

Evolutionary Maintainable Strategy and Origin of Aging

Kei-ichi TAINAKA

Department of Mathematical Science, Ibaraki University, Mito, 310, JAPAN

Abstract I present an evolutionary theory which is against usual Darwinian argument. So far, study of evolutionary game has been associated with the theory of "evolutionary stable strategy" (ESS). This theory is based on the consensus that natural selection happens on the scale of single individuals (genes): if a strategy increases the "Darwinian fitness" (the expected number of surviving offsprings in the next generation) of an individual, then it become the winner in the struggle with other strategies. The ESS theory thus determines which strategy becomes the winner in the contest with other strategies. However, the winner may go extinct during a long period, if its population size in stationary state is less than the minimum viable population, in other words, if the winner is endangered. The ESS theory disregards whether the winner is vulnerable or not. In the present paper, such long-term maintenace is explored by population vulnerable analysis (PVA). I apply both ESS analysis and PVA to a lattice ecosystem. Computer simulation on square lattice reveals that depending on the minimum viable population, PVA is more relevant than the ESS analysis. An established strategy is roughly determined by "evolutionary maintainable strategy" (EMS) which has the maximum value of steady-state density. We assume that a target species lives in several habitats which are geographically isolated from each other. According to the ESS analysis, EMS may be beaten by ESS in a certain habitat, whereas the former can survive in other habitats. This means that natural selection eventually acts not on individuals but on groups. In this case, the population size in stationary state becomes more important than the Darwinian fitness. Moreover, it is found from various simulations that EMS usually locates at a finite value of death rate, which indicates a positive meaning of death process.

1. Introduction

There has been a fundamental dispute for natural selection; that is, whether the selection happens on the scale of single individuals or on the scale of groups? Since the works

of Hamilton (1964) and Maynard Smith (1982) et al., many biologists have formed the consensus that natural selection acts on individuals (genes). However, the present paper revives the concept of group selection (Wynne-Edwards, 1962). I introduce evolutionary maintainable strategy (EMS) to explain the origin of aging.

2. Model

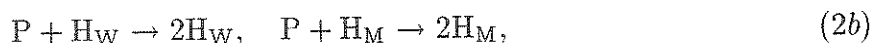
Consider, for example, the following lattice model:



where H, C and P represent an individual of herbivore, carnivore and plant, respectively. This system has been first reported as a voter model (Tainaka, 1993), but now I regard it as an ecosystem. The reaction (1d) means the death process of herbivore, so that the parameter d has the meaning of death rate of herbivore; with increasing d , the herbivore suffers loss, while plant gains a nutritional advantage. Provided that the reaction (1d) is neglected ($d = 0$), then the rule (1) is identical with the "Paper, Scissors, Stone" game (PSSG) (Tainaka, 1988; 1989; Rachebourg, et al., 1996) which symbolically represents ecological balance. We ask a question: which value (strategy) of d in the system (1) is established in the herbivore?

3. Evolutionary Stable Strategy (ESS)

First, usual game theory (ESS) (Maynard Smith & Price, 1973; Maynard Smith, 1982) is applied. This theory is based on the consensus that natural selection happens on the scale of single individuals (genes); if a strategy increases the Darwinian fitness of an individual, then it becomes the winner in the contest (struggle) with other strategies. To know ESS, we consider the following contest between a wild type of herbivore H_W and its mutant H_M :



where the herbivore H in (1) is replaced by H_W and H_M which are distinguishable by the death rate d in the reaction (2d): $d = d_W$ (or $d = d_M$) for H_W (or H_M). There is no direct interaction between these herbivores, so that they have the same niche.

Simulation is carried out by the lattice Lotka-Volterra model (LLVM) (Tainaka, 1988; 1989; Matsuda, et al., 1992). We briefly describe this simulation method. Initially, each

lattice site is occupied by one individual of three species. Ecosystem is updated by following two steps: (i) Choose a pair of neighboring lattice points randomly, and react them according to (2a) - (2c). (ii) Choose one lattice point randomly, and change it by (2d); when the point occupied by H_W (H_M) is selected, it becomes P by the probability d_W (d_M). If the restriction "neighboring" in the step (i) is neglected, then the dynamics is represented by the mean-field theory which is equivalent to the Lotka-Volterra model.

Simulation result of the contest (2) reveals that both herbivores H_W and H_M cannot coexist; the strategy which has larger value of d goes extinct. After this extinction, the ecosystem becomes equivalent to the system (1), and it evolves into a stationary state. From this survival contest, we conclude that the herbivore of $d \rightarrow 0$ is ESS. Hence, it is very hard from the ESS theory to explain the fact that the death rate of a species is finite.

4. Population Vulnerable Analysis

Second, the long-term persistence of the winner (herbivore) in the contest (2) is explored by population vulnerable analysis (PVA) (Soule, 1987) in the following simple procedure: i) We obtain the population size of the winner in stationary state against its death rate d . ii) If this size is less than the minimum viable population (MVP) (Thomas, 1990; Wilcove, 1993; Tainaka, K. & Itoh, 1996), the extinction of the winner is assumed to occur. Unfortunately the size of MVP for any single species can be difficult to ascertain. Here, we regard it as a parameter.

4.1 STEADY-STATE DENSITIES

In Figs. 1 and 2, the steady-state densities of species in the system (2) [system (1)] are depicted against the death rate d of herbivore H, where Figs. 1 and 2 are the results of mean-field theory (MFT) and lattice model (LLVM), respectively. If $d = 0$ (PSSG), three species have equal densities. With increasing d , a *counterintuitive* response is observed: the population size of H increases in spite of increase of d . On the other hand, the population size of carnivore (C) decreases. These results are obtained for both MFT and LLVM. However, in LLVM, the population of P decreases in spite of the increase of d . The carnivore disappears, when $d > d_c$, where $d_c = 1$ for MFT, and $d_c \sim 0.4$ for LLVM. After the extinction of carnivore ($d > d_c$), the system becomes equivalent to the contact process (Liggett, 1985), so that the herbivore conversely decreases with the increase of d . If $d > d_h$, the herbivore also goes extinct.

Note that the carnivore goes extinct by the increase of d . No one may believe such a cause, since the population of herbivore increases (*uncertainty of extinction*: Tainaka, 1994). Moreover, Fig. 2 exhibits "masked" competition: the adaptive move of herbivore (d approaches d_c) brings about the worst condition of both carnivore and plant. The masked competition, defined by steady-state densities, becomes clear in the case of lattice model.

4.2 EVOLUTIONARY MAINTAINABLE STRATEGY (EMS)

The steady-state density of herbivore (Figs. 1 and 2) has a peak at the extinction (phase transition) point of carnivore ($d = d_c$). We call such optimum strategy EMS. Now we describe the evolutionary meaning of EMS. We assume that the herbivore lives in several habitats which are geographically isolated from each other. According to the ESS analysis,

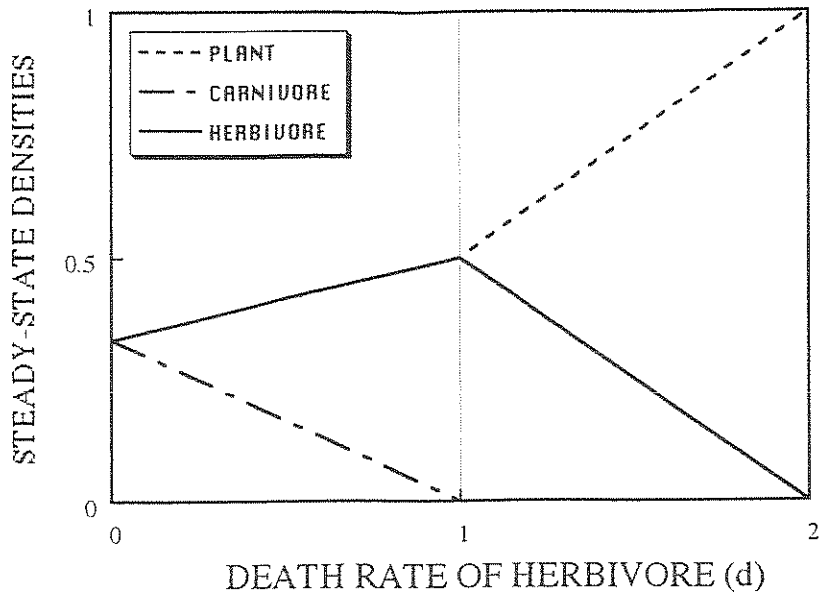


Fig. 1. The result of mean-field theory (MFT). The long-term average of densities for the system (2) [system (1)] are shown against the death rate d of surviving herbivore. The density of herbivore has a peak at the extinction point of carnivore ($d = d_c = 1$). The plant monotonically increases with d .

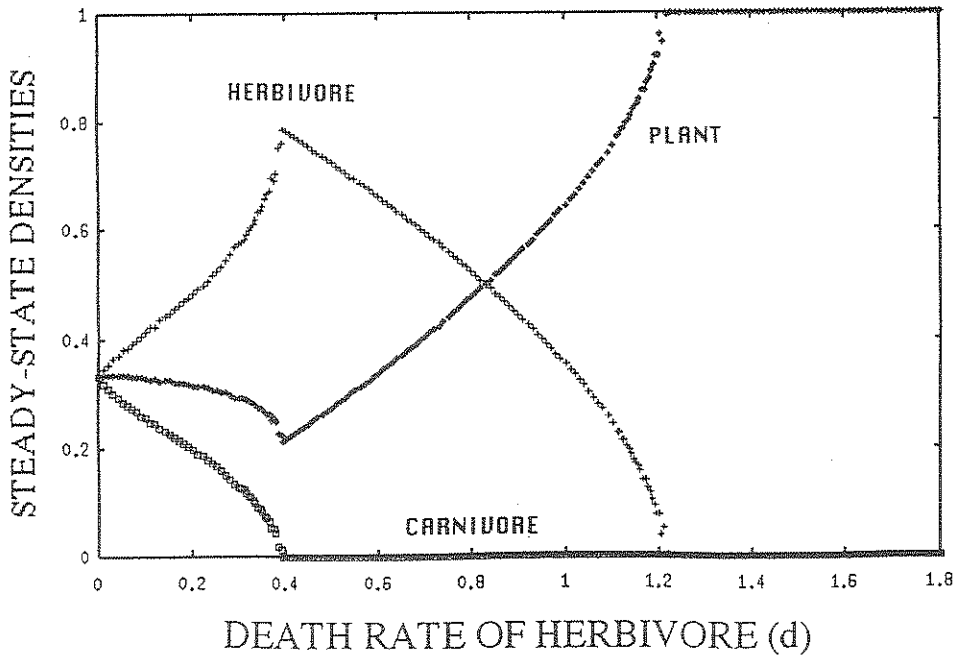


Fig. 2. Same as Fig. 1, but for the lattice model (LLVM). Each plot is obtained from the period $200 < t \leq 1000$ with 100×100 lattice. The density of herbivore has a sharp peak at the extinction point of carnivore ($d = d_c$). The optimum state for herbivore ($d = d_c$) corresponds to the worst condition for plant and carnivore (the masked competition).

the strategy of the least value of d becomes the winner in each habitat. However, the winner may go extinct during a long period, if its population size in stationary state is less than the minimum viable population (MVP), in other words, if the winner is endangered. When the MVP size is large, say $MVP = 0.6$ in Fig.2, only the strategies near the peak (EMS) can survive. While EMS may be beaten by ESS in a certain habitat, the former can survive in other habitats. Hence, the EMS theory explains the fact that the death rate of a species is finite. Another positive meaning of death process is indicated by the masked competition. Namely, it is necessary for any species to make genetic efforts to approach EMS; otherwise, the species may be forced to be ruined by efforts of other species [Red-Queen effect (Hamilton, 1980)].

4. 3 SELFSTRUCTURING EXTINCTION PATTERN

The difference between MFT and LLVM comes from the effect of spatial structure. Simulation of LLVM reveals that the spatial pattern is self-organized into a quasi-stationary state: the configuration of pattern dynamically varies, whereas average quantities, such as densities, are unchanged with time. To know a spatial correlation, we obtain the degree of clumping R_i of species i (Tainaka, 1994). When $R_i > 1$, the distribution of species i is clumped. In Fig. 3, the simulation result of R_i for species i ($i = H, C, P$) is depicted against d . This figure clearly reveals that when d approaches d_c (d_h), the degree of clumping of carnivore (herbivore) becomes rapidly high. We called such a cluster formation the "selfstructuring extinction pattern" (Kobayashi & Tainaka, 1997): when a species faces extinction, its contagiousness rapidly increases. The clumping behavior of carnivore may explain why the steady-state density of plant is decreased in spite of increase of d , and why the peak of EMS becomes sharp.

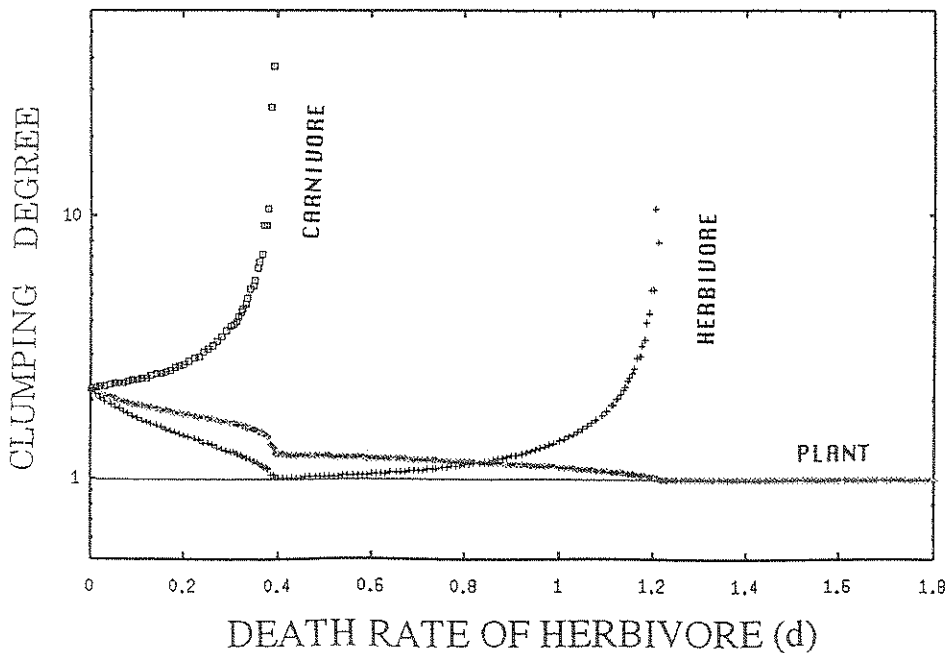


Fig. 3. The clumping degree R_i for species i ($i = H, C, P$) is plotted against d .

5. Concluding Remarks

I present an evolutionary theory which is against usual Darwinian argument. The present theory contains two processes of extinction: 1) the extinction of wild type or mutants after the contest in each habitat, and 2) the local extinction of endangered species. The characteristic time scale of process 1) is surely smaller than that of process 2). For the process 1), I apply usual ESS theory which is based on the consensus that natural selection happens on the scale of single individuals (genes); if a strategy increases the "Darwinian fitness" (the expected number of surviving offsprings in the next generation) of an individual, then it become the winner in the struggle with other strategies. On the other hand, I first deal with the process 2). I apply PVA to this process. When the size of MVP is considerably large, the process 2) is more relevant. In this case, the selection (the effect of MVP) acts on the scale of groups; the population size in stationary state becomes more important than the Darwinian fitness. Note that the geographical isolation of habitats plays an essential role for the establishment of EMS.

The system (1) is so simple, that it is expected that the similar peak as shown in Fig. 1 can be observed in many web models. If we take into account the spatial structure, we may easily obtain the peak, because in lattice models, the steady-state density frequently shows a counterintuitive nature (Tainaka, 1994; Sato, et al., 1994). While ESS is usually determined by intraspecies interaction, EMS strongly depends on the interspecific balance in ecosystems.

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