Statistical Mechanics of Population

—— *The Lattice Lotka-Volterra Model* ——

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To derive the consequence of heritable traits of individual organisms upon the feature of their populations, the lattice Lotka-Volterra model is studied which is defined as a Markov process of the state of the lattice space. A lattice site is either vacant or occupied by an individual of a certain type or species. Transition rates of the process are given in terms of parameters representing the trait of an individual such as intrinsic birth and death and migration rate of each type. Density is a variable defined as a probability that a site is occupied by a certain type. Under a given state of a site the conditional probability of its nearest neighbor site being occupied by a certain type is termed environs density of the site. Mutual exclusion of individuals is already taken into account by the basic assumption of the lattice model. Other interaction between individuals can be taken into account by assuming that the actual birth and death and migration rates are dependent on the environs densities. Extending the notion of ordinary Malthusian parameters, we define Malthusians as dynamical variables specifying the time development of the densities. Conditions for the positive stationary densities and for the evolutional stability (ES) against the invasion of mutant types is given in terms of Malthusians. Using the pair approximation (PA), a simplest decoupling approximation to take account of spatial correlation, we obtain analytical results for stationary densities, and critical parameters for ES in the case of two types. Assuming that the death rate is dependent on the environs density, we derive conditions for the evolution of altruism. Comparing with computer simulation, we discuss the validity of PA and its improvement.

§ 1. Introduction

Since Lotka and Volterra[1] studied population dynamics of interacting species of organisms, their models have been considered as basis for ecological processes, and a number of studies have been done on them. Kerner[2] has shown that the Lotka-Volterra model (LVM), which is described by a system of differential equations, admits a Liouville's theorem and a universal integral of 'motion'. On this basis he tried to develop statistical mechanics of LVM introducing the concept of microcanonical and canonical ensembles as well as a notion of temperature to LVM. Extending Kerner's studies, Goel, Maitra and Montroll[3] gave a good review of such models of interacting populations. They tried to obtain salient properties of populations which are rather insensitive to initial conditions and details of assumptions.

In their 'statistical mechanical' treatment of population dynamics, they regarded LVM as a first principle. However, in Lotka-Volterra type model parameters specifying the dynamical system are given in terms of groups and not in terms of individuals. Namely, the growth rate of population of each species called Malthusian parameter is given in terms of the intraspecific and interspecific interaction, and not in terms of the trait of each individual of a species, such as viability, fecundity, motility, and social behaviors such as helping or attacking towards neighbors. In this sense their treatment is not fully statistical mechanical, but rather

phenomenological. Because the spirit of statistical mechanics is to derive the macroscopic properties of the set of many particles from assumed properties of each particle. For instance, statistical mechanics has tried to derive hydrodynamic equation of motion from the equations of motion of the constituent particles. Likewise, it is desirable to study the logical relationship between the property of the population and that of the individual organism which constitutes the population.

Meanwhile, since Hamilton[4] sought for an 'unbeatable strategy' for the sex ratio in the presence of local competition of mates, the concept of theory of games has stimulated the development of evolutionary ecology. Here, the unit of selection is an individual, or ultimately is a gene rather than a species of organisms as a whole. This unbeatable strategy is now called 'evolutionarily stable strategy' or ESS, which is the stability of the wild-type against the invasion of a mutant of the same species. The mathematical theory of evolutionary ecology was excellently reviewed by Maynard Smith.[5] They are trying to understand the population on the bases of the act of individual organisms. However, in usual treatises of ESS the effect has been neglected that the difference of the trait between the invader and the wild-type may subsequently cause the difference in their respective environments. Organisms of different type may tend to form different environments which affect their respective fitnesses. For instance, altruists may live in an environment where mutual helping act is more prevalent, which may facilitate the former to invade the population of egoists.

Generally, the area in which each individual lives during its life is much smaller than the whole region inhabited by the total population of species. In LVM the biological environment affecting the growth rate of each species is represented by a set of population numbers or global densities of coexisting species. However, in reality it should be the local density that directly affects the fitness of each individual, and if the relevant local population number is small as on the verge of invasion or extinction, stochasticity cannot be ignored. Therefore, in order to get proper understanding how the feature of a population depends on various traits of an individual, stochastic dynamical models must seriously be studied. In physics, in order to understand how the feature of matter depends on the nature of atoms and molecules statistical mechanics is needed beyond thermodynamics. Also in population biology, we consider it worthwhile to regard LVM not as a first principle but as a model to be derived from more basic assumptions about the individual, and to study the feature of population beyond LVM. Our approach is nothing but to study population dynamics as a many body problem of statistical mechanics.

In statistical mechanics, in order to reduce mathematical complexity of many body problems in the continuous space, the lattice space has been found useful. The lattice gas model was shown to have a close relationship with spin models of magnetism not only classically but also quantum mechanically.[6] The lattice model is amenable to computer simulation and is suited to get a unified understanding of nature.

In population genetics, Kimura[7] introduced 'stepping stone model' to study the decrease of genetic correlation with distance in a geographically structured population. Although his motive of study was not for the approximation of the continuous

space for which Malécot[8] had studied, in effect Kimura's model can be regarded as a lattice model in which a site may contain a fixed number of individual organisms. Using the stepping stone model a number of studies have been done on the effect of geographical structure for the genetic correlation in a species. But the effect of individual traits and interactions between individuals was not fully studied.

In dynamical epidemiology, Kermack and McKendrick[9] introduced 'SIR model' which deals with dynamics of the change of population densities of susceptibles S, that of infected I, and that of recovered R. This model can be looked upon as a kind of LVM. Because the density of either predator or infected cannot grow without prey or host, and S and R can be associated with two different states of the host or prey, and the time development of both models is given as a dynamical system. In order to incorporate the spatial non-uniformity of these densities, as is necessary to study the spatial spread of pathogens, diffusion terms have been added to the traditional SIR-type model.[10] This approach is useful, but the range of applicability of such diffusion-reaction type treatment of the spread of pathogens, as well as the biological meaning of diffusion constants are to be questioned. Before such deterministic approach, the problem of spatial structure had been introduced and studied by the Markov process of the state of the lattice space under the name of 'contact process'. Recently, rigorous results as well as simulation results have been accumulated on the contact process.[11]

In such studies of the contact process, however, it is usually assumed for simplicity that in the lattice space each site is occupied by an individual which is either healthy or diseased. However, survival and extinction of species of organisms as well as their invasion and coexistence are important especially for ecological and evolutionary biology. As a lattice version of LVM the inclusion of the vacant site is inevitable for such a problem. In order to overcome the mathematical difficulty coming from the increase of a number of possible states of a site, we study the use of a decoupling approximation as a general tool. It would be worthwhile to study the lattice model as a microscopic version of the Lotka-Volterra model with the effect of local environment of individuals, which the original LVM has not properly considered. The purpose of this thesis is to give an introduction toward such studies. Prior to our studies Tainaka[12] had introduced the lattice Lotka-Volterra model (LLVM) and pointed out some interesting spatial patterns at a phase transition. However, at a moment his study is restricted to a case of a special interspecific interaction and without vacant site, while our object is for more generality. Early versions of the present study were already published,[13] but their treatment was not so systematic.

In the following, we give in § 2 the definition and the evolution equation of LLVM. Introducing the concept of environs densities and Malthusians, we derive conditions for the stationary state and for evolutional stability. In § 3 we apply these conditions to study a single species case as a simplest example. We obtain the densities at a stationary state in terms of the birth and death and migration rate under a pair approximation, which is the doublet decoupling approximation. We obtain the critical condition for the sustenance of the population. In § 4 we study the stability of the stationary state against the invasion of a mutant. Here, we consider a case in

which the death rate of an individual depends on its environs densities, hoping that it will give an insight to the evolution of altruism. Finally, we discuss in §5 use of LLVM and of the decoupling approximation, comparing our analytical result with the result of computer simulation.

§ 2.   The Lattice Lotka-Volterra Model (LLVM) and Malthusians

Consider the infinite lattice space in which the state of each lattice site is $+$, $-$, or 0. The state $+$ or $-$ represents the site being occupied by an individual of $+$ type or $-$ type and 0 represents the vacant site. A generalization to the case in which there are more than two types is straightforward, so that in this paper we only consider the case of two types for simplicity. In an infinitesimal time interval δt, the state of each occupied site changes to 0 with probability $d_\sigma \delta t$ by death, where d_σ is the *death rate* of σ type ($\sigma \in \{+, -\}$). Assume that each site has z nearest neighbor (n.n.) sites. Each pair of n.n. sites of state $(\sigma, 0)$, which means that one is of state σ and the other is of state 0, undergoes duplicated migration with probability $(b_\sigma/z)\delta t$, and the state changes to (σ, σ). We call b_σ simply *birth rate* of σ, althouth b_σ represents a possible maximum birth rate which is attained when all the z n.n. sites are vacant. We consider that unless there is enough room for the child to live, a born child cannot successfully survive to an adulthood. The value of b_σ may depend on other environmental situations, but in the simplest case we assume that it is a constant inherent to the type of an organism. The above pair of n.n. sites also undergoes the change of state from $(\sigma, 0)$ to $(0, \sigma)$ with probability $(m_\sigma/z)\delta t$ due to migration without duplication. We call m_σ *migration rate*. If the individual has no motility like a plant, we may put $m_\sigma = 0$. Moreover, if there is a birth by parasitism or infection, as mainly treated in dynamical epidemiology, we may assume that $-$type corresponds to a parasite, pathogen, or an infected individual, and the birth of $-$type may occur by infection or transmission from the n.n. site. Namely, we assume inside the framework of our LLVM that the state $(-, +)$ of n.n. pair changes to $(-, -)$ with certain probability proportional to the infection rate. In this paper, however, we only consider the case of birth by duplicated migration, and the case of birth by infection will be treated in a separate paper.[14]

Let $\rho_\sigma(x, t)$ be the probability that the state of the site at $x \in Z^d$ (site x) is σ at time t, where Z^d denotes the d-dimensional lattice space. Let $\rho_{\sigma\sigma'}(xx', t)$ be the probability that the state of site x is σ and the state of site x' is σ' at time t, where x and x' represent n.n. sites. The variable $\rho_\sigma(x, t)$ represents the *density* of $\sigma(\in \{+, -, 0\})$ at (x, t). Let us call $\rho_{\sigma\sigma'}(xx', t)$ for $(\sigma, \sigma' \in \{+, -, 0\})$ *doublet density*. The ordinary density can be referred to as *singlet density* as well. In this paper we only consider the uniform case in which these densities are independent of the coordinates x and x', so that in the following we suppress writing the coordinates. In LLVM clustering property has an important role for population dynamics due to nearest neighboring interactions so that we introduce the following notations. Let $q_{\sigma/\sigma'}$ be the conditional probability that a randomly chosen nearest-neighbor of σ'-site is σ-site ($\sigma, \sigma' \in \{+, -, 0\}$). Let also $q_{\sigma/\sigma'\sigma''}$ be the conditional probability that under a condition that a nearest-neighbor of σ'-site is σ''-site, another randomly chosen nearest-

neighbor of σ'-site is σ-site $(\sigma, \sigma', \sigma'' \in \{+, -, 0\})$. When σ is not 0, let us call these conditional probabilities $q_{\sigma/\sigma'}$ and $q_{\sigma/\sigma'\sigma''}$ representing the density of the n.n. of the site under consideration *environs density* of the site. In contrast singlet and doublet densities in this paper will be referred to as *global densities*.

According to the assumption of birth and death and migration processes, the time development of the densities is given by

$$\dot{\rho}_\sigma = \{-d_\sigma + b_\sigma q_{0/\sigma}\}\rho_\sigma , \tag{2.1}$$

$$\dot{\rho}_{\sigma\sigma} = -2\{d_\sigma + m_\sigma(1-z^{-1})q_{0/\sigma\sigma}\}\rho_{\sigma\sigma}$$
$$+ 2[b_\sigma\{z^{-1} + (1-z^{-1})q_{\sigma/0\sigma}\} + m_\sigma(1-z^{-1})q_{\sigma/0\sigma}]\rho_{0\sigma} , \tag{2.2}$$

$$\dot{\rho}_{\sigma\bar{\sigma}} = -[(d_\sigma + d_{\bar{\sigma}}) + m_\sigma(1-z^{-1})q_{0/\sigma\bar{\sigma}} + m_{\bar{\sigma}}(1-z^{-1})q_{0/\bar{\sigma}\sigma}]\rho_{\sigma\bar{\sigma}}$$
$$+ (b_\sigma + m_\sigma)(1-z^{-1})q_{\sigma/0\bar{\sigma}}\rho_{0\bar{\sigma}} + (b_{\bar{\sigma}} + m_{\bar{\sigma}})(1-z^{-1})q_{\bar{\sigma}/0\sigma}\rho_{0\sigma} . \tag{2.3}$$

$$(\sigma, \bar{\sigma} \in \{+, -\}, \sigma \neq \bar{\sigma})$$

By definition we have

$$\rho_{\sigma\sigma'} = \rho_{\sigma'\sigma} = \rho_\sigma q_{\sigma'/\sigma} = \rho_{\sigma'} q_{\sigma/\sigma'} \qquad (\sigma, \sigma' \in \{0, +, -\}) \tag{2.4}$$

and

$$\rho_0 = 1 - \rho_+ - \rho_- ,$$

$$q_{0/\sigma} = 1 - q_{+/\sigma} - q_{-/\sigma} . \tag{2.5}$$

When Eq. (2.1) is written in a form:

$$\dot{\rho}_\sigma = M_\sigma \rho_\sigma , \qquad (\sigma \in \{+, -\}) \tag{2.6}$$

$$M_\sigma = -d_\sigma + b_\sigma q_{0/\sigma} . \tag{2.7}$$

M_σ is usually called Malthusian parameter of σ. Since here M_σ is not a constant parameter but generally a dynamical variable, let us call M_σ simply *Malthusian of σ*. Likewise, we call the variable $M_{\sigma\sigma'} = \dot{\rho}_{\sigma\sigma'}/\rho_{\sigma\sigma'}$ *Malthusian of $(\sigma\sigma')$* which is written as:

$$M_{\sigma\sigma} = -2\{d_\sigma + m_\sigma(1-z^{-1})q_{0/\sigma\sigma}\} + 2[b_\sigma\{z^{-1} + (1-z^{-1})q_{\sigma/0\sigma}\}$$
$$+ m_\sigma(1-z^{-1})q_{\sigma/0\sigma}]q_{0/\sigma}/q_{\sigma/\sigma} \tag{2.8}$$

and

$$M_{\sigma\bar{\sigma}} = -[(d_\sigma + d_{\bar{\sigma}}) + m_\sigma(1-z^{-1})q_{0/\sigma\bar{\sigma}} + m_{\bar{\sigma}}(1-z^{-1})q_{0/\bar{\sigma}\sigma}]$$
$$+ (b_\sigma + m_\sigma)(1-z^{-1})q_{\sigma/0\bar{\sigma}}q_{0/\sigma}/q_{\sigma/\bar{\sigma}}$$
$$+ (b_{\bar{\sigma}} + m_{\bar{\sigma}})(1-z^{-1})q_{\bar{\sigma}/0\sigma}q_{0/\sigma}/q_{\bar{\sigma}/\sigma} . \tag{2.9}$$

Thus, Malthusians are given in terms of environs densities, and specify the growth of the global densities. In the stationary state with a positive density, the corresponding Malthusian must vanish.

We note from (2.4), (2.6) and the definition of Malthusian of $(\sigma\sigma')$ that

$$\dot{\rho}_{\sigma\sigma'} = \dot{\rho}_\sigma q_{\sigma'/\sigma} + \rho_\sigma \dot{q}_{\sigma'/\sigma} = (M_\sigma q_{\sigma'/\sigma} + \dot{q}_{\sigma'/\sigma})\rho_\sigma = M_{\sigma\sigma'}\rho_\sigma q_{\sigma'/\sigma} . \qquad (2\cdot10)$$

Thence, we obtain for $\rho_\sigma > 0$:

$$\dot{q}_{\sigma'/\sigma} = (M_{\sigma\sigma'} - M_\sigma)q_{\sigma'/\sigma} . \qquad (2\cdot11)$$

When the density ρ_σ of σ is infinitesimal, its time derivative is also infinitesimal according to $(2\cdot6)$ and $(2\cdot7)$. On the other hand, the time derivative of environs density $q_{\sigma/\sigma}$ is not infinitesimal but finite according to $(2\cdot11)$, $(2\cdot7)$ and $(2\cdot8)$. Note that even when $q_{\sigma/\sigma}$ is infinitesimal, the product $M_{\sigma\sigma}q_{\sigma/\sigma}$ becomes finite so long as $b_\sigma > 0$, due to a finite positive term $b_\sigma z^{-1}q_{0/\sigma}$. When the environs density $q_{\bar{\sigma}/\sigma}$ is finite positive, as is supposed usual for finite positive $\rho_{\bar{\sigma}}$, its time derivative is also finite according to $(2\cdot11)$, $(2\cdot7)$ and $(2\cdot9)$.

Therefore, on the verge of invasion or extinction of σ type, where its density ρ_σ is close to 0, the environs density $q_{\sigma'/\sigma}$ will reach a stationary state before the global density significantly changes. Thus, the environs density is a fast variable and the global density is a slow variable when the latter is infinitesimal. Then, we must have from $(2\cdot11)$ for $0 < \rho_\sigma \ll 1$:

$$M_{\sigma\sigma} = M_\sigma . \qquad (2\cdot12)$$

In addition if $\rho_{\bar{\sigma}} > 0$ we must have

$$M_{\sigma\bar{\sigma}} = M_\sigma . \qquad (2\cdot13)$$

It is to be noted that these equations hold in the low density limit $\rho_\sigma \to 0$, whether the population is stationary or not. Therefore, the condition for the invadability and sustainability of the σ type is given by

$$M_\sigma > 0 \qquad (2\cdot14)$$

together with $(2\cdot12)$ and $(2\cdot13)$.

Consider a population consisting only of $+$ type organisms and assume that it is in a stationary state with positive densities. Then, the following condition must be satisfied:

$$M_{++} = M_+ = 0 . \qquad (2\cdot15)$$

Here, we ask if few individuals of different type, say $-$type organisms appear in the population what will happen? Since the density ρ_- is very small at this moment, if the conditions

$$M_{--} = M_{+-} = M_- < 0 \qquad (2\cdot16)$$

are satisfied together with $(2\cdot15)$, then the density of $-$type will tend to 0 as time goes on and the original stationary state will persist; in other words, the stationary state is evolutionarily stable (ES).

If the stationary state is not ES, ultimately either the $+$type population goes to extinction, or both types coexist in the population. If the coexisting population ultimately reaches the stationary state, we must have:

$$M_{\sigma\sigma'}=M_\sigma=0 . \quad (\sigma, \sigma'\in\{+, -\}) \tag{2.17}$$

Thus, we have derived conditions for the sustainability, invadability and stationary state of a population in terms of Malthusians. Malthusians are given as a function of environs densities as variables and birth and death and migration rates as parameters. If the environs densities are known, then the global densities can be obtained by using (2·4) and (2·5). However, the number of unknown variables is generally larger than the number of equations.

For example, from $M_+=0$, we have rigorously

$$q_{0/+}=d_+/b_+ \tag{2.18}$$

at the stationary state of the population containing $+$ type organism. But we cannot determine the stationary density ρ_+ by (2·15), (2·8) and (2·5), since there 4 independent variables are involved against 2 independent equations. Therefore, in order to get useful results from the knowledge of Malthusians some approximations are necessary. We shall study it in the following sections.

§ 3. Single species case or lattice logistic model (LLM)

As a simplest case of LLVM let us consider single species of organisms, so that the state of a site is either $+$ or 0. Without loss of generality we set death rate $d_+ =1$, which means that an average lifetime of the organism is taken as a unit of time. We suppress writing suffix $+$ when no confusion is supposed to occur. We put

$$p\equiv q_{+/+} , \quad q\equiv q_{+/0} . \tag{3.1}$$

By (2·4) and (2·5) we have

$$\rho\equiv\rho_+=q/(1-p+q) . \tag{3.2}$$

In order to obtain the stationary density by (2·7), (2·8) and (2·15), we approximate:

$$q_{\sigma/\sigma'\sigma''}\cong q_{\sigma/\sigma'} . \tag{3.3}$$

We call this approximation *pair approximation* (*PA*) or *doublet decoupling approximation* (*DDA*). The decoupling approximation is based on the intuition that the effect of the second neighbor site will be less important than that of the nearest neighbor site. We shall discuss in § 5 the range of applicability of PA and its improvement by comparing with the result of computer simulation.

Using PA (3·3), Malthusians given by (2·7) and (2·8) become

$$M_+=-1+b(1-p) , \tag{3.4}$$

$$M_{++}=-2\{1+m(1-z^{-1})(1-p)\}+2[b\{z^{-1}+(1-z^{-1})q\}$$
$$+m(1-z^{-1})q](1-p)/p , \tag{3.5}$$

where we put $b\equiv b_+$ and $m=m_+$.

Now, from (2·15) we obtain the following stationary environs densities:

$$q_{+/+} = p = 1 - b^{-1},\tag{3.6}$$

$$q_{+/0} = q = \frac{(1-b^{-1})\{1+(1-z^{-1})\tilde{m}\} - z^{-1}}{(1-z^{-1})(1+\tilde{m})},\tag{3.7}$$

where we put $\tilde{m} \equiv m/b$. Thence, we obtain the stationary global density using (3.2):

$$\rho = \frac{(1-b^{-1})\{1+(1-z^{-1})\tilde{m}\} - z^{-1}}{(1-z^{-1})(1+\tilde{m}) - b^{-1}z^{-1}}.\tag{3.8}$$

For finite migration rate the global density ρ is smaller than the environs density p of the occupied site and is larger than the environs density q of the vacant site. In the infinite migration rate limit all the three densities become equal as in LVM. Thus, the Lotka-Volterra model corresponds to the infinite migration rate case of the lattice Lotka-Volterra model.

Consider the low density limit: $\rho \to 0$, where the environs density q tends to 0 by (3.2), and Malthusians (3.4) and (3.5) tend to the limit:

$$M_+^0 = -1 + b(1-p),\tag{3.9}$$

$$M_{++}^0 = -2\{1+m(1-z^{-1})(1-p)\} + 2bz^{-1}(1-p)/p,\tag{3.10}$$

Setting $M = M_+^0 = M_{++}^0$, we obtain for $|M| \ll 1$:

$$M = \frac{2\left\{1+\tilde{m}(1-z^{-1}) - \dfrac{z^{-1}}{1-b^{-1}}\right\}}{1 + \dfrac{2z^{-1}b^{-1}}{(1-b^{-1})^2}}.\tag{3.11}$$

For $M=0$, we have

$$b = b_c \equiv \frac{1+\tilde{m}(1-z^{-1})}{(1-z^{-1})(1+\tilde{m})}.\tag{3.12}$$

If $b > b_c$, then the population is sustained, since $M_+^0 = M > 0$, even when ρ happens to approach 0. On the other hand, for $b < b_c$, we have no stationary positive environs density in view of (3.7), and $M < 0$ for $\rho \to 0$. Thus, b_c is the critical birth rate for sustenance of the population. Note that b_c is a decreasing function of the relative migration rate $\tilde{m}$, and that the corresponding critical environs density $p_c = q_{+/+}$ is given using (3.6) by

$$p_c = \frac{z^{-1}}{1+\tilde{m}(1-z^{-1})}.\tag{3.13}$$

So far we have considered only the case in which all the organisms are of the same type. The model is just the lattice version of the so-called logistic model, which is a special case of LVM. In the next section we consider the invasion of a mutant type in the stationary population of a wild type.

§ 4. Evolutional stability of a stationary population

In the preceding section we have assumed that the death rate d_σ is a constant, so

that by taking an average lifetime as a unit of time we have set d_σ at 1 without loss of generality. However, in the presence of social interaction between organisms such as helping or attacking of animals or allelopathy of plants, the death rate may depend on the environs density.

To study the effect of such social interaction, let us assume as a simplest case that the death rate of an organism at site x is given by

$$d_\sigma(x) = 1 - \beta_- z^{-1} n_-(x), \quad (\sigma \in \{+, -\}) \tag{4·1}$$

where β_- is a constant parameter inherent to $-$ type, and $n_-(x)$ is a number of nearest neighbor sites of x which are occupied by $-$ type. Here, mutants are of $-$ type and the wild type organisms are of $+$ type.

The assumption (4·1) means that the wild type makes no social interaction and the death rate depends only on the number of mutants of the n.n. sites. If $\beta_- > 0$, the mutant is a helper, because it decreases the death rate of its neighbor. The helper is benevolent, because it helps neighbors to live without discriminating their types. It is altruistic, because the helping reduces its fecundity by decreasing a number of n.n. vacant sites for sending its children. In spite of such altruism the mutant may invade by increasing their number, because a helper may enjoy a reduced death rate by having more helpers in its n.n. sites than non-helpers, since the child of a helper is also a helper by assumption and the child is likely to live in the neighborhood of its parent. Whether the invasion of such altruists can actually happen is a subtle problem and needs a detailed analysis. In the following we look into this problem by studying the invadability of the $-$ type into the stationary population of the $+$ type according to the formulation developed in § 2.

Now, using PA, we get the following Malthusians in the limit of low density of the mutant, $\rho_- \to 0$:

$$M_-^0 = -(1 - \beta p_- \phi_-) + b(1 - p_-), \tag{4·2}$$

$$M_{--}^0 = -2[1 - \beta\{z^{-1} + (1 - z^{-1})p_-\phi_-\}] + 2bz^{-1}(1 - p_-)/(p_-\phi_-), \tag{4·3}$$

$$M_{+-}^0 = -[(1 - \beta z^{-1}) + \{1 - \beta(1 - z^{-1})p_-\phi_-\}]$$
$$+ b(1 - z^{-1})\{q_+(1 - p_-)/(p_-\psi_-) + q_-(1 - p_+)/(p_+\psi_+)\}. \tag{4·4}$$

Here, we have assumed for simplicity no migration, $m = 0$, and type-independent birth rate $b_\sigma = b(\sigma \in \{+, -\})$. We have put $\beta \equiv \beta_-$, and

$$p_\sigma \equiv q_{+/\sigma} + q_{-/\sigma} = 1 - q_{0/\sigma}, \tag{4·5}$$

$$p_\sigma\phi_\sigma \equiv q_{\sigma/\sigma}, \quad p_\sigma\psi_\sigma \equiv q_{\bar\sigma/\sigma}, \quad \phi_\sigma + \psi_\sigma = 1, \tag{4·6}$$

$$q_\sigma \equiv q_{\sigma/0}. \tag{4·7}$$

Because of the identity:

$$\rho_+ p_+ \psi_+ = \rho_- p_- \phi_- \tag{4·8}$$

and

$$\rho_\sigma = \rho_0 q_\sigma / (1 - p_\sigma) \tag{4.9}$$

we have

$$Q \equiv \frac{q_+(1-p_-)}{p_- \psi_-} = \frac{q_-(1-p_+)}{p_+ \psi_+} \tag{4.10}$$

so that we can rewrite (4.4) as

$$M_{+-}^0 = -2 + \beta\{z^{-1} + (1-z^{-1})p_- \psi_-\} + 2b(1-z^{-1})Q . \tag{4.11}$$

Remembering (2.15) and (2.16), we can discriminate the invadability of $-$ type referring to the sign of $M \equiv M_-^0 = M_{--}^0 = M_{+-}^0$, which can be obtained by solving the following simultaneous equations for $X \equiv p_-$, $Y \equiv p_- \phi_-$ and M:

$$M = -1 + \beta Y + b(1-X) , \tag{4.12}$$

$$M = -2 + 2\beta\{z^{-1} + (1-z^{-1})Y\} + 2bz^{-1}(1-X)/Y , \tag{4.13}$$

$$M = -2 + \beta\{z^{-1} + (1-z^{-1})Y\} + 2b(1-z^{-1})q_+(1-X)/(X-Y) . \tag{4.14}$$

For $\beta = 0$ both types have just the same traits, so that we must have $M = 0$. Then, we get from (4.12)

$$X = 1 - b^{-1} , \tag{4.15}$$

so that p_- is equal to $p_+ = p$ which is given by (3.6). From (4.13) and (4.14) we obtain

$$Y = z^{-1} \tag{4.16}$$

using $q_+ = q$ in (3.7) for $\tilde{m} = 0$. This indicates that for $|\beta| \ll 1$, the probability $q_{-/-}$ that the n.n. of the mutant site is also a mutant site is close to z^{-1}.

Therefore, we can solve (4.12)~(4.14) within the accuracy of the first order of magnitude of β by putting

$$X = 1 - b^{-1} + \delta X = p + \delta X , \quad Y = z^{-1} + \delta Y , \tag{4.17}$$

$$M = \beta z^{-1} - b \delta X \tag{4.18}$$

and assuming that δX, δY are infinitesimal. We obtain after somewhat lengthy calculations:

$$\delta X = z^{-1}\{1 + (2-z^{-1})(2-p)^{-1}(p-p_d)\}(1-p)\beta ,$$

$$\delta Y = z^{-2}\{(2-z^{-1})(2-p)^{-1}(p-p_d) - 2(1-z^{-1})\}\beta/2 , \tag{4.19}$$

$$M = z^{-1}(2-z^{-1})(2-p)^{-1}(p_d-p)\beta , \tag{4.20}$$

where

$$p_d = 1 - \frac{z-1}{z(2z-1)} = \begin{cases} \dfrac{5}{6} & (z=2) \\[2mm] \dfrac{25}{28} & (z=4) \end{cases} \tag{4.21}$$

is the demarcation environs density below which ($p < p_d$) a helper ($\beta > 0$) is invadable,

and above which $(p > p_d)$ an attacker is invadable in view of $(4 \cdot 20)$.

It is to be noted from $(4 \cdot 18)$ and $(4 \cdot 20)$ that M is a decreasing function of p, because the benefit of helping $z^{-1}\beta$ is independent of p, whereas the cost of helping $b\delta X$ increases with p. By $(3 \cdot 13)$ the minimum environs density p_c for sustenance of the wild type population is z^{-1} in the present case. Then, it is also notable that the range of p in which a helper is invadable is considerably wider than that in which an attacker is invadable; the ratio of their widths is 2 for $z=2$, and 6 for $z=4$.

The evolution of social behaviors of animals has been much debated; especially on the evolutional origin of altruism. Since Hamilton[15] has proposed kin selection theory against the group selection theory of altruism, they have tended to pay more attention to the kin-discriminating aspects of seemingly altruistic behavior. We do not deny its importance, especially for strong altruism in eusociality in which individuals of some caste completely lose fecundity. However, in the case of weak altruism as we have considered here, the above result may suggest that the kin recognition is not necessarily vital for its evolution, but too high environs density tends to suppress it and promote egoism instead. Although we must consider other factors for discussing the evolution of altruism, it is beyond the scope of this paper, and we proceed to the next section to discuss the validity of PA on which our analytical study is based.

§5. Comparison of pair approximation (PA) with computer simulation

In order to check the validity of decoupling approximations, we compared the stationary values of ρ_+, $q_{+/0}$, $q_{+/+}$ for lattice logistic model calculated by pair approximation and that obtained by Monte Carlo simulations (Fig. 1). Note that singlet decoupling approximation (SDA), which approximates $q_{\sigma/\sigma'}$ simply by ρ_σ, corresponds to the logistic model without any spatial structure. Figure 1 indicates that the pair approximation, that is doublet decoupling approximation (DDA), gives more accurate approximation than SDA.

We expect that triplet decoupling approximation (TDA), in which time development of the triplet densities $\rho_{\sigma\sigma'\sigma''}(\sigma, \sigma', \sigma'' \in \{+, 0\})$ is described by environs densities of double sites $q_{\sigma/\sigma'\sigma''}(\sigma, \sigma', \sigma'' \in \{+, 0\})$, should give better agreement with the simulation than DDA or SDA does. Figure 1 shows that this is really the case.

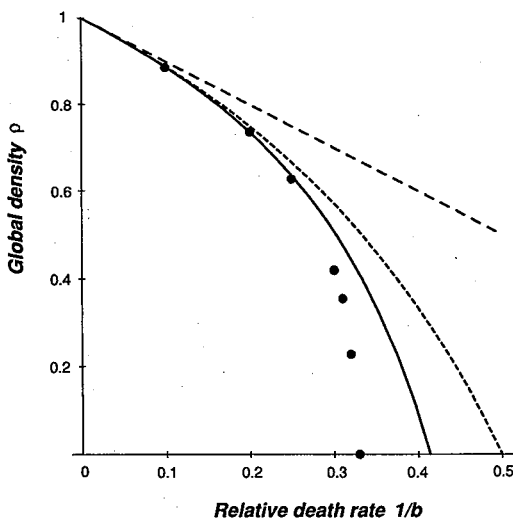As we can see in Fig. 1, DDA agrees

Fig. 1. Comparison of singlet density between singlet decoupling approximation (SDA), doublet decoupling approximation (DDA), triplet decoupling approximation (TDA) and Monte Carlo simulation.

Singlet densities are calculated by SDA, DDA and TDA. The simulation was conducted on the one-dimensional 10000 lattice torus for several values of b_+ with initial condition at $\rho_+=1$. Coarse dotted line, SDA; fine dotted line, DDA; solid line, TDA; circles, simulation.
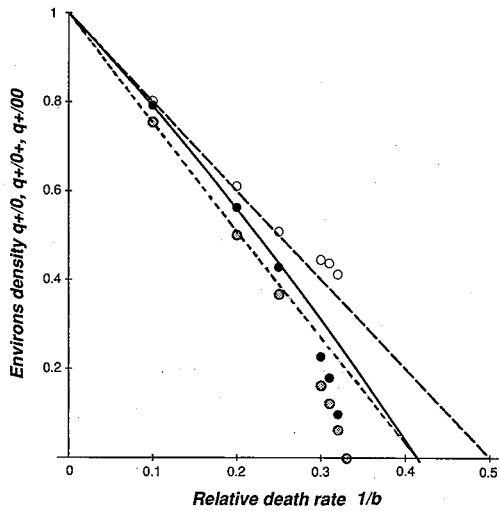
Fig. 2. Comparison between environs densities $q_{+/0}$, $q_{+/0+}$ and $q_{+/00}$ by TDA.

Differences between $q_{+/0}$, $q_{+/0+}$ and $q_{+/00}$ are shown. Curves are calculated by TDA. Solid line, $q_{+/0}$; coarse dotted line, $q_{+/0+}$; fine dotted line, $q_{+/00}$; filled circles, $q_{+/0}$; open circles, $q_{+/0+}$; gray circles, $q_{+/00}$. The condition for simulation is the same as in Fig. 1.
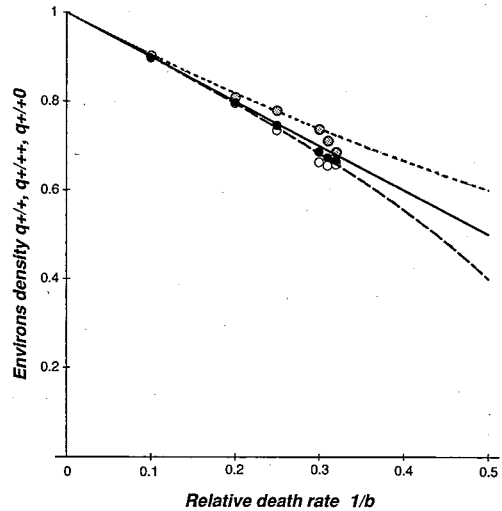
Fig. 3. Comparison between environs densities $q_{+/+}$, $q_{+/++}$ and $q_{+/+0}$ by TDA.

Differences between $q_{+/+}$, $q_{+/++}$ and $q_{+/+0}$ are not so significant compared to the ones between $q_{+/0}$, $q_{+/0+}$ and $q_{+/00}$. Curves are calculated by TDA. Solid line, $q_{+/+}$; coarse dotted line, $q_{+/++}$; fine dotted line, $q_{+/+0}$; filled circles, $q_{+/+}$; open circles, $q_{+/++}$; gray circles, $q_{+/+0}$. The condition for simulation is the same as in Fig. 1.

well at the high density of organism (say $\rho_+ > 0.5$), but not at low density. At the low density the difference between $q_{+/00}$ and $q_{+/0+}$ neglected in DDA will become serious, since even if $q_{+/00}$ approaches 0, $q_{+/0+}$ does not, reflecting the clustering property of organisms due to assumed nearest neighbor interactions. To improve this, we must incorporate triplet decoupling approximation (TDA).

Environs densities $q_{+/0+}$, $q_{+/00}$ calculated by TDA (see Appendix for the derivation) agree much better with that observed in Monte Carlo simulations (Fig. 2), and significantly differ from $q_{+/0}$ which is used in place of $q_{+/0+}$ and $q_{+/00}$ in DDA. It is notable that the difference between $q_{+/++}$ and $q_{+/+0}$ is relatively insignificant (Fig. 3). In regard of the comparisons between SDA, DDA and TDA, we expect that we can further improve approximation by increasing the order of decoupling.

§ 6. Conclusion

In our series of papers we have stressed the use of analogy between statistical physics and population biology. In the present paper we regarded individual organisms as constituents of a population, since the Lotka-Volterra model is primarily a model of population ecology and not of population genetics. However, from the mathematical point of view the constituent need not be an individual, nor the model need be considered only of ecology. It may be of population genetics and of dynamical epidemiology if we regard the constituent as a gene or a pathogen. In this sense,

such particle-like element of population biology may be termed 'replicon' broadly in its theoretical study. The vital property to be attached to the constituent element of population biology is that it undergoes birth and death with the law of heredity, besides its particle-like property. Particles as a constituent of matter behave independently of each other in the first approximation, and the interaction modifies their behavior; sometimes in a significant way. The variety of matter is disclosed in various environments under a given interaction characteristic to the constituent particles.

Owing to the action of birth and death with the law of heredity, the object of study of theoretical population biology can be much wider than that of statistical physics of matter. For instance, the latter has little to do with evolution nor to do with social or human science, whereas the former surely does, even though its extent is yet to be seen.

In this paper we have treated evolutional stability and the problem of altruism in a fashion of statistical mechanics. Corresponding to Hamiltonian in mechanics or in statistical physics, we have introduced the concept of Malthusian as a dynamical variable which specifies the dynamics of a population. By virtue of the notion of environs density, Malthusians can be given in terms of environs densities. Instead of starting from the deterministic dynamical system, we have set Markovian process as a first principle, because the biological system is inherently an open system, so that there is no reason to exclude stochasticity from the basic assumption. Thus, unlike the Hamiltonian dynamical system, our Malthusian dynamical system includes stochasticity in its background, which becomes apparent when the number of replicons become small as on the verge of invasion or extinction in a finite system.

As we have mentioned in Introduction, the Markovian lattice model has already been vigorously studied, and its scope is wider than the lattice Lotka-Volterra model studied here. For instance, the kinetic Ising model is one of typical examples of the Markovian lattice model, but we cannot reasonably associate the notion of Malthusian with it, because here the number of sites of a given state changes by the process of transition of state of each site without the process of reproduction. In contrast, in Malthusian dynamical system, without the process of reproduction a new state seldom appears; its appearance corresponds to a mutation process, but its rate is usually very small in reality. Thus, Malthusian dynamical system will have its common general feature distinguishing itself from other type of systems. The distinction of slow and fast variables on the verge of invasion, which we have shown in this paper, is one of such features. Our study has also indicated the use of decoupling approximation as a systematic approximation method. So far as we are aware, in contrast to the traditional study of statistical mechanics the study of approximation methods has been rather scarce in population biology. To have the systematic approximation method will be useful to know a global feature of a model and to give a good orientation in doing computer simulation to confirm the results.

There may be many possible directions toward which theoretical physics will progress. We hope that statistical mechanics of population as an extension of traditional statistical mechanics will be one of them.

Acknowledgements

Appendix

Here we derive several equilibrium values by triplet decoupling approximation (TDA). In contrast to doublet decoupling approximation (DDA), in which the time development of doublet densities in the system is considered, we must analyse master equations about triplet densities described as follows:

$$\dot{\rho}_{+++} = -3\rho_{+++} + b(1+q_{+/0+})\rho_{++0} + b\rho_{+0+},$$

$$\dot{\rho}_{++0} = -\{2+1/2b(1+q_{+/0+})\}\rho_{++0} + \rho_{+++} + 1/2b\rho_{+00} + 1/2b(1+q_{+/0+})\rho_{0+0},$$

$$\dot{\rho}_{+0+} = -(2+b)\rho_{+0+} + \rho_{+++} + bq_{+/00}\rho_{+00},$$

$$\dot{\rho}_{+00} = -\{1+1/2b(1+q_{+/00})\}\rho_{+00} + \rho_{++0} + \rho_{+0+} + 1/2bq_{+/00}\rho_{000},$$

$$\dot{\rho}_{0+0} = -\{1+b(1+q_{+/0+})\}\rho_{0+0} + 2\rho_{++0},$$

$$\dot{\rho}_{000} = -bq_{+/00}\rho_{000} + 2\rho_{+00} + \rho_{0+0}. \tag{1}$$

Note that $q_{\sigma/\sigma'\sigma''\sigma'''} = q_{\sigma/\sigma'\sigma''}$ in order to close these equations. Then using (1) we can get the time development of doublet densities:

$$\dot{\rho}_{++} = \dot{\rho}_{+++} + \dot{\rho}_{++0} = -2\rho_{++} + b(1+q_{+/0+})\rho_{+0},$$

$$\dot{\rho}_{+0} = (\dot{\rho}_{++0} + \dot{\rho}_{+0+} + \dot{\rho}_{+00} + \dot{\rho}_{0+0})/2 = -b/2(1+q_{+/0+})\rho_{+0} - \rho_{+0} + \rho_{++} + b/2q_{+/00}\rho_{00},$$

$$\dot{\rho}_{00} = \dot{\rho}_{+00} + \dot{\rho}_{000} = -bq_{+/00}\rho_{00} + 2\rho_{+0}. \tag{2}$$

Finally singlet densities change as follows from (2):

$$\dot{\rho}_{+} = \dot{\rho}_{++} + \dot{\rho}_{+0} = -\rho_{+} + bq_{+/0}\rho_{0},$$

$$\dot{\rho}_{0} = \dot{\rho}_{+0} + \dot{\rho}_{00} = -bq_{+/0}\rho_{0} + \rho_{+}. \tag{3}$$

From (1)~(3) we can get the following global densities and environs ones at equilibrium:

$$q_{+/0} = 1 - q_{0/0} = \frac{b^2 - 2b - 1}{b^2},\tag{4}$$

$$q_{+/0+} = 1 - q_{0/0+} = 1 - \frac{2}{b},\tag{5}$$

$$q_{+/00} = 1 - q_{0/00} = \frac{2(b^2 - 2b - 1)}{b(2b + 1)},\tag{6}$$

$$q_{+/+} = 1 - q_{0/+} = 1 - \frac{1}{b},\tag{7}$$

$$q_{+/++} = 1 - q_{0/++} = \frac{b(2b - 3)}{(b - 1)(2b + 1)},\tag{8}$$

$$q_{+/+0} = 1 - q_{0/+0} = 1 - \frac{2}{2b + 1},\tag{9}$$

$$\rho_+ = 1 - \rho_0 = \frac{b^2 - 2b - 1}{b^2 - b - 1}.\tag{10}$$

In Fig. 1 we use (10) as singlet density, in Fig. 2 (4)~(6) as environs densities around a vacant site and in Fig. 3 (7)~(9) as environs densities around an organism.

References

1) A. J. Lotka, J. Phys. Chem. **14** (1910), 271; Proc. Nat. Acad. Sci. U.S.A. **6** (1920), 410.
   V. Volterra, J. Cons. Perm. Int. Explor. Mer **3** (1928), 1; *Lecon sur la Theorie Mathematique de la Lutte pour le Vie* (Gauthier-Villars, Paris, 1931).
2) E. H. Kerner, Bull. Math. Biophys. **19** (1957), 121; Bull. Math. Biophys. **21** (1959), 217; Bull. Math. Biophys. **23** (1961), 141.
3) N. S. Goel, S. C. Maitra and E. W. Montroll, Rev. Modern Phys. **43** (1971), 231.
4) W. D. Hamilton, Science **156** (1967), 477.
5) J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge Univ. Press, Cambridge, 1982).
6) T. D. Lee and C. N. Yang, Phys. Rev. **87** (1952), 410.
   T. Matsubara and H. Matsuda, Prog. Theor. Phys. **16** (1956), 569.
   H. Matsuda and T. Tsuneto, Prog. Theor. Phys. Suppl. No. 46 (1970), 411.
7) M. Kimura and G. H. Weiss, Genetics **49** (1964), 561.
8) G. Malécot, *The Mathematics of Heredity* (W. H. Freeman and Company, San Francisco, 1969).
9) W. O. Kermack and A. G. Mckendrick, Proc. Roy. Soc. Ser. **A115** (1927), 700.
10) J. D. Murray, *Mathematical Biology* (Springer-Verlag, New York, 1989).
    S. Yachi, K. Kawasaki, N. Shigesada and E. Teramoto, Forma **4** (1989), 3.
11) A. M. De Roos, E. McCauley and W. G. Wilson, Proc. Roy. Soc. London **B246** (1991), 117.
    R. Durrett, Lecture Notes on Particle Systems and Percolation (Wadsworth & Brooks/Cole, California, 1988).
    R. Durrett and G. Swindle, Stoch. Proc. Appl. **37** (1991), 19.
    M. Katori and N. Konno, J. Phys. Soc. Jpn. **59** (1990), 877.
    N. Konno and M. Katori, J. Phys. Soc. Jpn. **59** (1990), 1581.
    T. M. Liggett, *Interacting Particle Systems* (Springer-Verlag, New York, 1985).
    D. Mollison, J. R. Statist. Soc. **B39** (1977), 283.
    T. Ootsuki and T. Keyes, Phys. Rev. **A33** (1986), 1223.
    K. Tainaka, J. Phys. Soc. Jpn. **57** (1988), 2588.
12) K. Tainaka and Y. Itoh, Europhys. Lett. **15** (1991), 399.
13) H. Matsuda, Prog. Theor. Phys. **66** (1981), 1078; *Animal Societies: Theories and Facts*, ed. Y. Itô, et al. (Japan Sci. Soc. Press, Tokyo, 1987), p. 67.
    H. Matsuda, N. Tamachi, A. Sasaki and N. Ogita, Lecture Notes in Biomathematics **71** (1987), 154.
14) K. Satō, H. Matsuda and A. Sasaki, submitted to J. Math. Biol.
15) W. D. Hamilton, J. Theor. Biol. **7** (1964), 1; *Animal Societies: Theories and Facts,* ed. Y. Itô, et al., (Japan Sci. Soc. Press, Tokyo, 1987), p. 81.