variations in the weight of the nestlings. . . . Lees has found similar large variations in the other small passerine species which he has weighed. In such species, the nestling can remain alive, and develop its feathers normally, although badly under weight, and the chief effect of undernourishment on a nestling is not death in the nest, but a reduced weight when it leaves the nest. The only comparative data so far available on the weights of nestling Starlings in broods of different sizes were obtained in 1947 by R. Carrick for three broods of different sizes, all raised by fully adult parents, all in the same locality, and all starting incubation on the same date. The results. . . fit the view that the average nestling weight decreases as brood-size increases, but many more data are needed before this point can be considered established.

POST-FLEDGING SURVIVAL IN SWITZERLAND

Those young which are below normal weight on leaving the nest might well have a reduced chance of subsequent survival. Moreover, any differences in their fledging weight associated with size of brood would tend to be intensified in the period immediately after leaving the nest, when the young are still dependent on their parents for a time; hence the greater the number of young, the less often each will tend to be fed. This means that the possible adverse effects of a large brood-size on survival can be revealed only if the data are extended to cover the period after leaving the nest. . . .

Should there be, in the period shortly after leaving the nest, a heavier mortality among the young from large than from small broods, then proportionately more individuals from small than large broods should survive to maturity. . . .

The results. . . are highly suggestive. In early broods, 5 is the commonest size of family. The recovery-rate for birds more than three months out of the nest is about the same for those coming from broods of 3, 4 or 5 young, in each case being around 2%. On the other hand, as soon as the brood-size exceeds 5, the recovery-rate falls. For individuals from broods of 6 it is only 1.7%, and for those from broods of 7–8 it is only 1.4%. If, now, the proportion of individuals recovered is multiplied by the original number of young in the brood (as in the right-hand column of table 6) [deleted], it is seen that, on the average, a brood of 5, 6 or 7 young gives rise to the same number of recoveries, about 0.1 per brood. If these recoveries are representative of the population, this must mean that an increase in brood-size between 5 and 7 young is approximately counterbalanced by an increase in proportionate mortality among the young, taking place in the period shortly after they leave the nest. . . .

The above data fit the hypothesis advanced earlier, viz. that when brood-size rises above the average, mortality also rises, so that productivity is not increased. Unfortunately, the proportion of birds recovered is so small that, despite the large numbers banded, the totals recovered are too small for the apparent differences in recovery-rate to be statistically significant. One could not expect bigger differences in the recovery-rates than those actually obtained, since, according to theory, the productivity per brood should be about equal for a brood of 5, 6 or 7 young, as in fact it is. (Had the young from broods of 6 or 7 survived less well, broods of 6 and 7 would have been less productive than broods of 5, and so would presumably have been extremely scarce.) Hence the lack of a significant result is due to the small number of recoveries, and not to the size of the difference found. For a significant result, about twice the present number of recoveries is needed, on the assumption that they are recovered in the same proportions. . . .

. . . in late broods 4 is the commonest size of family, and the recovery-rate falls from 2.2% in broods of 4, to 1.8% in broods of 5, and to about 1.4% in broods of 6. Once again, if the proportion of individuals recovered is multiplied by the number of young in the brood, it is seen that broods of 4, 5 and 6 young are about equally productive. Hence the results from late broods corroborate those from early broods. Unfortunately, the data are again too few for the result to be statistically significant. . . .

THE REGIONAL DIFFERENCE

It will be noted that in early broods the commonest number of young is 5 in Switzerland but only 4 in Britain, while in late broods it is 4 in Switzerland but only 3 in Britain. Lack showed that there was a widespread tendency for the average clutch-size of passerine birds to be larger in Central Europe than in Britain at the same latitude, and argued that a general trend suggests an adaptation. The data. . .fit in with this suggestion, since, in early broods, the survival-rate begins to decrease with a brood of more than 5 young in Switzerland, but with a brood of more than 4 young in Britain, while in late broods the decrease commences with a brood of more than 4 young in Switzerland but with a brood of more than 3 young in Britain. This presumably means that more food is available for young Starlings in Switzerland than in Britain, but there are as yet no data on this point. In the parallel case of the Swift (*Apus apus*) in the two regions, there is suggestive evidence that not only average clutch-size but also food supply is greater in Switzerland than in Britain.

Lack also showed a general tendency in passerine birds for average clutch-size to be higher in the north than the south of the European range. There are not yet sufficient data on this point for the Starling. . . .

POPULATION TURN-OVER

. . .the Starling has a lower reproductive rate in Britain than in Switzerland. While in both countries the Starling has been increasing in numbers in the last fifty years, the increase has probably been sufficiently slow to mean that the average number of young born each year is very nearly equal to the average annual mortality. The higher reproductive rate of Swiss than of British Starlings should therefore mean that the Swiss birds have a higher annual mortality than the British. This point can be tested by analysing the age at death of each banded bird later recovered. . . . This indicates that the mortality in the first year is 73% for Swiss but only 66% for British Starlings, while in later years it is 62% for Swiss and only 55% for British birds. These differences are statistically significant, and therefore support the above hypothesis. However, it is possible that the small percentage of recovered Starlings is slightly biassed as to age, as discussed in greater detail by Lack and Schifferli. It is scarcely necessary to add that, in a balanced population, a higher mortality-rate is an inevitable result of a higher reproductive rate. The types of danger to which Swiss and British Starlings are respectively subjected are a purely secondary consideration.

CONCLUSION

The data in this paper suggest that, as brood-size increases, the mortality among the young also increases, in such a way that the commonest brood-size found in nature is also the size with optimum productivity. This result appears to hold under the differing seasonal conditions of first and late broods, and the differing regional conditions of Switzerland, Holland and Britain. The facts therefore support the view that clutch-size is determined by natural selection acting through the survival of the young. . . .

THE ROLE OF WEATHER IN DETERMINING THE DISTRIBUTION AND ABUNDANCE OF ANIMALS

L. C. Birch—1957

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L. C. Birch is representative of those who consider populations to be regulated by factors largely external to the population and independent of the size of the population. Climate is an example of such a factor. H. G. Andrewartha and Birch, both of the University of Sydney, Australia, develop these concepts of population regulation in The distribution and abundance of animals (1954. Chicago, University of Chicago Press).

The thesis of this paper is that weather is a component of the environment of animals which effectively determines the limits to distribution and the abundance of some species. Short term and long term changes in weather determine short term and long term changes in distribution and abundance. That weather can be effective in determining the limits of abundance within the distribution of an animal has been doubted by some ecologists who believed that only "density-dependent" factors can "determine" the density of populations. Density dependent factors or as they have more recently been called "density-governing" factors are defined as those factors which "permit populations to grow when at relatively low densities, and oppose growth when the densities become relatively high" (see Nicholson). Weather is not classed as a "density governing" factor because it is claimed that it does not react to a change in density of animals. The upholders of this point of view maintain that in the absence of "density governing" factors populations would either grow without check or alternatively they would tend towards extinction.

We shall examine a partly hypothetical model, and illustrate it with examples, of how short term and long term changes in weather may influence the chance to survive and multiply in such a way as to prevent unlimited increase in numbers even in the absence of "density governing" factors. It will be shown in the same model that weather can operate in such a way that there will be little chance of extinction provided the fluctuations of weather are kept within limits which would need to be defined for each species. As these limits are approached the chance of extinction increases. Over a long period of time the chances of these limits being exceeded is greater than for a short period of time.

It is not contended that the numbers of all animals are determined primarily by weather nor that weather is more important than other components of environment. All components have a part to play. But in studying any one species it is usual to find that one component plays a primary role in determining numbers. Sometimes this is weather.

Weather is also a component of natural selection and so may play a part in determining the qualitative composition of a population. Selection through components of weather may change an animal's chance to survive and multiply and this will be reflected in changes in its distribution and abundance.

SHORT TERM CHANGES IN WEATHER

The grasshopper *Austroicetes cruciata* has a well defined distribution in south eastern Australia in a belt of country running roughly east to west. There is another grasshopper belt in western Australia which is separated from the eastern one by the Nullarbor desert. There the belt runs diagonally across the south western corner of the continent. . . . isopleths for moisture based on rainfall and evaporation. . . delineate quite nicely the distribution of the species. North of the distribution the country is too dry for the grasshopper to survive, south of the distribution it is too wet. . . . The contraction and expansion of the grasshopper belt in a north-south direction is associated with fluctuations of weather. Both these changes and the changes in abundance within the belt were studied by Andrewartha and Birch over a number of years. . . . From our understanding of these changes we built up a generalised diagram which summarises the situation [and] represents a section of the grasshopper belt from north to south. A central strip of country is inhabited permanently. Numbers there are likely to be higher than elsewhere. To the north and south the country is inhabited temporarily in sequences of favourable years. If we now select three localities within the grasshopper belt, one in the center, one in the north and one in the south, we might represent the change in abundance in time as in Figure 3. Locality A is a place where numbers are often high, locality B is a place which is unfavourably wet and numbers never so high. Locality C is a place which is so dry that grasshoppers become extinct in some years. Their presence in subsequent years is dependent upon dispersal from the south. . . . These changes are largely due to seasonal change in weather. Knowing the effect of weather on the survival of grasshoppers, Andrewartha and Birch were able to make an estimate of the chance, in each of these localities, of obtaining a sequence of years that would permit multiplication to plague numbers. At C the chance is extremely small. At A it is much greater. Conversely it would be true to say that the chance for survival and multiplication is small at B and C but high at A. This is a probabilistic way of looking at distribution and abundance. By introducing the idea of chance we have removed the necessity to consider whether temperature, rainfall and other components are "density-dependent" or "density-independent" factors. We do not deny the existence of density-dependent factors but we deny the assertion that populations can only be regulated by "density-dependent" factors. From the probabilistic point of view any component of environment might assume this role.

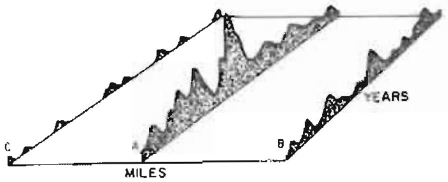

FIG. 3. *Hypothetical diagram, showing the change in mass of grasshoppers during many years in the localities marked A, B, and C, in Figure 2 [deleted]. (After Andrewartha and Birch, 1954).*

Let us now look more closely at how weather determines numbers at A, B and C so that grasshoppers are never so common at B and C as at A. Those who do not think that weather can regulate numbers argue that at a place such as C the weather is tolerable, otherwise the animals would not be there at all. If tolerable, then numbers will increase at C until a resource such as food runs short. So what really limits numbers at C is a shortage of an essential resource due to there being too many grasshoppers. In reply to this argument we would say that if weather at C remained tolerable all the time, then to be sure, numbers would increase until food or some other resource became limiting. But the situation at C is much more complex and this complexity alters the argument. Two characteristics of natural environments which have not been considered in this argument have to be taken into account. These are (a) fluctuations in the favourableness of weather and in other components of environment which affect survival and multiplication and (b) spatial patchiness of the environment. In other words we have to consider the heterogeneity of the environment in time and in space.

Consider the situation at C (Fig.3) which is within the distribution of the grasshopper but near the northern boundary. . . . There is only one generation of grasshoppers each year; they lay their eggs late in spring. During the summer and winter only the egg stage is present. The curve shows how the mass of grasshoppers might vary over a five year period. Each year without exception there is a crash in numbers after increase in bio-mass in the spring. But the increase in bio-mass is not the cause of the crash. The cause of the crash is the hot dry summer which inevitably follows the favourable season of spring. The earliness and extent of the crash in numbers will be determined by the earliness and severity of the unfavourable period. Likewise the upper limit to numbers each year is determined by the length and favourableness of the spring and the severity of the previous season. In the second year the unfavourable season was so severe that the grasshoppers were completely wiped out before they laid any eggs. The chance of this happening is high in the northern extremity of the distribution though it must be quite small in the more central localities. It is to be noted that in the third year grasshoppers were again present. We shall suppose that they arrived by dispersal from a locality, some ten miles or so south, which was more hospitable to grasshoppers in the previous season. . . .

The first point our model illustrates is that in an area of extreme unfavourableness in which the weather is sometimes intolerable for grasshoppers, it is still possible for grasshoppers to be found there. This is by virture of the patchiness of the environment.

Let us next consider what prevented grasshoppers from increasing indefinitely in both the locality in the north . . . and in a locality further south. . . . When the nymphs first hatch they are not likely to be short of food because this is the season of the year when the grass is growing most strongly. When swarms were present, the later stages sometimes experienced a shortage of food, not because there was insufficient grass in the area, but because it dried up before the grasshoppers could complete their development. It will be necessary to consider the nature of the food shortage at this stage in a moment. There is good evidence that grasshoppers do not suffer from food shortage while the grass is mostly green. Sheep share the pastures with grasshoppers and it is the aim of farmers to have enough dry grass standing in their paddocks to carry their flocks through summer. During the plague years 1935 to 1939 the number of sheep living in the pastures almost doubled. If there had been a shortage of dry food the farmers would most certainly have removed them. In other words the grasshoppers always left enough grass to provide

large stocks of dry grass in the summer.

The small amount of green food that is left at the end of the spring is related not to the number of grasshoppers but to the onset of the hot dry summer. It might be argued that the grasshoppers would then suffer from competition for the little food that was left. The green food that remained then consisted of short blades at the base of dried up tufts of grass. These green blades were sparsely scattered over many plants. The last grasshopper died of starvation before all the green food had disappeared. What was left it could not find at a rate fast enough to keep it alive. It is true that more grasshoppers will eat more food. But our observations convinced us that the total amount they ate was small in relation to what was available, even at the end of the season. Because grasshoppers find so little of the food that remains with the approach of summer the chance of a grasshopper finding food is independent of the number searching for it. This is the principle of the relative shortage of food described by Andrewartha and Birch. . . .

THE SELF-ADJUSTMENT OF POPULATIONS TO CHANGE

A. J. Nicholson—1957

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According to Nicholson, the density of a population is governed not by biotic and abiotic factors per se but by attributes of these elements (availability, accessibility, intensity, etc.). More important, however, is his contention that "the ability to adjust themselves to great changes in their environments" is inherent in all populations. The essence of this hypothesis and part of the empirical basis for it are found in this selection. The author is associated with the Commonwealth Scientific and Industrial Organization, Canberra, Australia.

For some years my method of approach to an understanding of population problems has been to use laboratory colonies of the Australian sheep-blowfly, *Lucilia cuprina* Wied., under precisely defined laboratory conditions. The method consists of introducing a small number of *L. cuprina* into a cage and, from then on, maintaining predetermined conditions constant, including the supply of such depletable requisites as food and water at a constant rate. The population is left entirely to its own devices and, apart from maintaining the predetermined conditions, the only action taken is to keep a careful day-to-day record of the numbers of individuals of some, at least, of the various developmental stages—supplementing this at times with other observations. . . .

L. cuprina is representative of the large group of animals which "scramble" for their food, the rate of supply of which is determined by factors other than the activity of the animals. With gross crowding such scrambling leads to much wastage of the governing requisite so that, with excessive numbers of animals, there is either excessive mortality or the fertility may be temporarily reduced below the replacement rate. This tends to produce violent oscillations in the size of the populations which are not caused by environmental fluctuations, and it generally limits the average density of the animals far below that which the supply of governing requisites could maintain if there were no wastage.

In contrast to this is the category of animals which "contest" for their limiting requisite. That is to say, each successful individual lays claim to a supply of requisites sufficient to maintain it, and to enable it to produce offspring. The unsuccessful individuals are denied access to critical requisites by their successful competitors. This kind of competition eliminates, or greatly reduces, the wastage of requisites, so permitting a relatively high density of animals to be maintained and, in addition, preventing such intraspecific oscillation as occurs in *L. cuprina*. There is room for only a certain limited number of individuals; consequently those which are unsuccessful in obtaining room "overflow" into less favourable parts of the environment from which critically important requisites are absent, or present in inadequate amounts. . . .

In the two categories of population regulation just discussed the amount and rate of production of the governing requisite, which is critical to the animals, is independent of their activities. There is another large and important category in which the activities of the animals not only influence the degree of depletion of their governing requisites, but also determine the amount produced. These are such phytophagous animals and predators as limit their own population densities by limiting the production of their host-plants or prey, thereby reducing these to the threshold levels, at which the enemies can find barely sufficient food to maintain their own numbers. . . . Note that "parasites" of the insect type are really predators, as their larvae eat their "hosts".

This category of population regulation is of exceptional interest because of the unexpected and varied results of interaction between animals and the organisms upon which they feed. The considerations which first caused me to consider population problems seriously conveniently illustrate the situation represented by this category.

Many years ago I was puzzled by the fact that the degree of infestation of citrus trees by scale insects appeared to be quite independent of the number of citrus trees in any particular area; for this indicated that the population of scale insects was directly influenced by the number of citrus trees—in spite of the fact that there was evidently space for far more scales on the foliage and branches, and that, as the citrus trees remained healthy, the food supply was presumably capable of supporting far more scale insects than it did. It occurred to me that the puzzling phenomenon could be due to the action of natural enemies, for the citrus trees not only provided food for the scale insects, but also constituted the area over which the enemies had to search. Simple considerations indicated that, if the number of scale insects was very high, large numbers of parasites would breed from them, and that these parasites, operating in the next generation, would collectively search the greater part of the foliage of the trees, so attacking most of the scale insects and causing their numbers to fall to a low level in the following generation. Continuing this kind of argument it became

clear that the numbers of scale insects and of their natural enemies should produce effects upon one another which would always tend to reduce over-large populations, and to allow very small populations to increase.

The mechanism visualized was that, if few enemies searched a large area, each would spend most of its time exploring previously unsearched areas; whereas if the searching enemies were numerous, each would spend most of its time searching previously explored areas within which most of the scale insects would presumably have been attacked already. Assuming that the enemies were fairly evenly or randomly distributed over the foliage, it was easy to construct a curve which represented quantitatively the reduction in the success of the searching individuals in exploring previously unexplored areas, in which the unattacked scales would presumably lie. This I called the "competition curve." . . . Using this curve it was possible to examine a number of hypothetical arithmetical examples by assigning arbitrary "powers of increase" to the hosts and "areas of discovery" (which represent the searching abilities of the parasites) to the parasites.

To my astonishment, no matter how I varied the two basic properties, the arithmetical examples indicated that the reactions between the two kinds of insects, although always of the right kind to oppose, and to change the direction of the current displacements, gave rise to oscillations in the numbers of both hosts and parasites, and these grew in amplitude with time! In other words, this simple system of corrective reaction was over-violent and proved to be intrinsically unstable. Subsequently Bailey confirmed and extended these conclusions by the use of mathematics.

Thus, in this situation, density-induced reactions were produced in populations of both kinds of interacting animals which were of the right sign to counteract departures from the equilibrium position but they were over-violent, so causing successively greater and greater over- and undershooting of the equilibrium position. The growth in amplitude of the oscillations is probably related to the fact that two systems of oscillation are involved. The well known predator-prey oscillations of Volterra lead to systems of sustained oscillations which may be referred to as "coupled oscillations". . . as they are due to a linkage between the two changing populations. Each as it passes its equilibrium density alters the direction of change of the other population; but Volterra's populations consisted of hypothetical animals with the curious property that they interacted from the moment they were born, which means that they were born fully mature. In contrast to this, insect hosts and their parasites require a considerable time to develop, and changes in density induced by interaction produce their effects only after the lapse of a generation. This tends to give rise to "lag-oscillations", such as were observed in the *Lucilia cuprina* cultures. The superimposition of these lag-oscillations upon the coupled oscillations seems to be the likely cause of growth in amplitude of successive oscillations, and of the consequent instability of this system of interaction.

Two arithmetically calculated examples are given in Figure 9 of this type of system, each example representing the interaction of a specific host and a specific parasite. That is to say, increase in the host density is limited solely by the action of one particular species of parasite, and the parasite attacks hosts of this species only, and so limits its own density by restricting that of its host. It will be seen that the violence of reaction is greater in B than in A, which illustrates the general conclusion

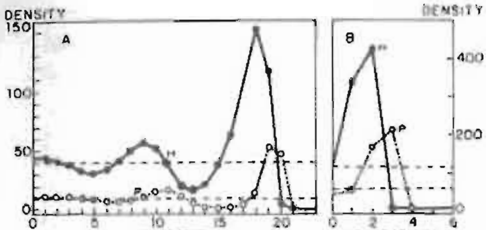

FIG. 9. *Calculated interspecific oscillations produced by interaction between a specific host and a specific parasite. Power of increase in A is 2, and in B it is 10 times per generation; all other properties and conditions are the same in the two systems illustrated. Heavy lines, host populations; dotted lines, parasite populations (shown at half the scale used for hosts); broken lines, steady densities.*

that the violence of oscillation mounts with increase in the "power of increase" of the host. . . . The magnitude of the "area of discovery" of the parasite does not influence the character of the oscillation. In both the examples given, it is assumed that initially one of the interacting species is at its equilibrium density whereas the other is displaced slightly from its equilibrium density. Only by making this assumption is it possible to show several successive oscillations for, otherwise, the violence of reaction is so great that one of the populations is quickly reduced to fractional numbers, and the other population follows—as is indicated in Figure 9 B. The graphs shown in Figure 9, and similar ones published elsewhere. . . are not intended to show what may be expected to happen to interacting hosts and parasites in nature, but simply to illustrate the probable underlying mechanism which leads to certain interesting events which are sometimes observed in nature. . . .

There is not sufficient time to discuss other categories of population regulation. . . I can only state that in all of these, just as in the three categories already discussed, it has been found that automatic compensatory mechanisms exist which permit the populations to adapt themselves to widely different circumstances by density-induced reactions. Because of much misunderstanding upon the point, I would like to stress that my investigations and theoretical considerations based upon them, do not imply that density governing reaction should operate upon a population at all times. At times populations may multiply without check, or their numbers may be progressively reduced over a period by adverse external factors, without there being any compensatory reaction during that period. In spite of this, it is necessary, and inevitable, that density-induced reaction should limit populations in relation to the prevailing environmental conditions from time to time at least, so determining the general levels of abundance from which the uncontrolled variations just spoken of may take place.

The foregoing considerations have shown that some kinds of animals, at least, induce reactions in their environments, and within their own populations, which bring about an automatic self-adjustment of their population densities at levels which are determined both by their own properties and by those of their environments. Theoretical considerations go farther than this . . . and indicate that no population can be persistent unless it has a mechanism of density-induced compensatory reaction to maintain it in being. . . .

COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION

Nelson G. Hairston, Frederick E. Smith, and Lawrence B. Slobodkin—1960

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In spite of acknowledging limited application, proponents of given population models tend to discuss them as all inclusive. It is at that point that the model encounters difficulty. Part of this difficulty arises from the heterogeneity of organisms in contrast to the homogeneity of the populations which provide the empirical basis for most of the models. The general pattern of population control which is developed in this brief, persuasive argument is an attempt by these three University of Michigan ecologists to reconcile diverse points of view.

The methods whereby natural populations are limited in size have been debated with vigor during three decades, particularly during the last few years (see papers by Nicholson, Birch, Andrewartha, Milne, Reynoldson, and Hutchinson, and ensuing discussions in the Cold Spring Harbor Symposium, 1957). Few ecologists will deny the importance of the subject, since the method of regulation of populations must be known before we can understand nature and predict its behavior. Although discussion of the subject has usually been confined to single species populations, it is equally important in situations where two or more species are involved.

The purpose of this note is to demonstrate a pattern of population control in many communities which derives easily from a series of general, widely accepted observations. The logic used is not easily refuted. Furthermore, the pattern reconciles conflicting interpretations by showing that populations in different trophic levels are expected to differ in their methods of control.

Our first observation is that the accumulation of fossil fuels occurs at a rate that is negligible when compared with the rate of energy fixation through photosynthesis in the biosphere. Apparent exceptions to this observation, such as bogs and ponds, are successional stages, in which the failure of decomposition hastens the termination of the stage. The rate of accumulation when compared with that of photosynthesis has also been shown to be negligible over geologic time. . . .

If virtually all of the energy fixed in photosynthesis does indeed flow through the biosphere, it must follow that all organisms taken together are limited by the amount of energy fixed. In particular, the decomposers as a group must be food-limited, since by definition they comprise the trophic level which degrades organic debris. There is no a priori reason why predators, behavior, physiological changes induced by high densities, etc., could not limit decomposer populations. In fact, some decomposer populations may be limited in such ways. If so, however, others must consume the "left-over" food, so that the group as a whole remains food limited; otherwise fossil fuel would accumulate rapidly.

Any population which is not resource-limited must, of course, be limited to a level *below* that set by its resources.

Our next three observations are interrelated. They apply primarily to terrestrial communities. The first of these is that cases of obvious depletion of green plants by herbivores are exceptions to the general picture, in which the plants are abundant and largely intact. Moreover, cases of obvious mass destruction by meteorological catastrophes are exceptional in most areas. Taken together, these two observations mean that producers are neither herbivore-limited nor catastrophe-limited, and must therefore be limited by their own exhaustion of a resource. In many areas, the limiting resource is obviously light, but in arid regions water may be the critical factor, and there are spectacular cases of limitation through the exhaustion of a critical mineral. The final observation in this group is that there are temporary exceptions to the general lack of depletion of green plants by herbivores. This occurs when herbivores are protected either by man or natural events, and it indicates that the herbivores are able to deplete the vegetation whenever they become numerous enough, as in the cases of the Kaibab deer herd, rodent plagues, and many insect outbreaks. It therefore follows that the usual condition is for populations of herbivores *not* to be limited by their food supply.

The vagaries of weather have been suggested as an adequate method of control for herbivore populations. The best factual clues related to this argument are to be found in the analysis of the exceptional cases where terrestrial herbivores have become numerous enough to deplete the vegetation. This often occurs with introduced rather than native species. It is most difficult to suppose that a species had been unable to adapt so as to escape control by the weather to which it was exposed, and at the same time by sheer chance to be able to escape this control from weather to which it had not been previously exposed. This assumption is especially difficult when mutual invasions by different herbivores between two countries may in both cases result in pests. Even more difficult to accept, however, is the implication regarding the native herbivores. The assumption that the hundreds or thousands of species native to a forest have failed to escape from control by the weather despite long exposure and much selection, when an invader is able to defoliate without this past history, implies that "pre-adaptation" is more likely than ordinary adaptation. This we cannot accept.

The remaining general method of herbivore control is predation (in its broadest sense, including parasitism, etc.). It is important to note that this hypothesis is not denied by the presence of introduced pests, since it is necessary only to suppose that either their natural predators have been left behind, or that while the herbivore is able to exist in the new climate, its enemies are not. There are, furthermore, numerous examples of the direct effect of predator removal. The history of the Kaibab deer is the best known example, although deer across the northern portions of the country are in repeated danger of winter starvation as a result of protection and predator removal. Several rodent plagues have been attributed to the local destruction of predators. More recently, the extensive spraying of forests to kill caterpillars has resulted in outbreaks of scale insects. The latter are protected from the spray, while their beetle predators and other insect enemies are not.

Thus, although rigorous proof that herbivores are generally controlled by predation is lacking, supporting evidence is available, and the alternate hypothesis of control by weather leads to false or untenable implications.

The foregoing conclusion has an important implication in the mechanism of control of the predator populations. The predators and parasites, in controlling the populations of herbivores, must thereby limit their own resources, and as a group they must be food-limited. Although the populations of some carnivores are obviously limited by territoriality, this kind of internal check cannot operate for all carnivores taken together. If it did, the herbivores would normally expand to the point of depletion of the vegetation, as they do in the absence of their normal predators and parasites.

There thus exists either direct proof or a great preponderance of factual evidence that in terrestrial communities decomposers, producers, and predators, as whole trophic levels, are resource-limited in the classical density-dependent fashion. Each of these three can and does expand toward the limit of the appropriate resource. We may now examine the reasons why this is a frequent situation in nature.

Whatever the resource for which a set of terrestrial plant species compete, the competition ultimately expresses itself as competition for space. A community in which this space is frequently emptied through depletion by herbivores would run the continual risk of replacement by another assemblage of species in which the herbivores are held down in numbers by predation below the level at which they damage the vegetation. That space once held by a group of terrestrial plant species is not readily given up is shown by the cases where relict stands exist under climates no longer suitable for their return following deliberate or accidental destruction. Hence, the community in which herbivores are held down in numbers, and in which the producers are resource-limited will be the most persistent. The development of this pattern is less likely where high producer mortalities are inevitable. In lakes, for example, algal populations are prone to crash whether grazed or not. In the same environment, grazing depletion is much more common than in communities where the major producers are rooted plants.

A second general conclusion follows from the resource limitation of the species of three trophic levels. This conclusion is that if more than one species exists in one of these levels, they may avoid competition only if each species is limited by factors completely unutilized by any of the other species. It is a fact, of course, that many species occupy each level in most communities. It is also a fact that they are not sufficiently segregated in their needs to escape competition. Although isolated cases of non-overlap have been described, this has never been observed for an entire assemblage. Therefore, interspecific competition for resources exists among producers, among carnivores, and among decomposers.

It is satisfying to note the number of observations that fall into line with the foregoing deductions. Interspecific competition is a powerful selective force, and we should expect to find evidence of its operation. Moreover, the evidence should be most conclusive in trophic levels where it is necessarily present. Among decomposers we find the most obvious specific mechanisms for reducing populations of competitors. The abundance of antibiotic substances attests to the frequency with which these mechanisms have been developed in the trophic level in which interspecific competition is inevitable. The producer species are the next most likely to reveal evidence of competition, and here we find such phenomena as crowding, shading, and vegetational zonation.

Among the carnivores, however, obvious adaptations for interspecific competition are less common. Active competition in the form of mutual habitat-exclusion has been noted in the cases of flatworms and salamanders. The commonest situation takes the form of niche diversification as the result of interspecific competition. This has been noted in birds, salamanders and other groups of carnivores. Quite likely, host specificity in parasites and parasitoid insects is at least partly due to the influence of interspecific competition.

Of equal significance is the frequent occurrence among herbivores of apparent exceptions to the influence of density-dependent factors. The grasshoppers described by Birch and the thrips described by Davidson and Andrewartha are well known examples. Moreover, it is among herbivores that we find cited examples of coexistence without evidence of competition for resources, such as the leafhoppers reported by Ross and the psocids described by Broadhead. It should be pointed out that in these latter cases coexistence applies primarily to an identity of food and place, and other aspects of the niches of these organisms are not known to be identical.

THE STUDY OF COMMUNITIES

At least as early as the time of Theophrastus it was recognized that different species show particular spatial relationships in groupings of one sort or another. The existence of assemblages and a seeming appearance of pattern in their composition and distribution have provided a considerable arena for ecological investigation.

Stimulated and oriented largely by the Danish botanist Eugene Warming at the turn of the century, the study of communities has been directed primarily towards plants. Considerable effort has been expended in the analysis of vegetational units (composition, physiognomy, stratification, distribution, etc.) and the investigation of such dynamic events as phenological and successional change. These studies on the general nature and composition of the plant community with respect to time and space were involved in reciprocal stimulation from concurrent theoretical developments and philosophical discussions.

Animal community studies were given major thrust by the English ecologist Charles Elton in the 1920's. Elton's concept of key industry animals functioning in integrating the community through a food chain focused attention on the relations of numbers of organisms and the nature of food chains and ecological niches. These aspects of community study are covered in the section on ecosystems.