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having space motions larger than 100 km
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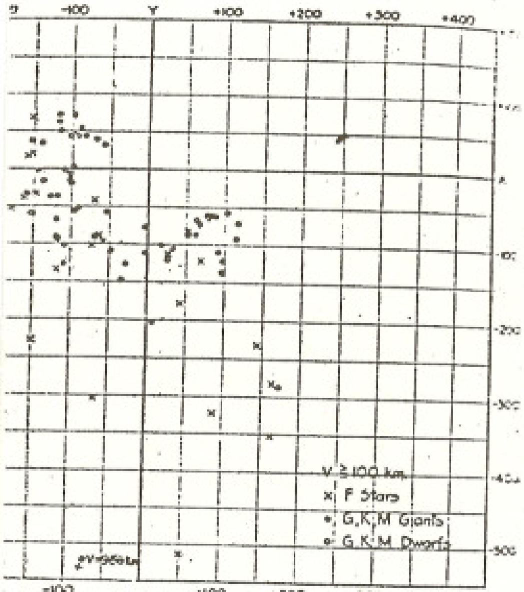

FIG. 2

ane of the velocities of stars having a speed greater

e of the first quadrant in the xy plane. N
km./sec. is moving in this direction, but
moving toward the third quadrant, a result
d by Adams and Joy[3] for stars of high radi

roph. J., Chicago, 53, 1921 (13).
oc., 79, 1919 (201).
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CONTRIBUTION TO THE ENERGETICS OF EVOLUTION*

By Alfred J. Lotka

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Communicated, May 6, 1922

It has been pointed out by Boltzmann[1] that the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy.[2] In accord with this observation is the principle[3] that, in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient[4] in directing available energy into channels favorable to the preservation of the species.

The first effect of natural selection thus operating upon competing species will be to give relative preponderance (in number or mass) to those most efficient in guiding available energy in the manner indicated. Primarily the *path* of the energy flux through the system will be affected.

But the species possessing superior energy-capturing and directing devices may accomplish something more than merely to divert to its own advantage energy for which others are competing with it. If sources are presented, capable of supplying available energy in excess of that actually being tapped by the entire system of living organisms, then an opportunity is furnished for suitably constituted organisms to enlarge the total energy flux[5] through the system. Whenever such organisms arise, natural selection will operate to preserve and increase them. The result in this case, is not a mere diversion of the energy flux through the system of organic nature along a new path, but an increase of the total flux through that system.

Again, so long as sources exist, capable of supplying matter, of a character suitable for the compositon of living organisms, in excess of that actually embodied in the system of organic nature, so long is opportunity furnished for suitably constituted organisms to enlarge the total mass of the system of organic nature. Whenever such organisms arise, natural selection will operate to preserve and increase them, provided always that there is presented a residue of untapped available energy. The result will be to increase the total mass of the system, and, with this total mass, also the total energy flux through the system, since, other things equal, this energy flux is proportional to the mass of the system.

Where a limit, either constant or slowly changing,[6] is imposed upon the total mass available for the operation of life processes, the available energy per unit of time (available power) placed at the disposal of the organisms, for application to their life tasks and contests, may be capable of increase by increasing the rate of turnover of the organic matter through the life cycle. So, for example, under present conditions,[7] the United States produce annually a crop of primary and secondary food amounting to about 1.37 × 10^{14} kilogramcalories per annum, enough to support a population of about 105 million persons (equivalent to about 88 million adults at the present rate of food consumption (4,270 kilogram-calories per adult per day). Suppose, as a simple, though rather extreme illustration that man found means of doubling the rate of growth of crops, and of growing two crops a year instead of one. Then, without changing the average crop actually standing on the fields, the land would be capable of supporting double the present population. If this population were attained, the energy flux through the system composed of the human population and the organisms upon which it is dependent for food, would also be doubled. This result would be attained, not by doubling the mass of the system (for the matter locked up in crops, etc., at a given moment would be, on an average, unchanged) but by increasing the velocity of circulation of mass through the life cycle in the system. Once more it is evident that, whenever a group of[8] organisms arises which is so constituted as to increase the rate of circulation of matter through the system in the manner exemplified, natural selection will operate to preserve and increase such a group, provided always that there is presented a residue of untapped available energy, and, where circumstances require it, also a residue of mass suitable for the composition of living matter.

To recapitulate: In every instance considered, natural selection will so operate as to increase the total mass of the organic system, to increase the rate of circulation of matter through the system, and to increase the total energy flux through the system, so long as there is presented an unutilized residue of matter and available energy.

This may be expressed by saying that *natural selection* tends to make the energy flux through the system a maximum, so far as compatible with the constraints to which the system is subject.

It is not lawful to infer immediately that *evolution* tends thus to make this energy flux a maximum. For in evolution two kinds of influences are at work: selecting influences, and generating influences. The former select, the latter furnish the material for selection.

If the material furnished for selection is strictly limited, as in the case of a simple chemical reaction,[9] which gives rise to a finite number of products, the range of operation of the selective influences is equally limited.

In the case of organic evolution the situation is very different. We have no reason to suppose that there is any finite limit to the number of possible types of organisms. In the present state of our knowledge, or rather our ignorance, regarding the generating influences that furnish material for natural selection, for organic evolution, an element of uncertainty enters here. It appears, however, at least *a priori* probable that among the certainly very large (if not infinite) variety of types presented for selection, sooner or later those will occur which give the opportunity for

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selection to operate in the direction indicated, namely so as to increase the total mass of the system, the rate of circulation of mass through the system and the total energy flux through the system. If this condition is satisfied the law of selection becomes also the law of evolution:

Evolution, in these circumstances, proceeds in such direction as to make the total energy flux through the system a maximum compatible with the constraints.

We have thus derived, upon a deductive basis, at least a preliminary answer to a question proposed by the writer in a previous publication.[10] It was there pointed out that the influence of man, as the most successful species in the competitive struggle, seems to have been to accelerate the circulation of matter through the life cycle, both by "enlarging the wheel," and by causing it to "spin faster." The question was raised whether, in this, man has been unconsciously fulfilling a law of nature, according to which some physical quantity in the system tends toward a maximum. This is now made to appear probable; and it is found that the physical quantity in question is of the dimensions of power, or energy per unit time, as was hinted by the writer on an earlier occasion.[11]

It may be remarked that the principle of maximum energy flux here set forth bears a certain outward resemblance to a principle enunciated by Ostwald:[12] "Of all possible energy transformations, that one takes place which brings about the maximum transformation in a given time." This principle of Ostwald's, however, is based on entirely different grounds from those here brought forward. It is not of general applicability, and in particular, its application to systems of the kind here considered does not appear warranted.

Addendum. Since the paragraphs above were penned, the writer has received from the booksellers a copy of Professor J. Johnstone's book, "The Mechanism of Life" (1921), in which (pp. 217–221) that author touches on matters closely related to those here discussed. Professor Johnstone draws, however, a somewhat different conclusion, namely that "In living processes the increase of entropy is retarded."[13] He points out that this is true, primarily, of plants; but that among animals[14] also natural selection must work toward the weeding out of unnecessary and wasteful activities, and thus toward the conserving of free energy, or, what amounts to the same thing, toward retarding energy dissipation.

This is perhaps not wholly convincing, for the first effect of the advent of animal organisms in a world peopled with a purely vegetable population, would certainly seem to be an acceleration of the process of dissipation. It appears, therefore, that at certain stages in the evolution of the system, at the least, life must have tended to increase rather than decrease dissipation. And even if animals ultimately evolve in the direction of decreased dissipative effect, they still remain essentially a dissipative type, as compared with plants, and, to make Professor Johnstone's argument conclusive, it would seem necessary to show, not merely that the animal organism evolves in that direction, but that the system of coupled transformers, plant and animal, as a whole has so evolved.

Professor Johnstone's conclusion is, however, not essentially incompatible with the one developed in this paper. Where the supply of available energy is limited, the advantage will go to that organism which is most efficient, most economical, in applying to preservative uses such energy as it captures. Where the energy supply is capable of expansion, efficiency or economy, though still an advantage, is only one way of meeting the situation, and, so long as there remains an unutilized margin of available energy, sooner or later the battle, presumably, will be between two groups or species equally efficient, equally economical, but the one more apt than the other in tapping previously unutilized sources of available energy.

There is here a problem that will call for further investigation. In particular, it remains to be established just what is the significance of the phrase "compatible with the constraints" which, in the presentation here given, modifies the maximum principle enunciated. The present communication is intended rather a preliminary than as an attempt to say the last word on the subject. More detailed discussion is planned for another occasion.

* Papers from the Department of Biometry and Vital Statistics, School of Hy... and Public Health, Johns Hopkins University, No. 59.

[1] *Der zweite Hauptsatz der mechanischen Wärmetheorie*, 1886 (Gerold, Vienna). ; *Populäre Schriften*, No. 3, Leipsic, 1905; Nernst, *Theoretische Chemie*, 1913, p... Burns and Paton, *Biophysics*, 1921, p. 8, H. F. Osborn, The Origin and Evolu... Life, 1918, p. XV.

[2] Compare also Sir Oliver Lodge, *Life and Matter*, 1906, pp. 139, 140.

[3] Lotka, A. J., *Ann. Naturphil*, 1910, pp. 67, 68; *Proc. Nat. Acad., Sci.*, 1921, pp. 195.

[4] Lotka, A. J., *Proc. Washington Acad.*, 5, 1915, pp. 360, 397.

[5] The term *energy flux* is here used to denote the available energy absorbed b... dissipated within the system per unit of time.

[6] As, for example, if the total mass of the system is capable of accretion, but o... a limited velocity, in which case the phenomenon of a moving equilibrium may p... itself. Compare Lotka, A. J., *Proc. Nat. Acad. Sci.*, 7, 1921, p. 168.

[7] Pearl, R., *The Nation's Food*, 1920, pp. 218, 203, 258, 80, 245; *Amer. J. Hyg...* 1921, p. 598.

[8] Owing to the fact that in existing organisms the anabiotic and catabiotic fu... are very largely segregated in different types (plants and animals), evolution w... operate upon systems or groups of at least two species, one species of autotroph... bions, and one of heterotrophic catabions.

[9] Compare Lotka, A. J., *Amer. J. Sci.*, 24, 1907, pp. 204, 216.

[10] Lotka, A. J., *Proc. Nat. Acad. Sci.*, 7, 1921, p. 172.

[11] *Idem.*, *Ann. Naturphil.*, 1910, p. 70. It is there suggested that the con... energy transformations associated with the maintenance of a steady state wou... ably be found to play the dominant rôle, while any "latent heat" effect a...

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change in the distribution of matter among the several species composing the ... would probably play a subordinate rôle; in contrast with the condition of affairs ... in ordinary physico-chemical systems. This is an obvious inference from the ...tion that the several species of organisms are distinguished much more by struc... differences than by differences in chemical composition.

...wald, W., *Lehrbuch der allgemeinen Chemie*, 1892, vol. 2, p. 37; Siebel, J. E ...d *of Mechanical Refrigeration*, 1915, p. 88. For a discussion of the validity and ...ns of Ostwald's principle see Helm G., *Die Energetik*, 1898, pp. 248; Neumann, ...iger *Berichte*, 1892, p. 184.

...t living organisms may be capable of retarding the energy flux through the sys...nature was suggested by the present writer in *Ann. Naturphil.*, 1910, p. 60.

...nstone, J., *The Mechanism of Life*, 1921, p. 220.

NATURAL SELECTION AS A PHYSICAL PRINCIPLE*

By Alfred J. Lotka

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Communicated May 6, 1922

In a paper presented concurrently with this, the principle of natural selection, or of the survival of the fittest (persistence of stable forms), is employed as an instrument for drawing certain conclusions regarding the energetics of a system in evolution.

Aside from such interest as attaches to the conclusions reached, the method itself of the argument presents a feature that deserves special ... The principle of natural selection reveals itself as capable of yield... information which the first and second laws of thermodynamics are not competent to furnish.

The two fundamental laws of thermodynamics are, of course, insufficient to determine the course of events in a physical system. They tell us that certain things cannot happen, but they do not tell us what does happen.

In the freedom which is thus left, certain writers have seen the opportunity for the interference of life and conciousness in the history of a physical system. So W. Ostwald[2] observes that "the organism utilizes, in manyfold ways the freedom of choice among reaction velocities, through the influence of catalytic substances, to satisfy advantageously its energy requirements." Sir Oliver Lodge also, has drawn attention to the guidance[3] exercised by life and mind upon physical events, within the limits imposed by the requirements of available[4] energy. H. Guilleminot[5] sees the influence of life upon physical systems in the substitution of guidance by choice in place of fortuitous happenings, where Carnot's principle leaves the course of events indeterminate. As to this, it may be objected that the attribute of fortuitousness is not an objective quality of a given event. It is the expression of our subjective ignorance, our lack of complete information, or else our deliberate ignoring of some of the factors that actually do determine the course of events. Admitting, however broadly, the directing influence of life upon the world's events, within the limits imposed by the Mayer-Joule and the Carnot-Clausius principles it would be an error to suppose that the faculty of guidance which the established laws of thermodynamics thus leave open, is a peculiar prerogative of living organisms. If these laws do not fully define the course of events, this does not necessarily mean that this course, in nature, is actually indeterminate, and requires, or even allows, some extra physical influence to decide happenings. It merely means that the laws, as formulated, take account of certain factors only, leaving others out of consideration; and that the data thus furnished are insufficient to yield an unambiguous answer to our enquiry regarding the course of events in a physical system. Whether life is present or not, something more than the first and second laws of thermodynamics is required to predict the course of events. And, whether life is present or not, *something* definite *does* happen; the course of events is determinate, though not in terms of the first and second laws alone. The "freedom" of which living organisms avail themselves *under the laws of thermodynamics* is not a freedom in fact but a spurious freedom[6] arising out of an incomplete statement of the physical laws applicable to the case. The strength of Carnot's principle is also its weakness: it holds true independently of the particular mechanism or configuration of the energy transformer (engine) to which it is applied; but, for that very reason it is also incompetent to yield essential information regarding the influence of mechanism upon the course of events. In the *ideal* case of a reversible heat engine the efficiency is independent of the mechanism. *Real* phenomena are irreversible; and, in particular, trigger action,[7] which plays so important a rôle in life processes, is a typically irreversible process, the release of available energy from a "false" equilibrium. Here mechanism is all-important. To deal with problems presented in these cases requires new methods,[8] requires the introduction into the argument, of new principles. And a principle competent to extend our systematic knowledge in this field seems to be found in the principle of natural selection, the principle of the survival of the fittest, or, to speak in terms freed from biological implications, the principle of the persistence of stable forms.

For the battle array of organic evolution is presented to our view an assembly of armies of energy transformers—accumulators (plants) and engines (animals); armies composed of multitudes of similar units the individual organisms. The similarity of the units invites statistical treatment, the development of a statistical mechanics of which the units shall be, not simple *material particles* in ordinary reversible collision of the type familiar in the kinetic theory, collisions in which action and reaction

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When the beast of prey A sights its quarry B, the latter may be said to enter the field of influence of A, and, in that sense, to collide with A. The energy that enters the eye of A in these circumstances may be insignificant, but it is enough to work the relay, to release the energy for the fatal encounter. And because evolution works with armies built up of similar units the seemingly erratic workings of the relay mechanism (in which action and reaction are not equal, and seem subject to no simple general law) are not, in effect, erratic, but range themselves according to law and order, for those species of units, those types of transformers, are picked out for survival, whose mechanism possesses certain definite properties. Thus the principle of natural selection makes its entry into dynamics.

Further elaboration of these concepts must be reserved for a future occasion.

In systems evolving toward a true equilibrium (such as thermally and mechanically isolated systems, or the isothermal systems of physical chemistry) the first and second laws of thermodynamics suffice to determinate at any rate the end state; this is, for example, independent of the amount of any purely catalytic substance that may be present. The first and the second law here themselves function as the laws of selection and evolution, as has been recognized by Perrin[9] and others, and exemplified in some detail by the writer, for the case of a monomolecular reversible reaction.[10]

But systems receiving a steady supply of available energy (such as the earth illuminated by the sun), and evolving, not toward a true equilibrium, but (probably) toward a stationary state, the laws of thermodynamics are no longer sufficient to determine the end state; a catalyst, in general, does affect the final steady state. Here selection may operate not only among components taking part in transformations, but also upon catalysts, in particular upon auto-catalytic or auto-catakinetic constituents of the system. Such auto-catakinetic constituents are the living organisms,[11] and to them, therefore the principles here discussed, apply.

That the principle of selection is competent to yield information beyond the scope of the laws of thermodynamics has been very clearly set forth independently, by H. Guilleminot.[12] The present writer has long realized that the principle is capable of such application; that it functions, as it were, as a third law of thermodynamics (or a fourth, if the third place be given to the Nernst principle). If he has not, before this date explicitly stated the case, this is mainly because his writings have followed a definite, systematic plan, announced in his early publications.[13] Viewing evolution as a change in the distribution of matter among the components of a physical system, the study of evolution naturally divides itself into two fields. The one, which might be termed the stoichiometry of evolution, deals with mass relations: the relative amounts of the different species of matter present, and the changes in these amounts the *kinetics* of evolution. The second field of study is the dynamics or *energetics* of evolution, the scope of which is sufficiently indicated by these terms. It appeared desirable to lay the foundation of the first, as the more elementary, of these fields, before proceeding to a systematic exposition of the second. This is the plan which has been closely followed by the writer in the past, and which it is hoped to develop in greater completeness in the future. Material held in reserve, and relating to the dynamics of evolution, will then be brought forward in its proper place. The present issue of this advance sheet is prompted by a recent reading of Guillemin's book, which, through a series of mishaps, has only recently come to the writer's hand.

*Papers from the Department of Biometry and Vital Statistics, School ... and Public Health, Johns Hopkins University, No. 60.

[1] These PROCEEDINGS, 8 p. 147.

[2] Ostwald, W., *Vorlesungen über Naturphilosophie*, 1902, p. 328.

[3] Sir Oliver Lodge, *Life and Matter*, 1906, p. 144.

[4] *Ibid.*, pp. 148, 149; *Nature*, 67, p. 595; 68, p. 31.

[5] Guilleminot, H., *La Matière et la Vie*, 1919, p. 121, et passim.

[6] This remark must be understood to apply only to that freedom which ar... the incompleteness of the first and second law as determinants of the cours... The writer does not here take sides, one way or another, in the controversie... free will, determinism, vitalism as distinguished from mechanistic concepti...

[7] Compare Lotka, A. J., *J. Washington Acad. Sci.*, 2, 1912, p.7 1; Guill... *loc. cit.*, p. 115; Johnstone, J., *The Mechanism of Life*, 1921, p. 49.

[8] Lotka, A. J., *Proc. Nat. Acad. Sci.*, 7, 1921, pp. 194, 196.

[9] Perrin, J., *Traité de Chimie*, 1903, vol. 1, pp. 142–143; Chowlson, O. D., *Le... Physik.*, 1905, vol. 3, p. 499; *Scientia*, 3, 1910, p. 51; Lotka, A. J., *Science Pr...* 1920, p. 406.

[10] For recent substantiation of some of the details of the presentation th... see Baly, E. C. C., *Nature*, vol. 109, 1922, p. 344.

[11] D'Arcy Thompson (*Growth and Form*, 1917, p. 132) attributes the ... of this concept to Chodat, quoted by Monnier, A. (*Publ. Inst. Bot. Un...* (7)- III, 1905. There seem to be, however, some earlier indications of ... thought. The following bibliography, which makes no pretense of compl... culled from works ready at hand: Errera, L., *Revue de l' Université de B...* 1899–1900. May issue; Ostwald, W., *Vorlesungen über Naturphilosophie*, 19... et seq.; Bastian, H. C., *The Nature and Origin of Living Matter*, 1905, p. ... Robertson, T. B., *Arch. Entwickelungsmechanik Org.*, 25, 1908, p. 581, 25, p. ... wald, Wo., *Die zeitlichen Eigenschaften der Entwickelungsvorgänge*, 1908; ... *Anat. Rec.*, 5, 1911, p. 373; Enriques, *Biol. Centralbl.*, 1909, p. 337; Lot... *Z. physik. Chem.*, 72, 1910, p. 511; 80, 1912, p. 159; *J. Phys. Chem.*, 14, 19... *Proc. Nat. Acad. Sci.*, 6, 1920, p. 275; Pearl, R., *Amer. J. Hygiene*, 1, 1921, p...

[12] Guilleminot, H., *loc. cit.*, p. 118, 154, et passim.

[13] Lotka, A. J., *Am. J. Sci.*, 24, 1907, p. 216; *Ann. Naturphil.*, 1910, p. 7...