CONTRIBUTION TO THE ENERGETICS OF EVOLUTION*

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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 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 Hygiene and Public Health, Johns Hopkins University, No. 59.

[1] *Der zweite Hauptsatz der mechanischen Wärmetheorie*, 1886 (Gerold, Vienna), p. 21; *Populäre Schriften*, No. 3, Leipsic, 1905; Nernst, *Theoretische Chemie*, 1913, p. 819; Burns and Paton, *Biophysics*, 1921, p. 8, H. F. Osborn, The Origin and Evolution of 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. 194, 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 by and dissipated within the system per unit of time.

[6] As, for example, if the total mass of the system is capable of accretion, but only at a limited velocity, in which case the phenomenon of a moving equilibrium may present 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. Hygiene*, **1**, 1921, p. 598.

[8] Owing to the fact that in existing organisms the anabiotic and catabiotic functions are very largely segregated in different types (plants and animals), evolution will here operate upon systems or groups of at least two species, one species of autotrophic ana 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 continuous energy transformations associated with the maintenance of a steady state would probably be found to play the dominant rôle, while any "latent heat" effect associated

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

[12] Ostwald, W., *Lehrbuch der allgemeinen Chemie*, 1892, vol. 2, p. 37; Siebel, J. E *Compend of Mechanical Refrigeration*, 1915, p. 88. For a discussion of the validity and limitations of Ostwald's principle see Helm G., *Die Energetik*, 1898, pp. 248; Neumann, C., *Leipziger Berichte*, 1892, p. 184.

[13] That living organisms may be capable of retarding the energy flux through the system of nature was suggested by the present writer in *Ann. Naturphil.*, 1910, p. 60.

[14] Johnstone, J., *The Mechanism of Life*, 1921, p. 220.

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*NATURAL SELECTION AS A PHYSICAL PRINCIPLE**

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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 note. The principle of natural selection reveals itself as capable of yielding 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 com-