

ABSTRACTS

of

Theory of Biomathematics and Its Applications V

Jan 13-16, 2009

INVITED LECTURE

*Jan 15, 2009
13:30-14:30*

Evolution in a host-parasite system

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Some organisms employ multiple defence strategies against their enemies, while others fail to employ a defence that seems obvious. We shall investigate three questions for host-parasite systems.

- Under what circumstances does it pay for a host to employ a given defence strategy against one of its parasites?
- If alternative strategies are available, how is the appropriate strategy chosen?
- When is it appropriate to employ multiple defence strategies against an enemy?

We shall illustrate our results in two cases of brood parasites and their hosts. The paper by Britton *et al.* (2007) contains more background details on the basic model and the analysis, but the extensions to the model and some of the results are new.

Reference

N F Britton, R Planqué and N R Franks, Evolution of defence portfolios in exploiter-victim systems, *Bull. math. Biol.* **69**(3), 957–988, 2007.

MINI-SYMPOSIUM

Mathematical Modeling of Pattern Formation

*Jan 14, 2009
9:30-12:00*

Phase field approach to cell aggregations

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Models for describing cell aggregates are necessary to understand the cell collective behaviors and the morphogenesis mathematically. In order to describe cellular patterns, several models have been reported, such as cell center dynamics [1], vertex dynamics [2], topological dynamics [3] and boundary dynamics models [4]. However, in our knowledge, there are no models depicting the shape of each cell, the local distribution of chemicals in the cells and their collective behaviors.

Therefore, we developed a new type of cell model, which is based on the phase field model. The time evolution keeping the local distributions of chemicals in the cells is available. One of the advantages of our model is that one can perform the numerical simulations without using the large computational memories. Numerical results for the basic phenomena of cell systems such as the cell division, the chemotaxis, and the cell adhesion will be presented as well as the detail explanations for the model.

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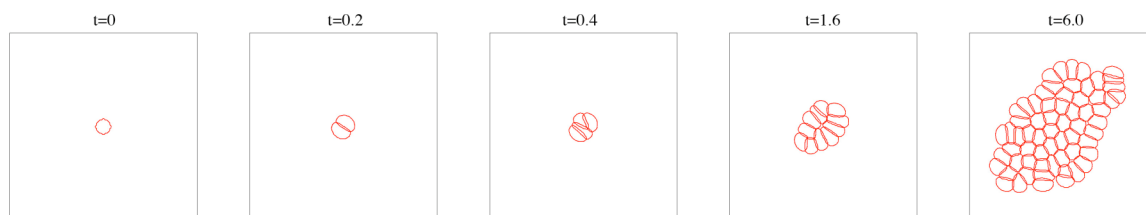


figure 1 : Cell divisions

Modeling lung branching morphogenesis

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Vertebrate lung has a tree-like structure. The structure is generated by repeated branching of epithelial tip during development, which is called branching morphogenesis. Many molecules are known to be involved in the formation of branches, but how the interaction of these molecules result in the formation of branch remain to be elucidated.

At first we choose the simplest possible experimental system that retain the ability to form branched structure. In this system, isolated lung epithelium in Matrigel forms a branched structure when culture medium is supplemented by fibroblast growth factor (FGF). We formulated this experimental system as two-species reaction-diffusion model, in which cells grows by consuming FGF molecule. According to the model, we could induce cyst-like pattern by increasing FGF concentration or facilitate FGF diffusion experimentally.

Next, we try to extrapolate the result to *in vivo* situation by examining avian lung development. Avian lung has both branched and cystic structure simultaneously during development, and we showed that the different FGF diffusion coefficient is responsible for the formation of cystic structure.

Despite all these efforts, the mechanism of branching morphogenesis *in vivo* remains to be elucidated. Mesenchyme tissue actively generates factors that influences branching morphogenesis, and changes shape according to the epithelial structure. It remains an open problem to extract the essential aspect of this complex phenomenon.

MINI-SYMPOSIUM

Mathematics of Population Dynamics

*Jan 14, 2009
14:40-17:10*

Linear Complementarity Problem and Stability of Lotka-Volterra Systems

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Abstract

The relationship between the linear complementarity problem and global stability (GS) of Lotka-Volterra systems is reviewed. Examples of the GS systems with interaction matrix belonging to P-matrix class are given. The case for the systems with nonlinear interactions is also discussed.

Key Words: linear complementarity problem, Lotka-Volterra equations, P-matrix, S_w .

References

- [1] Y. Takeuchi; Global Dynamical Properties of Lotka-Volterra Systems, World Scientific 1996.

Equilibrium structure of predator-prey systems determined by apparent competition

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A mathematical model for a system composed of multiple preys and a single predator is analyzed. In the system, preys indirectly compete with each other through a common predator. If there are no self-regulation in prey populations, competitive exclusion occurs and a single prey species dominates the system. On the other hand, if the predator is absent, the preys are decoupled and they definitely coexist. I will show that these two extreme cases help to understand the equilibrium structure of our intermediate case. In this analysis, a technique concerning complementarity problems and the index theorem for ecological systems are used to find a unique saturated equilibrium point. The generalization of these results is also discussed.

This is a joint work with Sebastian Schreiber, University of California, Davis.

Keywords: Competitive exclusion, Apparent competition, Complementarity problem, P-function

The competitive exclusion principle: a perspective of generalized epidemic model

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The competitive exclusion principle is one of the most interesting and important phenomena in the field of theoretical epidemiology and biology. We provide a strict and an elegant mathematical analysis related this phenomenon for an n -strain epidemic model by an average Lyapunov function theorem and some dynamical system theory. Further we can show that an equilibrium in which only the strain with the maximum basic reproductive number exists is globally asymptotically stable. This result was anticipated by Bremermann and Thieme in their 1989 paper where they showed that the equilibrium is locally stable — the global result has not been established previously.

Keywords: SIRS model; Competitive exclusion; Invasion problem; Globally asymptotically stable; Average Lyapunov function theorem

Models for competition in Immune system

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When n -different strains of virus infect a human body, there exists a competition of these strains for the resource, uninfected cells. If no immune response exists, only one strain whose basic reproductive ratio is largest persists. This is considered as an analogue of competitive exclusion in mathematical ecology. But it is shown in “Iwasa, Michor and Nowak, Some basic properties of immune selection, J. Theor. Biol. 229(2004)” that if there exist pathogen-specific immune responses, it becomes possible that more than one strains can coexist.

In this talk, we make an exposition of the above topic. We also introduce models by Inoue et. al. which incorporates infected cells and pathogens. When we use such models it is necessary to use Lyapunov functions which is originally considered in single strain model by Korobeinikov. We also make an exposition of Lyapunov functions of this type.

MINI-SYMPOSIUM

Mathematical Modeling of Life History Strategy

*Jan 15, 2009
9:25-12:15*

Optimal life-history models: why theoreticians should cooperate with empiricists

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I make an outline of the theoretical studies on optimal life history as an introduction of the satellite symposium entitled "Mathematical models for life history strategies". Under the premises that life history patterns observed in the field reflect a consequence of natural selection, evolutionary ecologists often attempt to seek the evolutionary cause, or ultimate mechanism of the focal phenotypic patterns. Apart from its proximate mechanism described by quantitative genetic models, the optimal life history (OLH) models provide us a significant perspective for understanding life history evolution. I briefly review how theoreticians construct and analyze OLH models by exemplifying the clines of optimal age and size at maturity along an environmental gradient, and then consider the relationship between theoretical and empirical works in life history evolution. It is strongly emphasized that empirical study is particularly needed for verifying premises that the model assumes rather than for checking the qualitative consistency between observation and model's prediction, when OLH models are constructed aiming to reveal the evolutionary causes of a particular life history pattern. Finally, I offer advice for accurately specifying the premises, classified into (1) fitness measures, (2) dependence and independence among traits, and (3) tradeoffs between life history components, and then refer to the importance of analyzing model's robustness to cope with the unknowable.

Resource dynamics and pollen-limitation can cause polymorphism of reproduction

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To investigate the evolution of reproductive behavior in perennial monoecious trees (e.g., oaks), we develop sex allocation models based on an extension of Satake & Iwasa's individual based model [1], including non linear resource dynamics and pollen-limitation. Our main assumptions are: 1) population size N is fixed, 2) distinguishing female flowering from fruiting, 3) random mating via wind pollination, 4) including large mutation step. The non-dimensionalized energy dynamics of an individual i ($i = 1, \dots, N$) is:

$$Y_i(t+1) = \begin{cases} Y_i(t) + 1 & \text{if } Y_i(t) \leq 0 \\ -R_c P(t)(1-r)Y_i(t) + 1 & \text{if } Y_i(t) > 0 \end{cases},$$

where $P(t) = ((1/N) \sum r[Y_i(t)]_+)^{-1}$ is the pollen efficiency, μ and R_c are positive constants, and r is an allocation ratio of the male flowering cost to the whole flowering cost. We define the invasion fitness $S_r(r')$ as long-term geometric mean of growth rate of a rare mutant, under the lottery process assuming all the empty sites will be filled instantly by offspring, described by:

$$S_r(r') = 1/T \sum_{t=1}^T \log \left[1 + \delta \left(\frac{1-r'}{2} \left(\frac{1-r}{1-r} + \frac{r'}{r} \right) \frac{[Y'(t)]}{\langle [Y_i(t)] \rangle_i} - 1 \right) \right],$$

where μ is the death rate of an individual.

Our results suggest that the fluctuating dynamics is favored for a considerably large parameter range together with a dimorphism of sex-ratio in population. In that case, according to the results of direct simulations, high r population shows an annual reproduction while low r population shows the diverse reproductive behaviors over time.

[1] Satake, A., Iwasa, Y., 2000. Pollen-coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *J. Theor. Biol.*, 203: 63-84.

Effect of stochasticity in visit of pollinator on resource allocation in a flower

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I develop a simple model to study the effect of the stochasticity in the availability of pollinator on evolutionarily stable (ES) resource allocation within a hermaphrodite flower of animal-pollinating plants. For simplicity, I consider trade-off in resource allocation between the attractive structure (petals etc.) and the female function (seeds and fruits) with neglecting the allocation to the male function (pollens and stamens).

I show that ES resource allocation does not much depend on the detail of the probability distribution of the number of pollinator visit on a flower, but on the probability that the flower fails to be visited.

I also find that:

- (1) When the flowers are self-incompatible, the ES allocation to the display monotonically increases as the availability of pollinators in the environment decreases.
- (2) When there is strong correlation among flowers in the number of pollinator visit, the ES allocation is larger than the case without the correlation.
- (3) When the flowers are self-compatible and engage prior selfing, the ES allocation monotonically increases as the availability of pollinators in the environment decreases to a threshold, under which it suddenly decreases to zero. Consequently, the ES allocation is a hump function of the effective selfing rate, rather than a monotonically decreasing function.

Evolution of overproduction of ovules: an advantage of selective abortion of ovules

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Overproduction of ovules within flowers, the production of ovules that are fertilized yet never become seeds, is widely observed in a variety of plants: many studies have reported seed:ovule ratios within flowers lower than 1. I developed two models to analyze the adaptive significances of overproduction of ovules.

In the first model, I reanalyzed the hypothesis that plants selectively abort ovules fertilized later to enhance the mean quality of resulting seeds, given that seeds fertilized with slowly growing pollen are of low quality genetically. I assumed that both superior and inferior pollen exist, the superior pollen growing faster to fertilize ovules, resulting in seeds of higher quality than those of ovules fertilized with inferior pollen. I found that, although selective abortion based on the order of fertilization can be advantageous, the parameter region favoring it is rather restricted. In addition, the degree of overproduction was low compared with that of natural plants.

In the second model, I hypothesized that it is advantageous for females to produce a uniform size of seeds, whereas it is advantageous for fertilized ovules to absorb more resources than this size. If there is a variance in resource absorption ability among fertilized ovules, non-uniform seeds are produced. Then, by overproducing ovules, females should select fertilized ovules with similar resource absorption rates, resulting in seeds of uniform size. A model analysis confirmed that this hypothesis works. In the model, the fertilized ovules of a plant consist of two genotypes which differ in resource absorption rate. I found that overproduction of ovules and selective abortion is advantageous if the difference in the resource absorption rates of the genotypes is large.

I hence concluded that the second model is likely as the factor selecting for overproduction of ovules.

Size dependent resource allocation with continuous growth in sedentary marine animals

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Sedentary marine animals, such as barnacles and parasitic marine bivalves, have diverse patterns of sexuality: simultaneous hermaphroditism, androdioecy (large hermaphrodites and dwarf males), dioecy (large females and dwarf males) and so on. We suggest that mating group size (MGS; the number of female-role individuals in a habitat) is an important factor to determine the sexual expressions. Individuals that constitute mating groups generally have size variation and resource allocation of each individual depends on its body size. We construct size dependent resource allocation model by incorporating resource acquisition exponent (α) and mortality (μ) as explanatory factors, where their body size changes continuously. The characteristic of our model is that the number of mating partners depends on body size of each individual, for example small individuals obtain fewer mating chances. We assume that all individuals may have potential to allocate their resources ($r(v)=v^\alpha$) to three usages (growth, male and female functions ($g(v)+m(v)+f(v)=1$), where v is the body size of individuals. However, these three resource usages do not coexist at the same time. That is, individuals allocate their resources to growth and male function ($g(v)+m(v)=1$) until they grow to a certain body size (called critical body size, v_c). On the other hand, those of body size v_c allocate their resources to male and female functions ($m(v_c)+f(v_c)=1$). As mortality (μ) increases and resource acquisition exponent (α) decreases, critical body size (v_c) becomes small and MGS is very small. In this case, dwarf males tend to appear and sexuality is androdioecy or dioecy. When mortality (μ) is small, critical body size (v_c) is large and MGS is large. In the latter case, sexual expression is simultaneous hermaphroditism.

MINI-SYMPOSIUM

Mathematics of Evolutionary Game Theory

*Jan 15, 2009
14:45-17:15*

Fixation probabilities in evolutionary game dynamics in finite diploid populations

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Fixation processes in evolutionary game dynamics in finite diploid populations are investigated. Traditionally, frequency dependent evolutionary dynamics is modeled as deterministic replicator dynamics. This implies that the infinite size of the population is assumed implicitly. In nature, however, population sizes are finite. Recently, stochastic processes in finite populations have been introduced in order to study finite size effects in evolutionary game dynamics.

One of the most significant studies on evolutionary dynamics in finite populations was carried out by Nowak et al (*Nature* 428). In their study, a natural definition of an advantageous mutation in a finite population was introduced by comparing the fixation probability of a mutant strategy with that of a neutral strategy. If the probability that the descendant of a single strategy α mutant invading a population of $(N - 1)$ strategy β individuals takes over the entire population is higher than the corresponding probability for the case of a neutral mutant, strategy α is advantageous. Further, it is shown that under weak selection, if the fitness of an α individual is higher than that of a β individual when the frequency of α individuals is $1/3$, strategy α is advantageous. This is called the “one-third law”.

In their study, it is assumed that the inheritance of strategies is asexual, i.e., the population is haploid. In this study, we apply their framework to a diploid population that plays a two-strategy game. In diploid populations, each individual has two homologous copies of each chromosome – one from its mother and the other from its father. We assume that there exist two alleles A and B on a single locus. Therefore, there are three genotypes AA , AB , and BB . Consider a process in which a pair of individuals – a male and a female – is chosen as parents for reproduction in proportion to their fitnesses, and their offspring replaces a randomly chosen individual. We assume that the individuals interact with each other through a game and that the genotype of the locus determines the strategy of the game. The fitness of an individual is determined through the game. The fixation probability of mutant allele A is defined as the probability that a population consisting of $(N - 1)$ genotype BB individuals and a genotype AB individual is eventually taken over by genotype AA individuals.

The fixation probability of a mutant allele in this diploid population is derived. Similar to the “one-third law” for a haploid population, there are several laws of criterion for the determination of advantageous mutant alleles. A “three-tenth law” for a completely recessive mutant allele and a “two-fifth law” for a completely dominant mutant allele are found; other cases are also discussed.

Evolution of male mating preference

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Theoretical and empirical research on sexual selection has mainly addressed decorative male traits and female preferences for such traits. However, there is increasing evidence of male mate choice for female traits in many species. Why do such male mating preferences evolve and how do they affect the evolution of female traits?

Several mathematical models of sexual selection of a male trait and a female preference have been proposed to reveal that the male trait and the female preference can sometimes coevolve. However, these models do not apply without modification to the case of a female trait and a male preference because of differences between the sexes, in particular because the fertility of a female is limited more by physiological constraints than her popularity (the number of males she attracts). Moreover, male preference may be costly. When many males are attracted to a particular female trait, such males are less likely to mate because attractive females have many candidates for a mate. So, a frequency dependent selection may act on male preference, which is a similar situation to evolutionary game theory.

I develop quantitative genetic models of a female trait and a male preference to show that a disagreement between the fertility maximum and the viability maximum of the female trait is necessary for directional male preference (preference for extreme female trait values) to evolve. Strong male preference can evolve when the popularity of a female has large effect on the number of her progeny that can reach maturity. I also show that males evolve to exhibit a stronger preference for females that are more feminine (less resemblance to males) than the average female when there is a sexual dimorphism caused by fertility selection which acts only on females.

Mutation-selection balance in n -strategy games

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We study a mutation-selection-balance equilibrium of general $n \times n$ matrix games. We consider the Moran process; in each update step a player is chosen for reproduction proportional to payoffs in the game, then he replaces one random player with his offspring. With probability u , a mutation occurs to the newborn. In this case he adopts one of the n strategies randomly. A strategy is favored by this selection-mutation process iff its equilibrium abundance is greater than the average, $1/n$. We find a surprisingly simple condition that specifies which strategies are favored. The condition is linear in mutation probability, u . Our results hold for weak selection limit, but for any mutation probability.

Spatial dynamics of cooperation and spite by conformist transmission

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Conformism is a type of social learning in which a learner tends to adopt a behavior which is played by the majority. Conformism is widely observed in human decision making. Consider a population of players who play two-strategy game. Assume that each player reconsiders and updates its strategy more likely when the current payoff is lower. In the reconsideration, the player surveys the other players' behaviors and copies it with conformism. In other words, we consider score-dependent social learning. We first derive the ODE for the frequency dynamics of the two strategies. Without conformism, it reproduces a replicator equation. If conformism exists, the weaker strategy (which is invaded by the other strategy in classic ESS analysis) can be locally stable. Second, we apply our results to public goods games, where investors modify the population average payoff but investors are vulnerable to the invasion of non-investors because investment is costly. Both the domination of investors and that of non-investors can be locally stable due to conformism. The system is bistable, but the basin of attraction of investor equilibrium is always small, independent of the efficiency of investment. Finally, we introduce spatial structure where players randomly move around and perform conformist transmission locally. The model is described by a scalar reaction diffusion equation. We show the existence of a traveling wave solution (TWS) that connects investor equilibrium and non-investor equilibrium. We also show that investor strategy will spread if and only if the efficiency of investment is negative. In other words, cooperation cannot spread but spiteful behavior can spread if conformism is strong, cost of investment is small, or the efficiency of spiteful behavior is strong. We also derive the analytic expression of the condition for spiteful behavior to spread.

CONTRIBUTED TALKS

The Walking Control on Drug-induced Locomotor Activity in Mice

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Cocaine is famous psychomotor stimulants that increases locomotor activity, elevates mood with rewarding euphoria and produces fearful and jittery aversive. However, the behavioral effects in the psychomotor activity are still remained unclear.

We have investigated the effect of cocaine on the mouse locomotor activity. A mouse freely walked around in the circular field 60cm in diameter, with the wall 40cm high. The mouse walk was recorded in the digital video camera, and it was taken into a personal computer as a movie file. After converting the movie file into sequential image file at 30 frames/sec, the centroid and n -th image moments were calculated.

The cocaine-applied mice showed higher activity during walking movement and with the walk in the central area of the field than the saline-applied control mice. We will also discuss the behavioral characters of cocaine-applied mice by using mathematical model.

Word-of-mouth versus mass media in rumor transmission

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Rumor transmission is considered as a social phenomenon that a remark spreads on a large scale in a short time through chain of communication. Its mathematical models, most of which are similar to the models describing the spread of infectious diseases because word-of-mouth and infectious diseases have much in common, have been constructed and investigated since the 1950s. They contain deterministic models expressed in terms of ODE or PDE system. On the other hand, the effect of outside source, mass media for example, can have a considerable effect on rumor transmission, although it is not taken into consideration in most of the existing rumor transmission models. For example, while many people, getting more conscious of global warming, take measures to it, some researchers voice on skepticism for it through mass media so extensively that the number of people who agree with the reserchers' skepticism is gradually increasing.

Here we discuss the effect of mass media on rumor transmission. For example, we report that, depending on parameters, supercritical bifurcation or subcritical bifurcation can occur in the following model:

$$\begin{cases} \dot{X}(t) = -\alpha X(t) \frac{Y(t)}{N(t)} - \delta X(t) \frac{Z(t)}{N(t)} + \eta_1 Y(t) + \eta_2 Z(t) - pX(t), \\ \dot{Y}(t) = \alpha X(t) \frac{Y(t)}{N(t)} - \gamma Y(t) \frac{Z(t)}{N(t)} - \eta_1 Y(t) + pX(t) + qZ(t), \\ \dot{Z}(t) = \gamma Y(t) \frac{Z(t)}{N(t)} + \delta X(t) \frac{Z(t)}{N(t)} - \eta_2 Z(t) - qZ(t), \end{cases}$$

where

$X(t)$: the number of susceptibles at time t ,

$Y(t)$: the number of spreaders at time t ,

$Z(t)$: the number of active stiflers at time t ,

$N(t) = X(t) + Y(t) + Z(t)$: the total population at time t ,

the effect of word-of-mouth is represented by parameters α , γ , δ , that of mass media p , q , and that of rumor modification η_1 , η_2 .

Analysis of network structure of a family tree

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Structure of a family tree of species with sexual reproduction is analyzed from the view point of network. The biparental individual including human beings has two parents, i.e., a father and a mother. Number of ancestors of each individual, therefore, increases exponentially, 2^G for past G generation and easily exceeds the total population size at that era. To resolve this paradox, some ancestors inevitably play multiple roles in the list of one's ancestors. This repetition is exhibited by a complex structure of ones genealogical tree, i.e., a diagram of individuals and connections between them which represent a parent-child relation. Structure of an ancestral tree and a similarity of two trees are analyzed for actual family tree of race horse. Comparison between simple model suggested by Derrida et al. is also exhibited.

Paradox of vaccination: is vaccination really effective against avian flu epidemics?

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Background

Although vaccination can be a useful tool for control of avian influenza epidemics, it might engender emergence of a vaccine-resistant strain. Field and experimental studies show that some avian influenza strains acquire resistance ability against vaccination. We investigated, in the context of the emergence of a vaccine-resistant strain, whether a vaccination program can prevent the spread of infectious disease. We also investigated how losses from immunization by vaccination imposed by the resistant strain affect the spread of the disease.

Methods and Findings

We designed and analyzed a deterministic compartment model illustrating transmission of vaccine-sensitive and vaccine-resistant strains during a vaccination program. We investigated how the loss of protection effectiveness impacts the program. Results show that a vaccination to prevent the spread of disease can instead spread the disease when the resistant strain is less virulent than the sensitive strain. If the loss is high, the program does not prevent the spread of the resistant strain despite a large prevalence rate of the program. The epidemic's final size can be larger than that before the vaccination program. We propose how to use poor vaccines, which have a large loss, to maximize program effects and describe various program risks, which can be estimated using available epidemiological data.

Conclusions

We presented clear and simple concepts to elucidate vaccination program guidelines to avoid negative program effects. Using our theory, monitoring the virulence of the resistant strain and investigating the loss caused by the resistant strain better development of vaccination strategies is possible.

Keywords: Epidemic model; Vaccination; Resistant strain; Paradox; Avian influenza

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A poor vaccine is really bad vaccine?

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Vaccination program can be effective for a control of avian influenza epidemic. But, the program is attended with risk of an emergence of a vaccine-resistant virus. Some theoretical researches predict that practice of vaccination program might increase a number of total infectious cases [1][2][3].

In this study, we evaluate an effectiveness of a vaccination program when a poor vaccine is used under an emergence of a vaccine-resistant virus and investigate an effect of the deterioration rate. As a result of analysis, we find that the poor vaccine can delay a timing of the emergence of a vaccine-resistant strain, and decrease the peak of the number of total infectious cases at the final phase of the epidemic. These results suggest that poor vaccines might give good effects for population level instead of bad effects for individual level.

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Threshold and stability results for an age-structured asymptomatic transmission model

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For the SEIR model, we think of E as a class of asymptomatic state with infectivity.

Such asymptomatic transmission model, we investigate the local and global stability for the steady state. We calculated an isolation ratio necessary to eradicate the infectious disease by isolating only infected individual.

Some Remarks on Time-Discrete Models for the Epidemic Population Dynamics

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感染症個体群動態に関する時間離散モデルについての考察

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In this work, we present a way of building a time-discrete model, especially related to the epidemic population dynamics, making use of the Royama's framework (Royama 1992; 瀬野 2007, 2008), which is sometimes called the 'first-principle' modelling, and further we analyze the derived discrete model to make some comparison to some typical ordinary differential equation models. Especially let us consider an epidemic population dynamics of nonfatal disease transmission, assuming that the total population size can be regarded as constant, say N , according to the epidemic time scale. The susceptible population on the k th day is denoted by S_k , and the infective by I_k . We assume the probability $P_k(i)$ that the number of contacts to other individuals by an individual is i in the k th day, and give the probability that the individual who contacts in j times to some infectives in the k th day successfully escapes from the infection by $(1 - \beta_k)^j$ ($0 < \beta_k < 1$). The parameter β_k corresponds to the probability that the susceptible is infected by a contact to an infective in the k th day. Besides, we assume the recovery probability q_k for an infective in the k th day, additionally with the probability m that the recovery successfully brings the immunity. The immune population on the k th day is denoted by R_k . The immunity is waned with probability θ per day. With these assumptions, we can derive the following discrete epidemic dynamics model for the susceptible frequency $\psi_k = S_k/N$, the infective $\phi_k = I_k/N$, and the immune $\eta_k = R_k/N$:

$$\begin{aligned}\psi_{k+1} &= \sum_{j=0}^{\infty} (1 - \beta_k \phi_k)^j P_k(j) \psi_k + (1 - m) q_k \phi_k + \theta \eta_k; \\ \phi_{k+1} &= \sum_{j=0}^{\infty} \{1 - (1 - \beta_k \phi_k)^j\} P_k(j) \psi_k + (1 - q_k) \phi_k; \\ \eta_{k+1} &= m q_k \phi_k + (1 - \theta) \eta_k,\end{aligned}\tag{1}$$

where $\psi_k + \phi_k + \eta_k = 1$ for any k . We show that this discrete model has the nature mathematically analogous to that of Kermack–McKendrick model if we assume that $P_k(j)$ follows a Poisson distribution. Furthermore, with a rational introduction of the time step size, we can show that the limit of the system (1) exactly corresponds to Kermack–McKendrick model.

Royama (1992) による数理モデリングを応用して、致死性の無視できる伝染病のある個体群における伝染ダイナミクスの数理モデルを考える (瀬野 2007, 2008)。考える伝染ダイナミクスの時間スケールでは、総個体群サイズの (伝染病に起因する以外の繁殖・死亡・移出入による) 増減は無視できるものとし、考えている個体群のサイズ (個体数) を N (定数) とする。第 k 日目 (開始時) の非感染 (伝染病感受性) 個体数を S_k , 感染 (伝染力保有) 個体数を I_k と表す。ある個体が 1 日に「延べ」 i 回, 他個体と接触する確率を $P_k(i)$ で与える。また, 第 k 日目の 1 日の間に感染した個体と j 回接触した非感染個体が感染から免れる確率を $(1 - \beta_k)^j$ で与える ($0 < \beta_k < 1$)。パラメータ β_k は, 第 k 日目において, 1 感染個体と接触した非感染個体が伝染病に感染する確率に相当する。さらに, 感染個体が 1 日の内に回復し, 感染力を失う確率を q_k で与える。ただし, 回復した個体に対して, 免疫獲得確率を m ($0 \leq m \leq 1$) とする。第 k 日目における免疫獲得個体数を R_k と表す。また, 免疫獲得個体が 1 日の内に免疫を失い, 感受性個体に戻る免疫失活確率を θ ($0 \leq \theta < 1$) で導入しておく。以上の仮定と設定により, 非感染者頻度 $\psi_k = S_k/N$, 感染者頻度 $\phi_k = I_k/N$, 免疫保有者頻度 $\eta_k = R_k/N$ の日変動を与える差分方程式系による数理モデル (1) を導くことができる。特に, $P_k(j)$ が Poisson 分布に従う場合, モデル (1) を解析することによって, Kermack–McKendrick モデルと同様の数学的性質を持つことがわかった。さらに, 合理的な手法で時間ステップを導入することによって, 系 (1) は, その極限において, Kermack–McKendrick モデルと一致することも示すことができた。

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Theoretical perspective of SHIV pathogenesis

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SHIV is a chimeric virus of HIV (Human Immunodeficiency Virus) and SIV (Simian Immunodeficiency Virus). In experimental infection, the existence of highly pathogenic strain and lowly pathogenic strain is confirmed. When the rhesus macaque is infected with the former strain, it develops into AIDS, but the macaque infected with the latter does not. In addition, it has been clarified, by an in vitro experiment, that the main differences of two strain are the viral productivity and the viral infectivity. In this research, we theoretically examine how the differences of two strains relate with the AIDS development in the rhesus macaque by applying the mathematical model.

Mathematical model for fermentation of Sake

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There are various kinds of fermented foods such that Sake, Soy sauce, and cheese. And, these are made by the activity of microorganisms. The mechanism of the microorganism in such foods can be considered using mathematical models. We researched about the brewing of Sake.

Sake has the highest alcoholic concentrations in world's brewages. It is due to the special technique "Heikou - fukuhakkou."

(simultaneous saccharification and fermentation)

Heikou - fukuhakkou

$$\left\{ \begin{array}{l} \frac{dS}{dt} = -aSM \\ \frac{dM}{dt} = bSM - cM \\ \frac{dG}{dt} = vSM - wGF \\ \frac{dF}{dt} = xGF - yF \\ \frac{dA}{dt} = zGF \end{array} \right.$$

S : Starch, M : Malt, G : Glucose, F : Ferment, A : Alcohol

a, b, c, v, w, x, y, z : constant

The fact that high glucose concentrations depresses the activity of sake yeast must be suitably incorporated into the model.

The advantage of "Heikou - fukuhakkou" cannot be explained only by the lower reproduction rate of sake yeast. And, both the lower fermentation rate and the lower reproduction rate are necessary to explain the advantage.

Mathematical analysis of age-structured HIV-1 model

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We consider an age-structured HIV-1 model which describes the dynamics of T cells and human immunodeficiency virus in vivo. T cells infected by HIV are divided into two classes; one is the class in which the reverse transcription is not get completed, the other one is class where the reverse transcription is completed.

First, we calculate the basic reproduction number $\mathcal{R}_0$ of this system, and formulate the stability condition of disease-free and endemic steady state. By using this model, we examine effects of reverse transcriptase inhibitor and protease inhibitor. Moreover, we consider the persistence of infected status.

Bursting oscillations and chaos in a prey-predator system with dormancy of predators

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We consider a prey-predator system with dormancy of predators

$$\begin{cases} \frac{dp}{dt} = r(1 - \frac{p}{K})p - f(p)z \\ \frac{dz}{dt} = k_1\mu(p)f(p)z + \alpha w - d_1z \\ \tau \frac{dw}{dt} = k_2(1 - \mu(p))f(p)z - \alpha w - d_2w, \end{cases} \quad (1)$$

where p and z denote the population densities of prey and predator, respectively, and w denote the population density of predator with dormancy state (resting eggs). r and K are the intrinsic growth rate and the carrying capacity of prey, respectively. k_1 and k_2 are increasing rates of predator in active and dormant states, respectively, and d_1 and d_2 denote the mortality rates of the active and dormant predator, respectively. α denotes the hatching rate, i.e., resting egg has the dormancy period with $1/\alpha$ on average. τ determines the time scale of the dynamics of resting eggs. $f(p)$ represents a functional response which is a positive strictly monotone increasing bounded function. A typical example of $f(p)$ is the Holling type II functional response defined by

$$f(p) = \frac{cp}{1 + chp}. \quad (2)$$

$\mu(p)$ is a switching function to control induction of dormancy, which is a positive strictly monotone increasing function with $0 < \mu(p) < 1$. A typical example of μ is

$$\mu(p) = \frac{1}{2} \left\{ 1 + \tanh \left(\frac{p - \eta}{\sigma} \right) \right\}, \quad (3)$$

where η and σ measure the switching level and sharpness, respectively.

In [1], we studied the bifurcation structure of (1) with respect to K , and showed that a stable coexisting equilibrium becomes unstable, and a stable periodic orbit appears through the Hopf-bifurcation. In this talk, we

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numerically show that the periodic orbits exhibit bursting oscillations and change to chaos as K increases considerably for appropriate parameter values. Moreover, according to the theory of [2], we give a partial justification for existence of bursting oscillations and chaos when τ is sufficiently large.

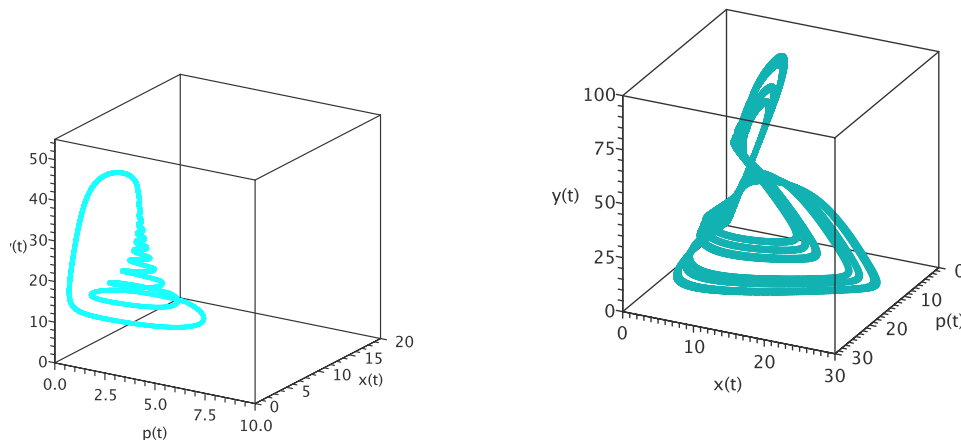


Figure. (Left) bursting oscillations. (Right) chaos.

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Option pricing theory of congestion with a time limit

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The net present values (NPV) and the option pricing theory for a queue and congestion with a time limit are proposed. The NPV and option theories are ordinary used in calculating a net payoff or an expected one of firms¹. In our previous work^{2,3}, we construct the new estimating theory of congestion by employing their pricing methods. These frameworks give us the information that the present values of congestion including future dynamics are effective or not. However, it is not enough to apply to practical problems, such as emergency evacuation from a building, an aircraft or an event place. Obviously, these problems are crucial from the point of view of the safety of human life. Therefore, we take account of the effect of a time limit to our system.

As a result of the presentation, the differences between the values of congestion with a time limit and those without a time limit are discussed. Furthermore, some empirical estimations of the parameters of our model concerning "human stress" are introduced (The concept of survival analysis makes possible to estimate the parameters).

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Speed of invasion for stochastic lattice model

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Ellner *et al.* (1998) approximately evaluated the speed of invasion for the simplest stochastic lattice model referred to as the lattice logistic model or the basic contact process with much accuracy. Their method “pair-edge approximation” considers the dynamics of the location for the front runner while the sites behind the front runner are assumed to be in the steady states obtained by ordinary pair approximation (Matsuda *et al.* 1992). The critical birth rate for population survival by pair-edge approximation gives better estimate than one by ordinary pair approximation. One of the next problems is to show how the estimate can be improved by applying the higher decoupling approximation to the steady states for the sites behind the front runner, especially in one-dimensional lattice space. Also we will challenge the case in two-dimensional lattice space.

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Coevolutionary and Diversity in Evolutionary Game Theory: Random Environment

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This talk is about the impacts of environmental variation on the game. Here environmental variation corresponds to the fitness variation.

In mathematical biology, we know that the player chooses Bet-Hedging strategy in the stochastic environment, if the fitness is “Geometric mean” and the player doesn’t, if it is “Arithmetic average” ([3]). In addition, Selten [4] showed that no mixed equilibria i.e., Bet-Hedging strategy, are evolutionarily stable when players can condition their strategies on their roles in a game. On the other hand, we know that Nash equilibrium in the game with randomly disturbed payoffs is always mixed strategy ([2]).

Thus, these results are discrepancy in spite of the similar model. Binmore and Samuelson [1] examines this discrepancy and reconciles these results. This study examines this discrepancy with the Replicator equation.

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Theoretical and Experimental Studies on Calling Behavior of Three Japanese Tree Frogs

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Synchronization has been observed in various systems including spontaneous behavior of living beings. We observed call alternation of two interacting Japanese tree frogs [1]: while an isolated frog calls nearly periodically, two frogs tend to synchronize almost in anti-phase π . Because of alternation of the two frogs, a system of the three frogs is frustrated and all the pairs cannot synchronize in anti-phase with each other. In this presentation, we introduce theoretical and experimental studies on calling behavior of three Japanese tree frogs. First, we modeled the calling behavior as a system of coupled phase oscillators and studied the dynamics by using bifurcation analysis and Lyapunov function analysis, which clarified the existence of various phenomena including a steady state with cooperative in-phase synchronization and competitive anti-phase synchronization, bistability, and asynchronization of the three oscillators [2,3]. Second, we experimentally observed several states of synchronization in calling of the three frogs [4]. Important future work includes theoretical modeling of many frogs and its empirical verification in real fields.

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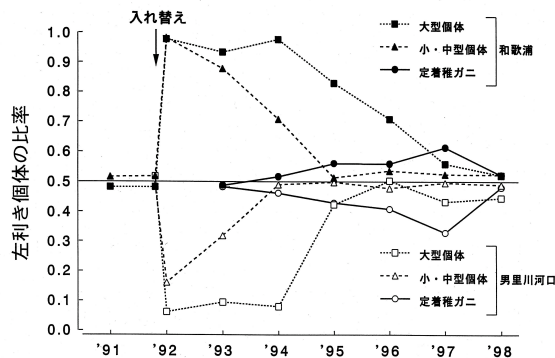
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Models of genetic system of the cheliped handedness in a fiddler crab, *Uca lactea*

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2つの干潟でのサイズ別に見た左右性の比率の年変化

Males of *Uca lactea* have an enormously large cheliped or large hand. Frequency of left handed individuals and right handed individuals are almost equal. Males use this large cheliped to court females and to fight, but not to feed. Females lack this large cheliped. It is an interesting problem what determines the side of this large male cheliped. Professor Hori in Kyoto University exchanged the right handed male individuals in Wakaura and the left handed male individuals in Onosato river. After the replacement, in Wakaura almost all males are left handed, while in Onosato river, almost all males are right handed. Graph is the dynamics of left handed male fraction, after the replacement. Since the fraction of left handed in

new-born deviates from 0.5 after '93, I deduced that handedness is genetically determined. The fraction of left handed in new-born is 0.5 in '92. Therefore, handedness is determined by the gene only from mother.

I constructed three models, where the gene only from mother determine children's handedness. The first model is that the handedness gene is on the X sex chromosome. The second model is that the gene is on a euchromosome and is affected by genomic imprinting. Genomic imprinting means that the gene from either mother or father expresses. The third model is that children's phenotype is determined by mother's genotype. This phenomenon is called maternal effect. I simulated three models and compared three models. In order to decrease the fraction of left handed in new-born from 5'th year to 6'th year, I introduced frequency dependednce and immigration of new-born.

All of three models, X chromosome model, imprinting model and maternal effect model can explain dynamics of handed fraction in male of a fiddler crab, *Uca lactea* after the replace experiment. To explain the decline of left handed fraction in mew-born from 5'th year to 6'th year, immigration of new-born is necessary.

The analysis of the effect of the discontinuity of the nutrient utilization to species diversity

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The multiple species coexistence is major issue in the ecology. There are many factors which promotes the species diversity (i.e. the environmental fluctuation, nonlinearity of nature etc.). Especially the coexistence of annual and perennial plant species are remained as the diversity problem. Now the difference between the annual and plant species is the production opportunity. That is, the annual plant species have opportunity to reproduce seed one time throughout their life, but the perennial plant reproduce seeds several time throughout their life. In this study, we consider how the strategy of the perennial affects to the species diversity. For the purpose we assume the discontinuous production function: perennial plant reproduce seeds for any nutrient level, but perennial plant reproduce seeds if the nutrient level is favorable to seed production otherwise they does not reproduce seeds. In this talk we give the results: 1) the relationship between the species diversity and seed production, 2) the relation between the species diversity and the strategy.

Keywords: Discontinuous seed production, Lottery model, coexistence of the plant species, population dynamics

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Density-vague dynamics of biological populations

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The nature of the negative feedback relationship between population growth rate and density is at the heart of population ecology. The existence and detection of density dependence has been, however, the subject of much controversy for the last 100 years. The consensus emerging from this prolonged debate is now that, when sufficiently long runs of data are available, ecologists should be able to detect density dependence from population time-series. The duration of a time series necessary to distinguish a regulated population trajectory from a random walk remains poorly understood. When plotting data on the form of the density-dependent relationship, ecologists have been confounded by considerable noise around each relationship, i.e. “density vagueness”; explaining this bivariate scatter has remained a largely unrealized goal.

Consider the biological system under environmental disturbances which is in the dynamical balance departing from and regressing toward an equilibrium population size. The ratio of the mean square successive difference to the variance in log-transformed population size measures elasticity in the system, and its reciprocal reads the equilibration time T_{eq} , i.e. the characteristic time scale of equilibration or crossover between the random-walking and the governed population. Analyzing long-term census data from major fish populations in the North Atlantic, I identify the equilibration time. The system appears nonstationary at time scales shorter than the equilibration time, possibly as long as a decade. I address the issue of density vagueness in the mathematical framework, and explain the duration (complementary time L_c) of a time series necessary to detect weak density dependence in a noisy system. It is difficult to judge whether the system is heading toward the equilibrium point in the time series of length less than the complementary time $L_c = [1 + 2 / (e^{1/T_{eq}} - 1)] \pi$. Failures to detect density dependence occur due to the uncertainty in the determination of the equilibrium population size associated with sample number. For the fish populations examined, observations covering a few decades are required to be able to disentangle density-dependent signals from external noise caused by environmental variations and variable harvest rates. Applying a proper coarse-graining procedure (at the time scale of T_{eq}) for time series analysis makes the negative relationship between population growth and abundance visible on these long runs of observation.

The mechanistic basis of population models with various types of competition

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The population dynamics of single species with seasonal reproduction are often modeled using difference equations. The explicit form of a discrete-time population model must be related to the behavior of individuals. In order to reveal the mechanistic basis of population models with various types of competition, we present a first-principles derivation of a discrete-time population model with a type of competition intermediate between scramble and contest. The derivation is formulated in a site-based framework, in which individuals are distributed among discrete resource sites, and based on an argument on the way of partitioning of resource among individuals. The derived model has parameters relating to the way of partitioning of resource, the intensity of competition, and the degree of spatial aggregation of individuals. Various population models exhibiting either scramble or contest competition can be obtained from the model in certain limits of its parameters. The model, thus, gives an integrated view which allows us to understand how various population models are interrelated with each other, and how the behavior of individuals affects the form of a corresponding model. Furthermore, extending the above argument, we also demonstrate that various population models exhibiting the Allee effect can be derived from first principles if assuming a population consisting of females and males.

Incoherence-coherence transition in the replicator-mutator equation with random interactions

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We study the behavior of the following replicator-mutator equation that is a general mathematical model with mutation in addition to interaction of strategies [1]:

$$\dot{x}_i = \sum_{j=1}^n x_j f_j(\mathbf{x}) Q_{ji} - \phi(\mathbf{x}) x_i$$
$$\begin{pmatrix} f_j(\mathbf{x}) = \sum_{i=1}^n a_{ij} x_i \\ \phi(\mathbf{x}) = \sum_{i=1}^n f_i(\mathbf{x}) x_i \end{pmatrix}$$

where f_j is fitness of species i and $\phi(\mathbf{x})$ is average fitness. This equation generally describes dynamics of complex adaptive systems in population genetics, social networks, and models of language evolution [2].

In the context of language evolution, each x_i denotes a rate of the number of speakers of a grammar i . The function ϕ is also called "coherence" since high value of it denotes only one grammar dominates (and all others extinct) and every speaker uses a same grammar coherently. The interactions $\{a_{ij}\}$ denote similarity between the grammar i and j and are all positive in definition. We assume symmetric mutation rate as $Q_{ij} = (1 - q)/(N - 1) = \text{const.}$ In general, the coherence ϕ increases with the self-replication rate $Q_{ii} = q$ and shows discrete transition. At a critical value $q = q_c$ coherence increases discontinuously from low to high value. In addition, below this threshold the system converges to a same equilibrium state from every initial condition, but above the threshold multiple equilibrium states appear.

For considering more general ecosystems, competitive interaction should be considered and, hence we study the replicator-mutator equation with Gaussian random interactions a_{ij} with both positive and negative values. If the average of the Gaussian distribution m is zero, discrete incoherence-coherence transition does not occur while if it is positive $m > 0$, discrete transition is observed. Transition for multiple equilibrium states are observed in both cases.

We also discuss other general properties of the replicator-mutator equation with random interactions and applicability of the model to general complex adaptive systems.

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Global bifurcation structures and parameter sensitivities of cardiac cell models

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There is a voltage difference between the inside and the outside of a cell (membrane potential) due to differences in ionic concentrations across the cell membrane. In the membrane, there are ionic channels which open and close dynamically to allow the passage of specific ions. When a stimulus is applied to the cell, ions pass through the channels, changing the membrane potential. This change is called the action potential. Action potentials are deeply related to vital activities including the heartbeat and information processing in the brain. If genetic or chemically-induced abnormalities of ionic channels arise, diseases such as arrhythmia and epilepsy may occur. These diseases are called ionic channel diseases or channelopathy, and many drugs are used for their clinical treatments. These drugs mainly change the conductances of ionic channels. It is, however, difficult to determine which change in the conductances is effective to treat these diseases in physiological experiments only. Therefore, computational models are widely employed to simulate the performances of cardiac cells.

The famous Hodgkin-Huxley (HH) equations describe the electric potential change of a neuronal membrane. Many mathematical cell models are based on the HH formalism. Because action potential waveforms of various parts of the heart are different in shape and amplitude, many models of different cardiac cells have been developed. For example, the Luo-Rudy dynamic model [1] and the Yanagihara-Noma-Irisawa model [2] represent the membrane potential changes in a ventricular and a sinoatrial node cell, respectively. In these models, a variety of bifurcation phenomena occur along with changes in parameters such as the conductance of ionic channels. In normal ventricular cells, the membrane potential converges to an equilibrium point without stimuli. An oscillatory solution, which bifurcates from the equilibrium point by a Hopf-bifurcation, causes an abnormal action potential. Although many researches have conducted simulation studies on the cardiac cell models in the past, few researches have analyzed bifurcation structures of these models since the cardiac models are very high-dimensional. In this research, we investigate the parameter sensitivities by bifurcation analysis in these models, and discuss the drug sensitivities of ionic channels. It is important to pay attention to sensitive ionic channels in the development of new drugs. We expect the result of this research to be useful in the treatment of tachycardia.

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Spatio-temporal Dynamics of Cell Proliferation and Differentiation in Colonic Crypts

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Colorectal cancer (CRC) is a major cause of death in developed countries. Consequently, it is an intensively studied neoplasm in human subjects, experimental animals, and cell culture. Here we describe a multipurpose mathematical model with easily-set parameters to simulate cell proliferation and differentiation in colonic crypts. This individual-based model focuses on cellular properties including position, size, maturity, and mitotic cycle time. Unlike cell population models, it permits visualization of spatio-temporal distributions during simulation. It also allows comparison of labeling index curves of colonic crypts. The results are consistent with data derived from experiments on normal human subjects. The model offers a useful adjunct to animal experimentation and provides an efficient way to test hypotheses regarding the complex processes underlying CRC.

Models of humoral immunity against multiple viral strains

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We analyze mathematical models for the dynamics of infectious disease and immune response within a host. We consider the following model:

$$\frac{dx}{dt} = \lambda - mx - \sum_{i=1}^n \beta_i x v_i, \quad (1)$$

$$\frac{dy_i}{dt} = \beta_i x v_i - a_i y_i, \quad (2)$$

$$\frac{dv_i}{dt} = k_i y_i - u_i v_i - p_i v_i z_i, \quad (3)$$

$$\frac{dz_i}{dt} = q_i v_i - d_i z_i, \quad (4)$$

where x is the number of uninfected cells, y_i is the number of cells infected by strain i , v_i is the number of viral strains, and the z_i is the number of immune cells specific to strain i . In the system without immune cells, only a strain with the maximum reproductive rate can survive in the steady state. However, in this model involving immune cells there can be coexistence of multiple strains in the steady state. Using the Lyapunov function, we can prove the global stability of the disease steady state. We can also examine the possibility of invasion of a new strain with the same way as Iwasa et al.(2004).

Traveling wave solutions to a malignant tumor invasion model

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I talk about traveling wave solutions to a system of partial differential equations related to a malignant tumor invasion model.

In 1999, Perumpanani et al. considered a mathematical model for malignant tumor cell invasion into connective tissue without cell diffusion, and they presented a three-component system and a two-component system reduced from the three-component one. In their study, traveling waves to the reduced two-component system were obtained numerically.

I prove the existence of smooth traveling wave solutions to the two-component system analytically, and I investigate their asymptotic behavior. In order to show the existence of traveling wave solutions, I consider heteroclinic orbits on a phase plane and construct an invariant region for the orbits. Concerning the behavior of the solutions, I apply the center manifold theory.

Travelling waves arising in the prey-predator invasion processes

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We consider the two kind of traveling waves which describe the invasion processes of the predator-prey system. The first one is the pursuit-evasion waves : Initially the whole space is occupied by the prey, and the predator is introduced in small region. Then, predator pursuits the prey and invade the place occupied by the prey. The second one is the invasion waves of the open space : Initially there is no species in the whole space, the prey and the predator are introduced in some small region. Then, the prey and the predator invade the open space at the same time. We discuss the existence of traveling waves and their minimal wave speeds by the singular perturbations and the numerical simulations.

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