



Competition and the Canonical Ensemble

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Received 8 December 1994; revised 10 April 1995

ABSTRACT

Gibbs' canonical ensemble model from equilibrium statistical mechanics furnishes solutions to Eigen's phenomenological rate equations under constant total organization in cases with or without mutability. The evolution of species with mutation under constant total organization reduces to the evolution of substantial virtual species without mutation under the same constant total organization. Application of the canonical ensemble model provides an exact correspondence between thermodynamic and biological parameters. In particular, evolutionary time, as the analog of temperature, emerges as a statistical aggregate of the condition of the evolving system.

1. INTRODUCTION

Eigen's (1971) phenomenological rate equations [1] under constant total organization have proved to be very useful tools for considering growth and selection of competing species. They are mathematically simple; and are capable of interpretation at various levels from the submolecular to the ecological. Although Eigen originally offered explicit solutions only in the absence of mutability, exact solutions in the presence of mutability were soon brought by Thompson and McBride [2], Jones et al. [3], and others. The purpose of this article is to show how these equations can be solved by Gibbs' canonical ensemble model [4]. This is initially counterintuitive, because the canonical ensemble is traditionally ascribed to equilibrium thermodynamics whereas the growth of populations is contingent on a separation from thermodynamic equilibrium. Even on closer examination the dual use of the canonical ensemble turns out to contain some subtleties. In thermodynamics the model describes the way a system settles into a state of maximal entropy at equilibrium. In the biological context, the model describes the way a system moves from a state of maximal entropy toward an ultimate state of certainty or zero entropy—the presence of a single master species or functionally coherent group of species. The

relationship between biology and thermodynamics is extremely complex and many-faceted. The dual applicability of the canonical ensemble provides a mathematical basis for one aspect of that relationship.

2. RANDOMNESS

Much of the controversy surrounding statistical mechanics arose from the long-standing lack of a solid basis for the underlying statistics. Measure theory provided a sound axiomatic foundation from the pure mathematics standpoint, but begged the question of the applicability of the axioms. Martin-Löf [5] finally gave an acceptable definition of randomness. The definition may be paraphrased as follows. Consider a scientific experiment that may have any one of N possible outcomes. By convention of modern science, a “scientific” experiment has to be repeatable and reproducible. The experiment is said to be *random* if no statistical test available to the experimenter can detect any pattern in repeated outcomes. It is very important to note that this definition is contingent on the power of the apparatus available. Rolling a die under casino conditions should be random. On the other hand, if equipment such as a high-speed precision camera were available, it would be possible to predict the outcome of each roll from the initial motion of the die, and experiment would no longer be random.

The basic concepts of entropy and probability follow from the concept of randomness. For a random experiment with N outcomes, the *entropy* is

$$H = \log N. \quad (2.1)$$

The *probability* $\pi(x)$ of any one particular outcome x of the random experiment is

$$\pi(x) = N^{-1}. \quad (2.2)$$

The probability $\pi(x)$ represents a fair stake to buy into the following game: Win one unit if the outcome of the experiment is x . Randomness of the experiment means that there are no winning strategies in this game. The entropy (2.1) measures one’s ignorance about the outcome of the experiment. If you let someone else run the experiment and instead question them afterwards as to what the outcome was, then the number of yes/no questions required to elicit the outcome would be $H/(\log 2)$.

The above formulae are too narrow to be of general use, where one wishes to deal with nonrandom experiments. These may be modeled using an underlying random experiment whose set of outcomes, called the *phase space*, has N elements. The phase space is completely

partitioned into a set $\xi = \{C_1, \dots, C_r\}$ of mutually exclusive subsets called *states*. The partition ξ represents the nonrandom experiment (also denoted ξ) of sampling an outcome x from the phase space and locating the state C_i in which it lies. If the state C_i contains n_i outcomes of the underlying random experiment, each of whose outcomes has probability N^{-1} according to (2.2), then the probability $p_i = p(C_i)$ of the state C_i is given as

$$p_i = n_i N^{-1}. \quad (2.3)$$

The state C_i may be regarded as a random experiment in its own right. Select an outcome from C_i . The entropy of this random experiment, according to (2.1), is

$$H(C_i) = \log n_i. \quad (2.4)$$

If you perform experiment ξ and obtain the result C_i , then your ignorance will have been reduced by $\log N - \log n_i = -\log p_i$. This happens with probability p_i . Thus the average loss of ignorance or gain in knowledge obtained on performing experiment ξ is its *entropy*

$$H(\xi) = - \sum_{i=1}^r p_i \log p_i. \quad (2.5)$$

The entropy $H(\xi)$ satisfies the inequality

$$0 \leq H(\xi) \leq \log r. \quad (2.6)$$

Equality obtains on the left in (2.6) if and only if $p(C_i) = 1$ for some i . If you already know in advance that ξ will come up with state C_i , then you gain no knowledge by performing the experiment. Equality obtains on the right in (2.6) if and only if $p(C_i) = r^{-1}$ for each i . The most informative experiments are those designed so that all their different outcomes are equally likely. In particular, randomness of an experiment is characterized by its entropy.

3. THE CANONICAL ENSEMBLE

For the experiment $\xi = \{C_1, \dots, C_r\}$ considered in the previous section, absolute randomness—complete ignorance about the outcome—was characterized by unconstrained maximization of the entropy $H(\xi)$, attaining the value $\log r$ according to (2.6). In practice it may be possible to assign a numerical value E_i to each state C_i , for example the number of spots on the face of a die or an energy in electronvolts. If the

expected value

$$E = \sum_{i=1}^r p_i E_i \quad (3.1)$$

is known, then the nonnegative probabilities p_i , which have to satisfy the relationship

$$1 = \sum_{i=1}^r p_i, \quad (3.2)$$

are determined by the assumption of relative randomness: no pattern is discernible in repeated outcomes except for maintenance of the expected value E . This is equivalent to maximization of the entropy $H(\xi)$ subject to the constraints (3.1) and (3.2). Note that these constraints are linear in p_i , while $H(\xi)$ is a concave function of the p_i . It follows (e.g., §5.7 of Lancaster [6]) that the maximization problem has a unique solution, recognized by the zeros of the partial derivatives of the Lagrangean function

$$L(p_i, \alpha, \beta) = - \sum_{i=1}^r p_i \log p_i + \alpha \left(1 - \sum_{i=1}^r p_i \right) + \beta \left(E - \sum_{i=1}^r p_i E_i \right). \quad (3.3)$$

The stationarity conditions $\partial L / \partial p_i = 0$ lead to $\log p_i = -(1 + \alpha) - \beta E_i$ or $p_i = \exp(-\beta E_i) / \exp(1 + \alpha)$. Substituting into (3.2), noting that α is independent of i , one obtains

$$p_i = \exp(-\beta E_i) / Z(\beta) \quad (3.4)$$

with the *partition function* or *Zustandsumme*

$$Z(\beta) = \sum_{i=1}^r \exp(-\beta E_i). \quad (3.5)$$

The value E from (3.1) is recovered as

$$E = -dZ/d\beta; \quad (3.6)$$

on the other hand, this equation may yield β . The entropy $H(\xi)$ may be recovered via

$$- \sum_{i=1}^r p_i \log p_i = \sum_{i=1}^r p_i [(1 + \alpha) + \beta E_i]$$

as

$$H(\xi) = \log Z + \beta E. \quad (3.7)$$

Note that (3.4)–(3.7) are just consequences of the assumption of randomness of ξ relative to (3.1) and the attribution of the numerical value E_i to each state C_i . There is no inherent reason for such an experiment ξ to be inappropriate as a model in certain biological circumstances. An experiment ξ with probabilities random subject to (3.1) is called a *canonical ensemble* because it generalizes the models of that name in (equilibrium) statistical mechanics.

A correspondence with thermodynamics arises when the E_i and E are energies in suitable units. Introducing *Boltzmann's constant* K , the *thermodynamic entropy* is

$$S = KH. \quad (3.8)$$

The temperature is

$$\Theta = 1/K\beta. \quad (3.9)$$

The thermodynamic potential is

$$\Psi = \log Z(\beta). \quad (3.10)$$

The Helmholtz free energy is

$$F = -K\Theta\Psi. \quad (3.11)$$

Equation (3.7) then reduces to

$$F = E - \Theta S. \quad (3.12)$$

All this formalism is available in the general context of the canonical ensemble, although the appropriate units may vary from case to case. In the applications to competition models given below, (3.10) represents a cull count, while (3.11) represents an average cull rate.

4. COMPETITION WITHOUT MUTABILITY

The simplest application of the canonical ensemble (with nonthermodynamic parameters) to a biological context arises in Eigen's [1] phenomenological rate equation for the case of constant overall organization and negligible mutability. Consider r species $1, \dots, r$. Suppose that the i th species has a known net growth rate E_i . In other words, if a

population of n_i units of the i th species is allowed to develop without constraint, its rate of change is given by

$$\dot{n}_i = E_i n_i. \quad (4.1)$$

Note that the units of the quantity E_i in Equation (4.1) are $(\text{time})^{-1}$. Now suppose that the r species are brought together in a joint population maintained at a constant count N (e.g., by control of a common food supply). Thus the birth of one individual has to be compensated by the death of another, not necessarily of the same species. If n_i now represents the number of individuals of species i present in the joint population, its rate of change is given by

$$\dot{n}_i = (E_i - E) n_i. \quad (4.2)$$

Summing the Equations (4.2) over i , constancy of the joint population amounts to

$$0 = \sum_{i=1}^r \dot{n}_i = -NE + \sum_{i=1}^r n_i E_i. \quad (4.3)$$

Consider the experiment ξ of capturing a random individual from the population and determining its species. State C_i corresponds to the i th species. Equations (2.3) and (4.3) yield the constraint

$$E = \sum_{i=1}^r p_i E_i \quad (4.4)$$

on the experiment ξ . If *nothing else is assumed to be known* (including the initial values of the n_i), then the canonical ensemble is the appropriate model for ξ , and (3.4) determines the probability of C_i as

$$p_i = \exp(-\beta E_i) / Z(\beta) \quad (4.5)$$

with

$$Z(\beta) = \sum_{i=1}^r \exp(-\beta E_i). \quad (4.6)$$

To interpret this, set

$$t = -\beta. \quad (4.7)$$

Since the dimensions of E_i are $(\text{time})^{-1}$, the dimensions of the Lagrange multiplier t are those of time. Indeed, rewriting (4.5) and (4.6) in terms of t yields

$$p_i = \frac{\exp(E_i t)}{\sum_{j=1}^r \exp(E_j t)} \quad (4.8)$$

or

$$n_i = \frac{N \exp(E_i t)}{\sum_{j=1}^r \exp(E_j t)}. \quad (4.9)$$

It is instructive to compare (4.9) with a conventional solution of (4.2). The conventional solution uses the Ansatz

$$n_i = \frac{N x_i}{\exp \int_0^t E(\tau) d\tau}, \quad (4.10)$$

which leads to the linear equations

$$\dot{x}_i = E_i x_i. \quad (4.11)$$

In deriving (4.9), nothing was assumed to be known about the initial distribution of the n_i . The canonical ensemble model, maximizing the entropy $H(\xi)$, thus selects the maximum entropy initial distribution

$$n_i(0) = N/r, \quad (4.12)$$

i.e., $x_i(0) = r^{-1}$. With this initial condition, the conventional solution of (4.2) is

$$n_i = \frac{N \exp(E_i t)}{r \exp \int_0^t E(\tau) d\tau}. \quad (4.13)$$

Comparison with (4.9) yields the partition function

$$Z(t) = \sum_{j=1}^r \exp(E_j t) = r \exp \int_0^t E(\tau) d\tau. \quad (4.14)$$

As a potential, the thermodynamic potential (3.10) is determined only to within an additive constant. Using (4.14), one may thus express the “thermodynamic potential” in the present context as the “energy integral”

$$\Psi = \int_0^t E(\tau) d\tau. \quad (4.15)$$

By (4.4), $E(t)$ is the cull rate necessary to hold the total population constant. Thus (4.15) represents the total number of individuals lost to population control over the first t time units. The “Helmholtz free energy” (3.11) becomes the average cull rate

$$F = \frac{1}{t} \int_0^t E(\tau) d\tau \quad (4.16)$$

over the first t time units.

5. SPECIFIED INITIAL CONDITIONS

In solving (4.1) under unknown initial conditions, the canonical ensemble technique assumes the maximum-entropy initial distribution (4.12). However, the technique may be adapted to take account of precise knowledge of the initial values $n_i(0)$. Set

$$d = \text{gcd}\{n_i(0) | 1 \leq i \leq r\}, \quad (5.1)$$

the greatest common divisor of the initial quantities $n_i(0)$. The single species i , with its unconstrained growth rate E_i , may then be considered as

$$a_i = n_i(0) / d \quad (5.2)$$

distinct, equally numerous species i_1, \dots, i_{a_i} , each with unconstrained growth rate E_i . Let n_{ij} denote the size of the population ij . Then n_{ij} satisfies the equation

$$\dot{n}_{ij} = (E_i - E)n_{ij}. \quad (5.3)$$

Since

$$n_i = \sum_{j=1}^{a_i} n_{ij}, \quad (5.4)$$

the n_i satisfy (4.2). The initial condition $n_i(0) = a_i d$ then corresponds to a uniform initial distribution

$$n_{ij}(0) = d \quad (5.5)$$

for all the species ij . The canonical ensemble technique solves (5.3) as

$$n_{ij} = \frac{N \exp(E_i t)}{\sum_{i=1}^r a_i \exp(E_j t)}. \quad (5.6)$$

Using (5.4), one then obtains the solution

$$n_i = \frac{N n_i(0) \exp(E_i t)}{\sum_{j=1}^r n_j(0) \exp(E_j t)} \quad (5.7)$$

of (4.2) subject to known initial values $n_i(0)$. The partition function in this case is

$$Z(t) = \frac{1}{d} \sum_{j=1}^r n_j(0) \exp(E_j t) = \frac{N}{d} \exp \int_0^t E(\tau) d\tau. \quad (5.8)$$

The “thermodynamic potential” may again be taken to be given by (4.15), with the same interpretation as a count of culled individuals. Similarly, the “Helmholtz free energy” (4.16) is again interpretable as the average cull rate over the first t time units.

6. COMPETITION WITH MUTABILITY

In the presence of mutations, Eigen’s phenomenological rate equation for the case of constant overall organization $N = \sum_{i=1}^r n_i$ takes the form

$$\dot{n}_i = -E n_i + \sum_{j=1}^r A_{ij} n_j. \quad (6.1)$$

Positive off-diagonal terms A_{ij} of the $r \times r$ matrix A represent mutations from species j to species i . Assuming that the matrix A has r distinct real eigenvalues, the canonical ensemble technique provides a partial analysis of (6.1). To this end, it is helpful to rewrite (6.1) in vector-matrix form as

$$\dot{\mathbf{n}} = (A - E) \mathbf{n}. \quad (6.2)$$

Here, as usual, the scalar E is considered as the scalar matrix EI with I the $r \times r$ identity matrix. Let Q be an $r \times r$ matrix whose columns Q_j , for $j = 1, \dots, r$, are eigenvectors of A , say

$$AQ_j = \lambda_j Q_j, \quad (6.3)$$

ordered so that $\lambda_1 > \lambda_2 > \dots > \lambda_r$. Normalize the eigenvectors as follows. If $\sum_{i=1}^r Q_{ij} \neq 0$, choose Q_j with $\sum_{i=1}^r Q_{ij} = 1$. If $\sum_{i=1}^r Q_{ij} = 0$, choose Q_j with $\sum_{i=1}^r |Q_{ij}| = 1$ and with the first nonzero term of the sequence $Q_{1j}, Q_{2j}, \dots, Q_{rj}$ being positive. (This normalization of eigenvectors Q_j with $\sum_{i=1}^r Q_{ij} = 0$ is purely conventional.) Since the columns of Q form a basis of \mathbb{R}^r , there are unique scalar functions $m_1(t), \dots, m_r(t)$ such that

$$n = \sum_{j=1}^r m_j(t) Q_j. \quad (6.3)$$

This expression is to be contrasted with the expression

$$n = \sum_{j=1}^r n_j(t) I_j \quad (6.4)$$

of the vector n as a linear combination of the columns I_j of the identity matrix I . The column I_j represents one individual of the species j . By analogy, the column Q_j of Q will be considered to represent one individual of *virtual species* j . (In the present context, the virtual species are candidates for the concept of "environ" as discussed by Patten [7]). Consider a population determined by a vector n . According to (6.4), it can be described by the presence of n_j individuals of species j . According to (6.3), it could then equally be described by "the presence of m_j individuals of virtual species j ." It is this latter description that facilitates application of the canonical ensemble technique. The virtual species j is said to be *substantial* if and only if $\sum_{i=1}^r Q_{ij} \neq 0$, i.e., if and only if $\sum_{i=1}^r Q_{ij} = 1$ according to the normalization. Now substitution from (6.3) into (6.2) gives

$$\begin{aligned} \sum_{j=1}^r \dot{m}_j(t) Q_j &= \dot{n} = (A - E)n \\ &= \sum_{j=1}^r m_j(t) (A - E) Q_j \\ &= \sum_{j=1}^r m_j(t) (\lambda_j - E) Q_j. \end{aligned}$$

Equating coefficients of Q_j yields

$$\dot{m}_j = (\lambda_j - E)m_j \tag{6.5}$$

for each virtual species j . On the other hand, substitution from (6.3) into the constraint

$$N = \sum_{i=1}^r n_i \tag{6.6}$$

of constant overall organization gives

$$N = \sum_{i=1}^r n_i = \sum_{i=1}^r \sum_{j=1}^r m_j(t) Q_{ij} = \sum_{j=1}^r m_j(t) \sum_{i=1}^r Q_{ij}$$

or

$$N = \sum'_j m_j, \tag{6.7}$$

where \sum'_j denotes summation restricted to substantial virtual species j . The insubstantial virtual species make no contribution to the overall organization. The reduction performed for the case of r distinct real eigenvalues of A may be summarized as follows.

THEOREM

Eigen's phenomenological rate equation for the evolution of species in the presence of mutation, and subject to constant overall organization N , yields the phenomenological rate equation for the evolution of substantial virtual species in the absence of mutation, subject to the same constant overall organization N .

The equation for the evolution of the substantial virtual species in the absence of mutation can then be analyzed by the canonical ensemble technique, as discussed in previous sections. In particular, it should be noted that the dominant virtual species 1 is substantial if the nonnegative matrix $B = A - I \min\{A_{ii} | A_{ii} < 0, 1 \leq i \leq r\}$ is *primitive* in the sense of Birkhoff [8]. Indeed, the matrices A and B have the same eigenvectors, and the Perron-Frobenius Theorem ([8], Theorem XVI. 4.5) shows that B has a positive dominant eigenvector.

7. TWO EXAMPLES

To help fix the ideas of the previous section, it is useful to work through a couple of examples. First, consider the equations

$$\dot{n}_1 = 18n_1 + 9n_2 - E(t)n_1, \quad (7.1a)$$

$$\dot{n}_2 = 18n_1 + 14n_2 + 10n_3 - E(t)n_2, \quad (7.1b)$$

$$\dot{n}_3 = 5n_2 + 10n_3 - E(t)n_3. \quad (7.1c)$$

The virtual species are $\mathcal{Q}_1 = [3/8, 4/8, 1/8]^T$ with unconstrained growth rate (eigenvalue) 30, $\mathcal{Q}_2 = [-3/4, 2/4, 5/4]^T$ with eigenvalue 12, and $\mathcal{Q}_3 = [1/4, -2/4, 1/4]^T$ with eigenvalue 0. The first two virtual species are substantial, whereas \mathcal{Q}_3 is not. Equations (7.1) for the counts n_i ($i = 1, 2, 3$) of species i reduce to the equations

$$\dot{m}_1 = 30m_1 - E(t)m_1, \quad (7.2a)$$

$$\dot{m}_2 = 12m_2 - E(t)m_2 \quad (7.2b)$$

for the counts m_j ($j = 1, 2$) of the substantial virtual species j . Virtual species 1 is dominant; i.e., the ultimate proportions of species 1, 2, 3 are 3:4:1. The behavior of (7.1) is best summarized with the aid of Figure 1, where the coordinates (p_1, p_2, p_3) are barycentric coordinates representing the relative mixes of species 1, 2, 3. Physically realizable configura-

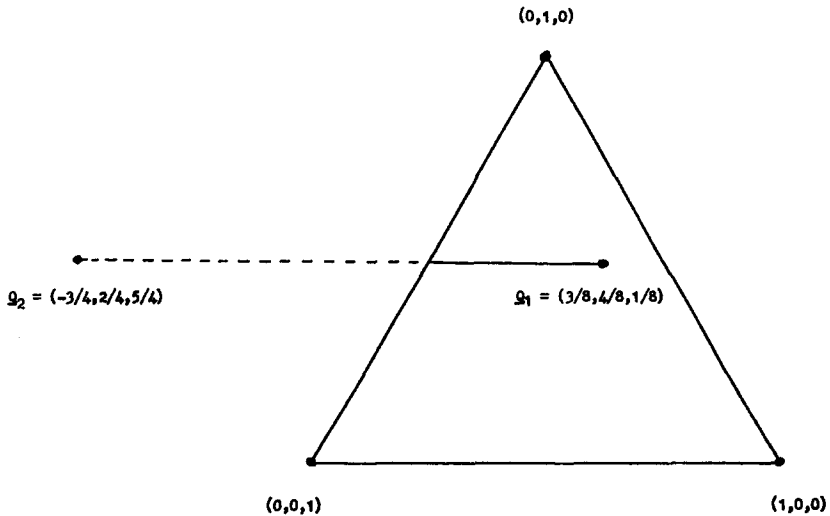


FIG. 1.

rations lie on the 2-simplex spanned by the corner points representing pure concentrations of the various species. Biologically viable configurations are restricted to the intersection of this 2-simplex with the 1-simplex spanned by the endpoints representing pure concentrations of the substantial virtual species. Whatever the original position within the 2-simplex of the point describing system (7.1), initial carnage will move it rapidly to the 1-simplex $\{(1-p)Q_1 + pQ_2 | 0 \leq p \leq 1/3\}$. The point will then drift gradually toward Q_1 . The insubstantial virtual species Q_3 represents a nonviable combination of species; and for this reason does not impinge on a canonical ensemble analysis of the system.

Now consider the equations

$$\begin{aligned}\dot{n}_i &= -D_i n_i + A_i n_{s+i} - E(t) n_i, \\ \dot{n}_{s+i} &= A_i n_i - D_i n_{s+i} - E(t) n_{s+i}\end{aligned}\quad (7.3)$$

for $i=1, \dots, s$, with $A_1 - D_1 > A_2 - D_2 > \dots > A_s - D_s > 0$. They are simple versions (without mutation) of the phenomenological equations for self-reproduction based on complementary recognition, as considered by Eigen [1 (§IV.2)] and by Thompson and McBride [2]. The virtual species are $Q_i = (1/2)I_i + (1/2)I_{s+i}$ and $Q_{s+i} = (1/2)I_i - (1/2)I_{s+i}$ for $i=1, \dots, s$. The Q_i are substantial, whereas the Q_{s+i} are not. For the purposes of canonical ensemble analysis, (7.3) reduces to

$$\dot{m}_j = (A_j - D_j) m_j - E(t) m_j \quad (7.4)$$

for $j=1, \dots, s$. The canonical ensemble technique describes the evolution of the combined populations of complementary pairs, in particular the eventual dominance of the master pair $\{1, s+1\}$, but does not concern itself with the differences between n_i and n_{s+i} represented by the insubstantial virtual species Q_{s+i} .

8. CONCLUSIONS

Application of the canonical ensemble model is not limited to equilibrium thermodynamics. With different units for the numerical quantities involved, the model yields solutions to the phenomenological rate equations for the case of constant total organization. These different uses of the model provide an exact correspondence between thermodynamic and biological parameters (contrasting with more formal analogies such as those of Demetrius [9]). The most striking of these corre-

spendences arises from the common interpretation of the Lagrangean multiplier β of (3.3) as an (inverted) temperature Θ (3.5) and as time t (4.7). Temperature is a statistical aggregate of (macroscopic parts of) a thermodynamic system. Similarly, the time parameter (4.7) is a large-scale statistical aggregate of evolving systems such as (4.2) and (6.5). It is qualitatively different from the local absolute Newtonian time inherent in Newton's dot notation in Equations (4.2) and (6.5).

If one's interests are primarily concerned with the use of the phenomenological rate equations in the biosciences, then one may naturally be inclined to question the need for an alternative approach such as that furnished by the canonical ensemble technique, given that "classical" analytic solutions have become available since the publication of Eigen's work. There are two aspects of the canonical ensemble approach that are particularly significant from this point of view. The first aspect is its ability to yield solutions to the equations without the assumption of known initial conditions. There are many contexts in biology where one engages in the study of an already existing, well-established system without having access to its initial state. A good mathematical model of such a system should not then have to have initial conditions imposed on it, because these would necessarily be artificial. The second relevant aspect of the canonical ensemble approach is its emphasis on the intrinsic time parameter (4.7), as opposed to the external, Newtonian time that more properly belongs to physics. This emphasis suggests the determination of the intrinsic "system age" of a natural system as an object of biological study. For example, one might envisage the ecosystem of a geographical area subject to occasional cataclysms such as major floods or forest fires. The system's intrinsic "clock" is restarted after each cataclysm, independently of the continuous passage of calendar time.

Preparation of the phenomenological equations with mutability for solution by the canonical ensemble technique focuses on the concept of virtual species; and in particular on the distinction between substantial and insubstantial virtual species. Virtual species appear to be the kind of "elementary particle" proposed by Patten [7]. Further clarification of the relative roles of substantial and insubstantial virtual species is called for.

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