

Evolutionarily Stable Strategies of Dispersal : Mathematical Models and Analysis

江副, 日出夫

<https://doi.org/10.11501/3132414>

出版情報 : 九州大学, 1997, 博士 (理学), 論文博士
バージョン :
権利関係 :

Evolutionarily Stable Strategies of Dispersal:
Mathematical Models and Analysis

江 副 日 出 夫

①

**Evolutionarily Stable Strategies of Dispersal:
Mathematical Models and Analysis**

Hideo Ezoë

Department of Natural Science
Osaka Women's University
Dansen-cho, Sakai
Osaka 590, Japan

Dissertation
submitted in partial fulfillment of the requirements
for the degree of

DOCTOR OF SCIENCE

in Biology
Division of Science
Graduate School of Kyushu University

Contents

Preface, 2

1 Evolution of Condition-Dependent Dispersal:

A Genetic-Algorithm Search for the ESS Reaction Norm

- 1.1 Introduction, 5
- 1.2 model, 7
- 1.3 Neural network model of reaction norm and genetic algorithm, 12
- 1.4 Reaction norm of learned network, 16
- 1.5 Correlation of environment between sites, 17
- 1.6 Discussion, 19
- 1.7 Figures, 23

2 Optimal Dispersal Range and Seed Size in a Stable Environment

- 2.1 Introduction, 32
- 2.2 model, 34
- 2.3 Evolutionarily Stable Dispersal Strategy, 35
- 2.4 Discussion, 38
- 2.5 Appendix: Individual-Based Computer Simulation, 41
- 2.6 Figures, 43

Acknowledgment, 46

References, 47

Preface

Dispersal is one of the fundamental components common to life histories of almost all species, the means of which are full of variety. Larger animals which are equipped with wings, legs, tails, and fins can migrate by themselves for long distance, although smaller animals and other organisms such as plants and microorganisms can disperse by help of wind, stream, tide, and other animals including the human. Even if means of dispersal are passive, organisms often develop structures advantageous for dispersal: wings of planthoppers, feathers of dandelion's seeds, colorful nutritious fruits of many endozoochorous plants, etc.

Many theoretical and empirical studies so far have revealed that the dispersal in spatially heterogeneous and even homogeneous habitats strongly affects on the population dynamics as well as the genetic ones. For example, the system of competitive or prey - predator species can be maintained by the difference between the dispersal ability of each species (Huffaker, 1958; Hanski, 1983; Nee and May: 1992). On the other hand, the population living in the heterogeneous environment may extinct for larger dispersal rate because of excessive emigration from favorable patches (Shigesada *et al.*, 1986). Theoretical studies on population dynamics with dispersal have mainly been done adopting metapopulation models (Hanski and Gilpin, 1991; Hanski and Gilpin, 1997) and reaction - diffusion models (Okubo, 1980; Shigesada and Kawasaki, 1997), although in recent years increasing researchers becomes engaged in studying lattice models (Matsuda *et al.*, 1987; Durrett and Levin, 1994; Durrett and Levin, 1997; Harada *et al.*, 1995; Harada and Iwasa, 1996; Kubo *et al.*, 1996; Nakamaru *et al.*, 1997).

Yet why do organisms disperse, or, what benefit do dispersers gain at the cost of dispersal, such as energy loss for migration itself, physiological cost of developing structures for dispersal, and additional cost of mortality? Hamilton, who was interested in the wing polymorphism within insect species, and May were first to show that the trait for dispersal evolve even when the patchy habitats are stable and the mortality cost of dispersal is extremely high (Hamilton and May, 1977; Hamilton, 1996). They analyzed the evolutionarily stable strategy (ESS), which are defined as the strategy that when the most of the population adopted that strategy, no mutants who adopt other strategy can invade (Maynard Smith, 1982). Many ESS dispersal models have been developed, most of which are more realistic extensions of Hamilton and May (1977) (e.g. Crespi and Taylor, 1990; Ozaki, 1995).

In general, however, mathematical models considering realistic factors may

often be so complicate that it is difficult to derive the explicit criteria for ESS as well as ESS solutions itself. In the first chapter of this article, I apply genetic algorithm combined a neural network to calculate the ESS dispersal rate when the quality of patches are different from each other. Genetic algorithm are a method of optimization analogous to the evolution of organisms(Holland, 1985) and recently it has been applied to evolutionary ecology (e. g. Toquenaga et al., 1994). On the other hand, neural network is analogous to nervous systems of organisms, which has been studied mainly in computer science, and it has also been applied to behavioral ecology (e.g. Enquist and Arak, 1993; Enquist and Arak, 1994). In this article I used a neural network in order to construct the variety of reaction norm functions of individuals.

In the second chapter, I develop a new model to evaluate ESS dispersal range. In the three model used to study population dynamics with spatial structure, metapopulation models cannot deal with dispersal range explicitly, although those models have been applied most widely to study the evolution of dispersal. On the other hand, it is difficult for reaction-diffusion models to deal with the difference in the strategies and fitness of each individual, that is a reason why that models have seldom been applied to evolutionary ecology. Lattice models are the most flexible in the three models, while in the most case theoretical analysis is almost impossible and computer simulation is often an unique method for analysis. The model I propose in the second chapter is a simple and abstract one such that an approximated ESS solution can be evaluated by theoretical and numerical analysis, although it can predict the results of the more realistic individual-based computer simulation, which proves the promising possibility of that model.

In the following I summarize the content of each chapter in more detail.

Chapter 1: Evolution of Condition-Dependent Dispersal: A Genetic-Algorithm Search for the ESS Reaction Norm

Many insects produce two types (winged and wingless) of offspring that greatly differ in dispersal ability. The fraction of the two often depends on quality of the local habitat and crowding experienced by the mother. Here we studied the condition-dependent dispersal that is evolutionarily stable. The model is also applicable to annual plants that produce two types of seeds differing in dispersal rate. Assumptions are: the population is composed of a number of sites each occupied by a single adult. The total number of offspring produced by a mother depends on the environmental quality of the site which varies over the years and between sites. The ESS fraction of dispersing type as a function of the quality of the habitat (or ESS reaction norm) states that no disperser should be produced if habitat quality m is smaller than a critical value

k. If *m* is larger than *k*, the number of dispersers should increase with *m* and that of nondispersers should be kept constant. Second, we developed an alternative way of searching for the ESS: the reaction norm is represented as a three-layered neural network, and the parameters (weights and biases) are chosen by genetic algorithm (GA). This method can be extended easily to the cases of multiple environmental factors. There was an optimal (relatively wide) range of mutation rates for weights and biases, outside of which the convergence of the network to the valid ESS was likely to fail. Recombination, or crossing-over, was not effective in improving the success rate. The learned network often shows several characteristic ways of deviation from the ESS. We also examined the case in which the quality of different sites are correlated. In this case the ESS fraction of dispersers increases both with the quality of the site and with the average quality of the whole population in that year.

Chapter 2: Optimal Dispersal Range and Seed Size in a Stable Environment

The evolutionarily stable (ESS) dispersal range for annual plants is studied in a stable environment when there is a trade-off between seed survivability and dispersal range via seed size. Larger seed size is more beneficial in the competition for safe sites, but likely to be dispersed shorter and to suffer competition among siblings. Previously Hamilton and May (1977) found that the dispersal can be adaptive in a stable environment to reduce competition among sibs, but they assumed that dispersers can go to all the patches equally likely, which is not suitable for many terrestrial plants with limited dispersal range. In this article I discuss the evolution of dispersal range for wind dispersed seeds when dispersal range is tightly coupled with seed size. I assume that the density of dispersed seed follows two-dimensional normal distribution function, with variance decreasing with seed size. Due to the trade-off between the seed number and the survivability of a seedling offspring, there is a seed size \tilde{w} that maximizes the product of the two quantities. This is the optimal seed size when size-dependent dispersal is neglected. The ESS seed size considering the size-dependent dispersal w^* is also calculated by neglecting the effect of spatial clumping of relatives. Under the environment unfavorable for seed dispersal, the ESS seed size w^* can be much smaller than the optimal seed size \tilde{w} , but there is a lower limit for the ESS dispersal range even in the extremely sticky environment. Even if the dependency of seed survivability on the seed size is so weak that the cost of long range dispersal is small, the ESS seed dispersal range cannot become very large. These results are confirmed by individual-based computer simulations with more realistic assumptions considering spatial clumping of non-sib relatives.

Chapter 1

Evolution of Condition-Dependent Dispersal: A Genetic-Algorithm Search for the ESS Reaction Norm*

1.1 Introduction

Many life history traits as well as behavioural or morphological traits show environmental plasticity -- the phenotypes depend strongly on the environmental conditions experienced by the individuals or by their mothers. A typical example is "phase change" of insects, which produce two types of offspring (winged and wingless) that greatly differ in dispersal ability. Wing polymorphism of insects has been observed in many taxa, including aphids (Kawada, 1987; Liu, 1994), plant hoppers (Denno, 1994), crickets (Masaki and Shimizu, 1995; Tanaka, 1994; Zera and Mole, 1994), and beetles (Aukema, 1995). For wing polymorphism of aphids, it is known that the phenotype is controlled by the food quality and availability, temperature (Liu, 1994) and the frequency of physical contacts with conspecifics, indicating the degree of crowding (Kawada, 1987).

Cost-benefit analysis and comparative studies between species and between different populations of the same species revealed that the evolution of dispersal tendency depends on the habitat persistence (Denno, 1994). Solbreck (1995) summarized the study of the habitats and resource density of a lygaeid bug in a patchy landscape over a seventeen year period and concluded that migration is more likely to evolve if the habitat is patchy, per capita food resources greatly fluctuate, and the relative favorability of patches changes between years (see also Gatehouse, 1994).

Because the evolutionary advantage of different fractions of the two types within a brood depends on their frequency in the population, and on the environmental condition experienced by the mothers, the evolutionary outcome can be calculated by game models (e.g. Crespi and Taylor, 1990; Ozaki, 1995). The population structure

* This Chapter was done in collaboration with Professor Yoh Iwasa. The original paper is accepted for publication in *Researches on Population Ecology*.

commonly assumed is as follows (e.g. Hamilton and May, 1977; Comins et al., 1980; Cohen and Motro, 1989; Crespi and Taylor, 1990): The population is composed of a large number of sites, each occupied by a single adult. Each mother can produce offspring that are either of the dispersing type or of the nondispersing type. The nondispersers stay in their natal sites but dispersers migrate out to a different site. Dispersal is accompanied by a considerable risk of mortality. Individuals settled in a site after a dispersal stage, both residents and migrants compete with each other, and only one per site wins and survives to maturation. The strategy of each mother is the fraction of dispersers among her offspring, which may change with the quality of the environment. The details of the assumptions may differ, concerning the number of adults remaining in each site, the mode of genetic inheritance (sexual or asexual), the cost of dispersal, and the fluctuation of environmental quality. A similar model is also applicable to terrestrial plants that produce two types of seeds differing in dispersal rate (e.g. seeds with or without pappus).

In this paper we first show that the ESS fraction of dispersers among offspring is dependent on the total number of offspring produced by a mother. If the environmental quality fluctuates between sites and over the years, each mother should decide the fraction of dispersers among her offspring depending on the quality of the site.

Evolutionary game models have been quite successful in providing tools for the understanding of the diversity of life history patterns and animal behaviors in nature (Maynard Smith, 1982), examples including the hatching schedule of herbivorous insects (Ezoe, 1995). However, traditional methods of obtaining the evolutionarily stable strategy often require us to specify an explicit mathematical expression including one or a few free parameters to choose. This procedure in effect gives a class of reaction norm, or how the organisms change their phenotypes depending on the environment. The validity of the ESS computation critically depends on the choice of the candidate functions, and sometimes a wrong choice of a class of functions results in qualitatively different conclusions (e.g. an example in sex change of fish, see Iwasa (1991)). More importantly, the need to specify the functional form makes it difficult to consider organisms' response to multiple environmental factors. To overcome these difficulties, we need a more flexible methodology to search for the ESS reaction norm without specifying much in advance what it is like.

In the second half of this paper, we propose an alternative method of finding an ESS reaction norm -- we construct candidate reaction norms expressed in terms of a three-layer neural network, which is known to be flexible enough to simulate any complex functional form (Ishikawa, 1990). Then we can choose a number of

parameters, weights and biases, included in the network to realize a reaction norm that is close to the ESS.

The usefulness of the neural network modelling of an organism's reaction to diverse stimuli is most clearly shown by the studies of the evolution of female mate preference for males of various shapes and patterns (Enquist and Arak, 1993, 1994; Johnstone 1994) or pollinator choice of flower shape (Arak and Enquist, 1993). A neural network was also adopted to express a reaction norm of each individual in group formation process of birds (Toquenaga et al., 1994). However, in these and other papers using neural network models, an explicit ESS solution is not available, hence we cannot confirm that the network is close to the valid ESS. In the present paper, we apply the neural network modelling to the case in which an explicit ESS solution is also available, and we examine carefully the conditions in which the new method converges to the valid ESS.

In doing the random search for suitable parameter values, we face a common problem of being trapped in local peaks if we adopt the usual gradient methods for optimization. To overcome this difficulty, we here use a genetic algorithm (or GA) (Holland, 1985; Davis, 1990; Michalewicz, 1994). The parameters are stored as an array, and a population of these arrays with some variation is generated. Through an evolutionary operation including reproduction, survival, competition, dispersal, and crossing-over, the evolutionarily stable array of parameters are found. We may regard this procedure as a simplified simulation of genetic evolution.

In this paper, we study the performance of the method for different choices of parameters in genetic algorithm procedures, such as mutation rates, variance of mutation, and crossing-over.

1.2 Model

We consider a population consisting of many sites (or local habitats), in each of which only a single adult survives, as is assumed in Hamilton and May (1977). The reproductive success in a site depends on the "quality" of the environment, which fluctuates among sites and over generations. Let m be the resource level at a site. We first study the case of uncorrelated environmental fluctuation, in which m is a stochastic variable, independent between sites and over generations following the

identical probability distribution $f(m)$. Later we consider the case in which m may be correlated between sites in the same generation.

The adults produce two types of offspring: dispersers and nondispersers. We here assume that the costs of producing a dispersing offspring and a nondispersing offspring are the same.

The fraction of dispersing offspring of a mother is denoted by v , which satisfies $0 \leq v \leq 1$. It may be affected by the genotype of the parent as well as by the quality of the environment m in general. In this paper we do not specify the mechanism for the control of wing dimorphism although simple genetic models have been proposed considering juvenile hormone (JH) level influencing the traits of migratory syndrome (e.g. Fairbairn, 1994).

In this model one generation cycle consists of three stages:

1. **Reproduction:** At the start of a season, an adult produces offspring which may be either of the dispersing type or of the nondispersing type. The number of eggs produced by an adult depends on the environmental condition fluctuating between years. Resource level of a patch m is equal to the number of offspring (eggs or seeds) produced in a patch. We call m the quality of the environment. The fraction of migrants is a function of both the mother's genotype and the quality of the patch. Let $v(m)$ be the fraction of dispersing type as a function of the total number of offspring m , given for a particular genotype of the mother. Hence $mv(m)$ is the number of dispersing type offspring and $m(1-v(m))$ be the number of offspring staying in the patch.
2. **Dispersal:** Dispersing type daughters emigrate from the natal site and settled into other patches chosen at random. Dispersal type offspring produced from all the sites are pooled and then redistributed randomly. Hence migrants from a site arrive at any of the other sites with equal probability. The survivorship during migration is p (< 1).

The loss due to migration appears not only as reduced survivorship but also reduced fecundity, which is the cost of migration capability (Roff and Fairbairn, 1991; Tanaka, 1994; Zera and Mole, 1994; Zera and Denno, 1997), but for simplicity of argument we here neglect this effect.

3. **Competition:** After the dispersal stage, competition occurs among individuals in each site. Only one individual wins and reproduces. The probability of being the winner is the same between migrants and residents.

From the assumption of asexual reproduction, the interests of a mother and her daughter are the same. Environment in the next generation is unpredictable. The evolutionarily stable strategy (ESS) for the mother is simply to maximize the expected number of sites in which one of her offspring is the winner. We here assume that the

final population includes a single genotype that is evolutionarily stable although natural insect populations are often genetically polymorphic with respect to the propensity to produce winged and wingless types (Roff, 1994a, 1994b).

Evolutionary stable reaction norm:

Consider a mother with a genotypic reaction norm of v , indicating that she produces dispersing type offspring with fraction $v(m)$ in the patch of quality m , in the population where a single genotype denoted by \bar{v} is common. Let $\phi(m)$ be the expected number of surviving offspring produced by her if the resource level is m . Due to competition among individuals, the number of surviving offspring $\phi(m)$ also depends on the common genotype \bar{v} . Hence it should be expressed as a function of resource level m , the migration strategy of itself $v(m)$, and the migration strategy of competitors $\bar{v}(m)$. The fitness of the genotype in a population, denoted by W , is the average of $\phi(m)$ with respect to the distribution of resource level m . Using the symbol $E_m[\cdot]$ for the average with respect to the quality of a site m experienced by the mother, the fitness is written as:

$$W = E_m[\phi(v(m), m | \bar{v}(\cdot))] \quad (1a)$$

The number of surviving offspring produced by a mother is the sum of two terms:

$$\phi(v(m), m | \bar{v}(\cdot)) = E_c \left[\frac{m(1-v(m))}{m(1-v(m)) + c} \right] + mv(m)pE_m \left[E_c \left[\frac{1}{1 + m'(1-\bar{v}(m')) + c} \right] \right] \quad (1b)$$

The first term of the right hand side of Eq. (1b) is the probability that one of her nondispersing offspring survives in the natal site, and the second term is the the expected number of the surviving offspring that disperse to other sites. The product $m(1-v(m))$ in the first term is the number of offspring remaining in the natal site. c is the number of competitors that invaded from other sites; it follows a Poisson distribution with average $\bar{w} = E_m[pm \bar{v}(m)]$. In Eq. (1b), $E_c[\cdot]$ indicates the average with respect to c , the number of invading competitors. Because they have the same competitive ability, the probability of a mother's offspring winning the site is simply the fraction of her offspring among all the individuals arriving there.

Dispersers are first pooled and then redistributed over all the sites. Because the whole system includes a large number of sites, we can neglect the probability that more than one of the dispersers produced by a mother settles on the same site. In the second term of Eq. (1b), $mv(m)$ is the number of offspring that disperse from the site and p is the survivorship of dispersers. The success rate of an individual arriving safely on a site is simply the inverse of the total number of individuals arriving there. It is the sum of the number of residents $m'(1-\bar{v}(m'))$, the number of migrants from the other patches c , and 1, indicating itself. $E_m[\bullet]$ indicates the average with respect to the quality of sites m' .

The evolutionarily stable reaction norm of this model is given by a function $v(m)$ that achieves the highest fitness in a population dominated by individuals of the same type. The maximum of the fitness W is achieved by choosing v given resource level m . This can be done simply by choosing the optimal $v(m)$ that maximizes ϕ for each given m . Noting that fraction v is constrained to be within an interval $0 \leq v \leq 1$, we have the following relation at the ESS:

$$\frac{\partial \phi}{\partial v} = 0 \quad , \quad \text{if } 0 < v < 1 \quad , \quad (2a)$$

$$\frac{\partial \phi}{\partial v} \leq 0 \quad , \quad \text{if } v=0 \quad , \quad (2b)$$

$$\frac{\partial \phi}{\partial v} \geq 0 \quad , \quad \text{if } v=1 \quad , \quad (2c)$$

because migration fraction v is chosen to be the optimal value in the population dominated by the same type. Equation (2a) implies that $\partial \phi / \partial v = 0$ if both dispersers and nondispersers are produced at the ESS. We calculate the partial derivative with respect to v with $v(m')$ fixed, and then set $v(m) = \bar{v}(m)$:

$$\begin{aligned} \frac{\partial \phi}{\partial v} &= E_c \left[\frac{-mc}{(m(1-v(m))+c)^2} \right] + mp E_{m'} \left[E_c \left[\frac{1}{1+m'(1-\bar{v}(m'))+c} \right] \right] \\ &= m \left\{ E_c \left[\frac{-c}{(m(1-v(m))+c)^2} \right] + [\text{a term independent from } m \text{ and } v] \right\} . \end{aligned} \quad (3)$$

For $0 < v < 1$, Eqs. (2) tells that Eq. (3) is zero. Hence $m(1-v(m))$ is independent of m . By considering other cases ($v=0$ or 1), we have

$$\bar{v}(m) = \begin{cases} 1 - \frac{k}{m}, & \text{for } m \geq k \\ 0, & \text{for } 0 \leq m < k \end{cases} \quad (4)$$

Equation (4) implies that no disperser should be produced if the total number of offspring is small ($m \leq k$) but some dispersers should be produced if the total number of offspring exceeds a critical level k . The optimal value of k which satisfies $\partial\phi/\partial k = 0$ depends on the distribution of patch quality $f(m)$. The expected number of offspring ϕ given by Eq. (1b) is the sum of the two terms: indicating the fitness from nondispersing offspring, and the fitness from dispersing offspring. We compare their marginal increase when k increases by unit amount. The partial derivative of the first term of ϕ with respect to k is,

$$\frac{d}{dk} \left(E_c \left[\frac{k}{k+c} \right] \right) = E_c \left[\frac{k}{(k+c)^2} \right] \quad (5a)$$

which indicates the marginal increase of fitness through producing nondispersing offspring by using larger k . The partial derivative of the second term of Eq. (1b) is,

$$\begin{aligned} -p E_m \left[E_c \left[\frac{1}{1+m'(1-\bar{v}(m'))+c} \right] \right] \\ = -p \left(E_{m' \geq k} \left[E_c \left[\frac{1}{1+k+c} \right] \right] + E_{m' < k} \left[E_c \left[\frac{1}{1+m'+c} \right] \right] \right) \end{aligned} \quad (5b)$$

which indicates the decreasing rate of success from dispersing offspring when she uses larger k . For $\partial\phi/\partial k = 0$ to hold, these two must be equal in magnitude.

The optimal k can be obtained by iterative computation as follows:

- [1] First, set k to zero.
- [2] Then, calculate the average number of invaders in a patch $\bar{w} = E_m [pm\bar{v}(m)]$ using Eq. (4).

- [3] We examine whether k satisfies the optimization condition $\partial\phi/\partial k = 0$. For small k , the sum of Eq. (5a) and Eq. (5b) is larger than zero. If the magnitude of Eq. (5a) becomes smaller or equal to the one of Eq. (5b) from the first time, which means $\partial\phi/\partial k \leq 0$, k is regarded as an appropriate value. Otherwise we increase k and go back to step [2].
- [4] Iterate step [2] and step [3] until Eq. (5a) becomes small or equal to Eq. (5b).

A result similar to Eq. (4) has been obtained in several previous theoretical works on the evolution of dispersal rate (e.g. Crespi and Taylor, 1990; Ozaki, 1995).

1.3 Neural network model of reaction norm and genetic algorithm

In the model studied in the present paper, the evolutionarily stable reaction norm can be calculated explicitly. This is, however, not possible in general. For such cases we need to simulate the evolutionary replacement of genes that cause individuals to have a different reaction norm $v(m)$. In a typical case, we first choose a class of candidate functions that include a few parameters determining the shape of the function, and then examine the "evolution" of these parameters. The choice of the class of candidate functions is very important for the success of this method, because we will not be able to reach a correct answer if the chosen class of functions does not include a function similar to the correct ESS solution. To avoid such a situation, we need to choose a class of candidate functions that are sufficiently flexible to imitate any complex form of functions.

Neural network model of reaction norm

To formulate the reaction norm, we use a neural network of feed forward type which is a method to generate an input-output relationship in a very flexible way. A neural network gives the fraction of migrant v (output) as a function of quantities that might affect the decision making of the organism, such as the environmental quality of the patch m . Figure 1 illustrates the structure of the neural network we used, which has been adopted in modelling the regulatory region of developmental genes (Takeda, 1993; Takeda and Iwasa, 1997).

The neural network is composed of three layers (input, intermediate, and output layers). First and second layers contain multiple units (neuron), but the third is a single unit. Each unit receives input from the units in the previous layer and give output to some units in the next layer. Let x_k be the input of the system, and y_k be the output of the k -th neuron in the input (first) layer:

$$y_k = \frac{1}{1 + \exp(-x_k + a_k)} \quad , \quad (6a)$$

which is a sigmoid function increasing from 0 to 1, and the transition is centered around a_k . We call a_k "bias" in this paper. Let z_j be the state of the intermediate layer which is

$$z_j = \frac{1}{1 + \exp\left(-\sum_k w_{kj} y_k + b_j\right)} \quad , \quad (6b)$$

where w_{kj} is the "weight" of neuron y_k in affecting the state of intermediate layer z_j . Parameter b_j is the bias for the j -th neuron of the intermediate layer. The output of the system is:

$$v = \begin{cases} 0 & \sum_k w'_j z_j \leq 0 \\ \sum_k w'_j z_j & 0 < \sum_k w'_j z_j < 1 \\ 1 & \sum_k w'_j z_j \geq 1 \end{cases} \quad , \quad (6c)$$

where w'_j is the weight for the signal from the j -th neuron in the intermediate layer. Weights (w_{kj} , w'_j) and biases (a_k , b_j) may vary between individuals in the population. Equations (6a) and (6b) are of a sigmoidal function, while Eq. (6c) is linear. We found that the network cannot produce a good result if sigmoidal functions are assumed for the third layer as well. The function for the neurons in the output layer was chosen as Eq. (6c), in order to realize zero output.

It has been proved that, with suitable choice of the weights, a three-layer neural network can imitate any complex input-output relationship if the number of neurons in the intermediate (hidden) layer is large (Ishikawa, 1990). However whether or not we can search for the set of parameters that gives a sufficiently accurate input-output relationship is a question that requires separate examinations.

To imitate a function of a single independent variable, i.e. $k = 1$, we used seven neurons in the intermediate layer, determined after trial and error and considering the limitation of available computational resources. As explained later, we used a larger network for the case of multiple input ($k = 2$).

The neural network models are especially useful if the number of input variables is large, and if we have no prior information on the shape of correct ESS. On the other hand in these cases, we cannot compare the neural network model with the exact ESS solution. To examine the degree of deviation of the network model and the condition in which it gives the correct answer, we here apply the neural network model to the simple case in which the explicit solution is separately obtained.

Genetic algorithm

We adopted a genetic algorithm to "evolve" the neural network and to obtain the evolutionarily stable reaction norm. Genetic algorithm is an engineering method to search for the optimal solution by the operations of mutation and selection in a hypothetical population of sequences, where each sequence codes for a method of designing or controlling the object to optimize. It has been used quite extensively in engineering when a mathematically tractable model of the object is difficult to construct (Holland, 1985), and has also been adopted in behavioral ecology (Sumida et al., 1990; Toquenaga et al., 1994; Johnstone, 1994; Kamo et al., 1997), in the evolution of signalling (Enquist and Arak, 1993; Johnstone, 1994), and in human sociobiology (Johnstone and Franklin, 1993).

The method can be regarded simply as an efficient technique to search for the evolutionarily stable state, rather than a simulation of genetic dynamics, but it may also be regarded as a simplified computer simulation of evolutionary process, although we did not attempt to make biologically plausible assumptions on the genetic system coding for the networks. We call a set of parameters of a neural network (a_k , w_{kj} , b_j , and w'_j) the "genotype" of an individual, which determines the strategy responding to the environment.

In our simulations for the case of single input model, the "genotype" of an individual was a set of 22 parameters (weights and biases) of a neural network. These numbers were arranged on four series, $\{a_k\}$, $\{w_{kj}\}$, $\{b_j\}$, and $\{w'_j\}$, each of which is called "chromosome". The population was composed of $N=100$ individuals, which represent adults occupying 100 sites. In each time step, which we call a generation, there were the following operations (Fig. 2a):

1. Mutation: Each parameter experiences mutation with the probability of u_w for weights, and with the probability of u_b for biases (a_k, b_j) in each generation. If mutation occurs for one of the weights or biases, then it is added by a random variable following a normal distribution with mean 0 and variance σ^2 (Fig. 2b).
2. Crossing-over: Crossing-over is the procedure comparable to genetic recombination, as it allows the construction of a mixture of genomes of different individuals. However, unlike genetic recombination, crossing-over in the genetic algorithm used in our simulation occurs in a stage separate from the process of reproduction or multiplication. With probability of r , recombination rate, another individual is randomly chosen, two recombinants are made and replace the original two individuals. We adopted two different ways to produce recombinants from given two individuals. The first one is "separate-chromosome mode" in which we choose one of the two parents randomly and independently for each parameter sets, treated as if each parameter sets are coded in different chromosomes (Fig. 2c). The second is "bound-chromosome mode" in which three chromosomes ($\{w_{kj}\}$, $\{b_j\}$, and $\{w'_j\}$) are bound with each other at the both ends so that there are linkage between parameters on the different chromosomes (Fig. 2d). This mode of crossing-over is more likely to preserve the local structure of the neural network than the first mode.
3. Reproduction: Each individual reproduces according to the quality of the site m .
4. Dispersal: The fraction of offspring that should disperse is computed based on the reaction norm generated by the neural network with parameters for the individual. A nondispersing offspring would stay in the natal site where it was born. A dispersing individual is killed randomly with probability $1-p$, and if it survives, it would land on one of the sites different from the parent.
5. Selection: After the migration stage, all the individuals successfully land on a site, both migrants from other sites and residents, are equal in the chance of winning the sites. One of them is randomly chosen and contributes to the following generation.

The initial condition was composed of 100 individuals whose weights and bias were randomly generated from a uniform distribution independently between individuals. After 100,000 generations, the system converged to the equilibrium and was then run additional 1000 generations during which mutation and recombination were suppressed. After this 1000 generations, the population becomes dominated by the type of the highest fitness. We then generate the fraction of dispersing offspring for different values of input factors using the network in the final population -- which is the reaction norm obtained by the method of neural network - genetic algorithm modelling.

1.4 Reaction norm of learned network

We assumed that the number of eggs laid by individuals followed an independent uniform distribution. After 100,000 generations, the reaction norm generated by the trained network reached an approximate asymptote.

We evaluated the success of convergence of a neural network trained by the genetic-algorithm by comparing the reaction norm of the network and the one predicted analytically by Eq. (4). To quantify the failure of convergence, we use V , defined as the sum of squared difference of the number of migrants $mv(m)$ between these two values over a range of m used in our computation ($1 \leq m \leq 100$).

Examples of the reaction norm generated by the trained network are illustrated in Fig. 3a. Solid lines are true ESS computed by Eq. (4). Vertical axis indicates the fraction of dispersing offspring $v(m)$ for different quality variable m . Circles are for the run in which the reaction norm generated by the trained network is fairly close to the analytical result. Figure 3b shows the same data as Fig. 3a, except for indicating the number of dispersing offspring $mv(m)$.

When the neural network failed to converge to the ESS, the reaction norms often shows one of the several characteristic patterns. Figure 3a illustrates a few typical cases. Diamonds show a typical pattern of constant dispersal rate independent of the site quality experienced by the mother. In contrast, triangles show another typical case in which dispersal rate generated by the network is a step function -- no migration occurs for density below a threshold and dispersal rate is almost a constant for density above it. It is convenient to evaluate the goodness of the convergence V , the sum of squared difference of the migrant $mv(m)$ between the one predicted by the network and the valid ESS given by Eq. (4). We evaluated $V=215$ for circle plots, but $V=7134$ and $V=3174$ for diamonds and triangles, respectively.

To distinguish parameter sets for good convergence and for bad convergence, plotting the average values of V gave no clear result because the case in which the process failed to converge would show a very large V . Instead we counted the number of times in which the 5 replicates for each set of mutations for weights and biases V was smaller than 1000, which are listed in Fig. 4a-h.

The effect of mutation rates:

Figure 4a illustrates cases of no recombination ($r = 0$). Each box is distinguished by the number of runs among 5 replicates that resulted in $V < 1000$.

Mutation rate for biases are examined for 5 levels: $u_b = 0.001, 0.0001, 0.00001, 0.000001,$ and 0.0 ; mutation rate for weights are examined also for 5 levels: $u_w = 0.05, 0.01, 0.001, 0.0001,$ and 0.00001 . Mutational variance was fixed $\sigma^2 = 100$. There are a range of optimal mutation rates for good convergence. With a very large mutation rate for the biases, and with both large and small mutation rates for the weights, no runs converge to the valid ESS.

We have also examined the network with a larger mutational variance $\sigma^2 = 400$. The results are shown in Fig. 4b. The performance was not very different from the case with $\sigma^2 = 100$.

The effect of crossing-over rate:

Figure 4c-f show the results for positive crossing-over rate: $r = 0$ (Fig. 4a), $r = 0.005$ (Fig. 4c), $r = 0.01$ (Fig. 4d), $r = 0.02$ (Fig. 4e), and $r = 0.05$ (Fig. 4f). The separate chromosome mode was adopted.

From these results, we can conclude that the recombination improves the fraction of good convergence, although too large rate of recombination prevents the network from convergence. However the effect is not very large.

There were no difference detected between different modes of recombination and different rates of recombination. For example, Fig. 4g shows the case with $r = 0.01$ with bound-chromosome mode was also examined, but it was not more successful than the corresponding separate-chromosome mode (Fig. 4d).

Although based on small number of replications, we conclude that recombination would not create a large improvement in convergence among the range of parameters we examined.

1.5 Correlation of environment between sites

Next we consider the case in which the environmental qualities in different sites are positively correlated as might be caused by the global environmental change such as temperature, moisture etc.. In such a case, the organism can improve its fitness by knowing not only the quality of its own site but also the average quality over the population in the same generation, because a higher quality in other sites indicates more

competitors. To be specific, we assume that the environmental quality of the i th site in year t is:

$$m_{i,t} = \bar{m}_t + \xi_{i,t}, \quad (7)$$

where \bar{m}_t is the general quality of year t , and $\xi_{i,t}$ is the deviation of the environmental quality in site i from the average over all the sites of the same year. We assume $E[\xi_{i,t}] = 0$.

A mother should determine the fraction of dispersing offspring by knowing both $m_{i,t}$ the quality of the environment and \bar{m}_t the average quality of all the environment, indicating abundance of competitors invading the site. We assume that \bar{m}_t is known based on some additional information. Let $v(m_{i,t}, \bar{m}_t)$ be the fraction of dispersing offspring. The fitness W is the average of the expected number of offspring from a mother experiencing the quality of the site m in a generation with average quality of \bar{m}_t , and its genotype is $v(m_{i,t}, \bar{m}_t)$:

$$\begin{aligned} \phi(v(m, \bar{m}), m, \bar{m} | \bar{v}(\bullet, \bullet)) = & E_c \left[\frac{m(1 - v(m, \bar{m}))}{m(1 - v(m, \bar{m})) + c} \mid \bar{m} \right] \\ & + mv(m, \bar{m}) p E_m \left[E_c \left[\frac{1}{1 + m'(1 - \bar{v}(m', \bar{m})) + c} \mid \bar{m} \right] \mid \bar{m} \right], \quad (8) \end{aligned}$$

where \bar{v} is the genotype dominating the population. In Eq. (8), the number of competitors c is assumed to follow a Poisson distribution with the average of $\bar{w} = E_m[p m \bar{v}(m, \bar{m}) | m]$. $E_c[\bullet | \bar{m}]$ and $E_m[\bullet | \bar{m}]$ are now the conditional averages when \bar{m}_t is given.

For fixed \bar{m} , the optimization of ϕ with respect to m is the same as before and the optimum fraction of dispersers is given by Eq. (4). However the threshold k depends now on \bar{m} .

$$\bar{v}(m, \bar{m}) = \begin{cases} 1 - \frac{k(\bar{m})}{m}, & \text{for } m \geq k(\bar{m}) \\ 0, & \text{for } 0 \leq m < k(\bar{m}) \end{cases}, \quad (9)$$

where $k(\bar{m})$ is determined numerically from Eq. (5).

The evolutionarily stable reaction norm thus calculated should depend both on the environmental quality of the site m in which the parent experiences and the average environmental quality of the whole population \bar{m} . Figure 5 illustrates that the predicted ESS number of dispersing offspring increases with the environmental quality of the generation \bar{m} .

We have also done genetic algorithm search for the ESS. The neural network indicating the reaction norm of the parent should have two input factors: the environmental quality of the patch $m_{i,t}$ and the average environmental quality in that year \bar{m}_t . The neural network needs to be larger to be able to "learn" the reaction norm for two input factors, than the case for one input. We used a neural network of 2 neurons in the input layers and 11 neurons in the intermediate layer. Thus the total number of parameters included in a network is 46. Parameters of mutation rates are $u_b = 0.000001$, $u_w = 0.001$, mutation variance is $\sigma^2 = 100$, and recombination rate is $r = 0.1$ (separate-chromosome mode), which are the value for the fastest convergence in the last section.

Results of the GA training are plotted in Fig. 5 by dotted lines. The network could learn to respond to both the quality of the current site and the average quality of the whole population. A genetic algorithm search for the ESS solution successfully converged to the ESS solution.

1.6 Discussion

Many aspects of life history evolution can be formulated as the condition-dependent decision making of a phenotype, and then can be modelled as a mapping from input variables (e.g. density, temperature, food level, fat content etc.) to the phenotype (e.g. fraction of dispersal type, sex ratio, timing of reproduction, size of maturation, diapause). The mapping may give a probability for a certain life history event to occur under given conditions.

In this paper we have been analyzing the condition-dependent dispersal in which each individual offspring is either a dispersing type or a nondispersing type. The dispersal dimorphism of insects has been considered as a condition dependent strategy adopted under unpredictable environments (Gatehouse, 1994; Roff, 1994a, 1994b).

The present model is also applicable to those plants in which some seeds have pappi with large dispersing ability while other seeds have none (Geritz, 1995). The dispersal range of seeds of most terrestrial plants are much smaller than the whole range of the population, and we may need to consider the evolutionarily stable dispersal range rather than the dichotomy of dispersing and nondispersing seeds (Ezoe, unpublished manuscript). For terrestrial plants, the dispersal tendency is likely to change with successional status (Olivieri et al., 1995).

The traditional approach of evolutionary game theory and optimization requires us to specify a set of feasible strategies within which the optimal strategy is sought. Specifying a feasible strategy set would require at least a rough picture of what the ESS solution should be. The limitation of mathematically tractable cases has restricted the range of questions we can answer and hence our scope on the evolutionary processes. One way to overcome this difficulty is to start with a flexible class of candidate functions, which is likely to include the one close to the true ESS. To model a potentially complex function from input to output, a neural network model is useful. Then we can use a random search method, such as the genetic algorithm to identify the evolutionarily stable type.

Introducing neural network models sometimes allows us to handle complex biological traits that cannot be done by traditional modelling techniques. This is illustrated most clearly by the evolutionary theory of female mate preference for a male with an exaggerated ornament. Most models of sexual selection, both quantitative genetic and signalling game models, discuss the evolution of a single male trait (e.g. Lande, 1981, Iwasa et al., 1991; Pomiankowski et al., 1991; Grafen, 1990), and a few analyze the evolution of multiple (just two) traits (Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994; Johnstone, 1995). Enquist and Arak (1993) introduced neural network modelling of female visual system in order to discuss the preference evolution for the male's shape or pattern, and let them evolve to discriminate males of the correct species from those of the wrong species. A three-layered neural network was used to represent the female's mate preference, which consists of 6 by 6 receptor cells arranged on a regular square lattice, 10 hidden cells, and one output cell. They reported that the trained networks were attracted by "supernormal stimuli" where there was a greater response to an exaggerated form than to the images used as the correct species for training. Arak and Enquist (1993) trained networks to discriminate flowers that had petals of different lengths, which again resulted in a bias in pollinators' preference. The evolution of symmetrical visual patterns was discussed in Enquist and Arak (1994) and Johnstone (1994). Thus a new set of questions started to be asked once neural network modelling was introduced. Recently, Kamo et al. (1997) have

examined Enquist and Arak's (1993) model in detail and reported that the same network model often shows no supernormal stimuli, contrary to Enquist and Arak, which illustrates the need for careful examination of the training procedures in neural network modelling.

An efficient way of searching for the evolutionarily stable network is the genetic algorithm, which imitates the population genetic dynamics and evolution in the computer. Genetic algorithms have been adopted in behavioral ecology to search for the optimal solution in a complicated situations, such as to dawn chorus of birds as the dynamic optimization of energy budget (Sumida et al., 1990).

In this paper, we examined the fraction of cases with good convergence to the ESS for different mutation rate, mutation variance, recombination rate, and the mode of recombination. We found that there is a range of "optimal parameter sets" that allow the fastest convergence to the valid ESS with a high probability. A limited numerical study in this paper suggests the need for a more extensive study of the general rules: e.g. when the convergence to the ESS is fast, how much time is needed to reach the equilibrium, and how robust is the method?

The neural network modelling may not be simply a way to calculate the ESS. For example, the use of neural network modelling in the sensory system has identified many nonadaptive natures of the evolved network, such as supernormality, peak shift, generalization, propensity for symmetric shape and simple coloration (Enquist and Arak, 1993; 1994, Johnstone, 1994). These are unlikely to be explained by the optimization or evolutionary stability, and yet they are considered to be meaningful properties that may explain many features of the female sensory system and exaggerated male traits.

The same kind of arguments may also be very useful for the evolution of life history decision making. In this paper, we observed that the neural network did not converge to the exact ESS but instead it converged often to the pattern showing a constant migration rate or a step function of quality (Fig. 3). Since the genetic algorithm can be regarded as a simplified simulation of evolutionary processes, this result implies that the selective difference between the true ESS and these nonoptimal patterns was probably not very great. In such a situation, and in a finite population, it should not be surprising if the system has an inherent bias of evolution toward one of these patterns rather than the true ESS. If there is a propensity to evolve a reaction norm with some characteristic biases, as suggested by Fig. 3, this might explain some of the reaction norms shown by organisms in the field. In such a case, the systematic deviation of the reaction norm to evolve from the valid ESS is not an artefact of the method, but can suggest a particular propensity to a pattern that is easy to evolve. This possibility needs more careful examination.

The formalism of expressing the reaction norm as a neural network and adjusting the weights and biases by genetic algorithm may become a useful approach in the near future, because the speed of computers is rapidly increasing. Using neural network modelling of the reaction norm and training by genetic algorithm, we may construct a network having a variety of cues that are available to the organisms in their decision making. After training with the genetic algorithm, we will end up with the neural network that reacts only to one of a few essential cue(s), suggesting that organisms too might evolve to use only those few cues.

1.7 Figures

Figure 1 Illustration of a three-layer neural network. Note the number of neurons in this figure is differ from the network we used to simulate the reaction norm.

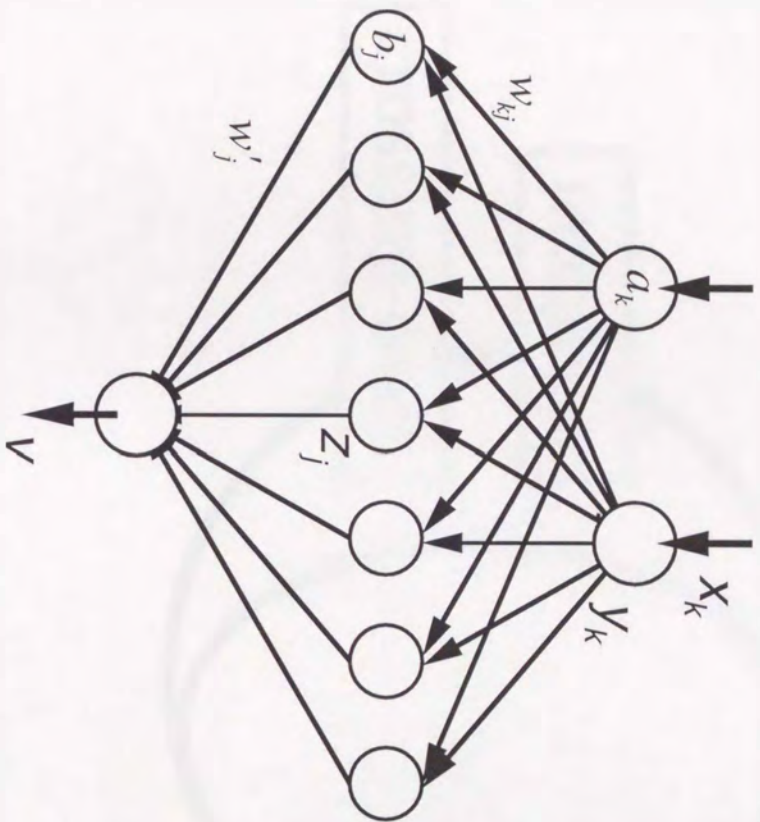
Figure 2 Scheme of a genetic algorithm:(a) the generation cycle, (b) mutation, (c) crossing-over (separate-chromosome mode), (d) crossing-over (bound-chromosome mode). During the last 1000 generations of each trial we used excluding mutation and crossing-over (the inner cycle in (a)).

Figure 3 (a) Reaction norms (the fraction of dispersing offspring) $v(m)$ obtained by the genetic algorithm training of the neural network. Solid lines are the true ESS computed by Eq. (4). Circles are for the reaction norm of a trained neural network with $V=215$ (successful convergence). Diamonds are for that of a network with $V=7134$ (not successful in convergence), in which the reaction norm is a constant fraction of dispersing offspring irrespective of the total number of offspring produce. Triangles are for another case of failure in convergence with $V=3174$. In this case no dispersal offspring is produced below a certain threshold level, and a high dispersal rate above it.
(b) Plotting The same data as (a), except for the vertical axis indicating the number of dispersing offspring $mv(m)$.

Figure 4 The number of times in which the trained network converged successfully to the valid ESS. Cases with different mutation rates of threshold levels (a_i and b_i), and mutation rates of weights (w_{ij}) are shown. The brightness of each box indicates the numbers of replicates that ended up with good convergence ($V < 1000$) among five replicates. (a) $r = 0$, $\sigma^2 = 100$. (b) $r = 0$, $\sigma^2 = 400$. (c)-(f) are positive recombination rate: (c) $r = 0.005$, (d) $r = 0.01$, (e) $r = 0.02$, and (f) $r = 0.05$, with separate-chromosome mode, and $\sigma^2 = 100$. (g) $r = 0.01$ with bound-chromosome mode, and $\sigma^2 = 100$.

Figure 5 Reaction norms for the case of two inputs signals, in the environment in which productivity in different habitats are correlated. The plots indicates the output of the the trained network and the lines indicates the optimal reaction norm obtained analytically. The average quality of sites is: (a) $\bar{m} = 65$, (b) $\bar{m} = 50$, and (c) $\bar{m} = 35$.

Fig. 1



input layer

intermediate layer

output layer

Fig. 2a

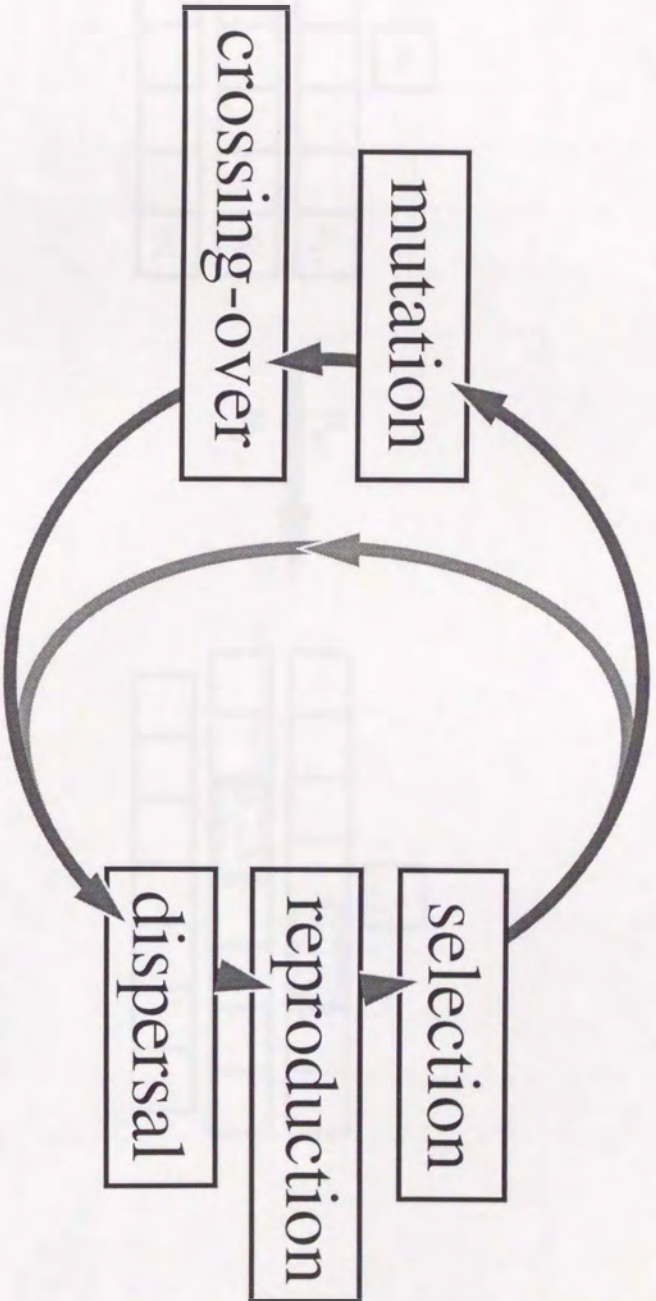


Fig.2b

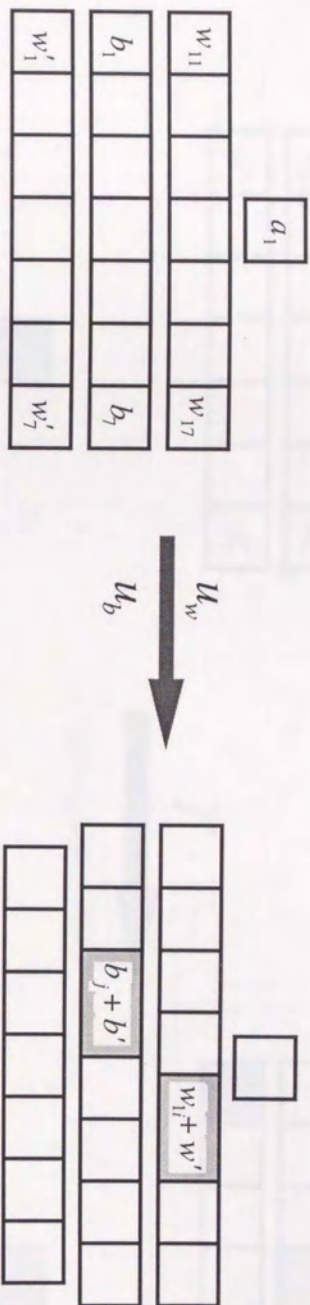


Fig.2c

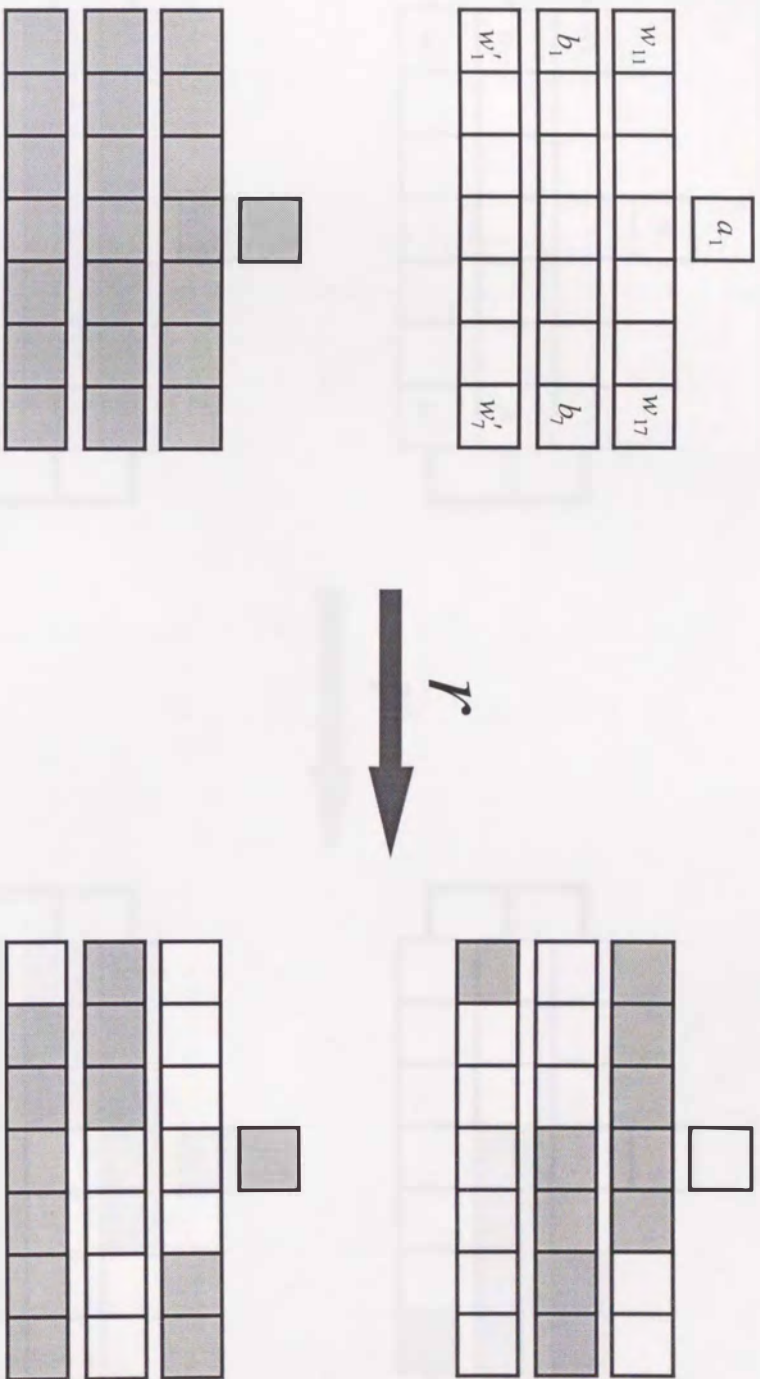


Fig. 2d

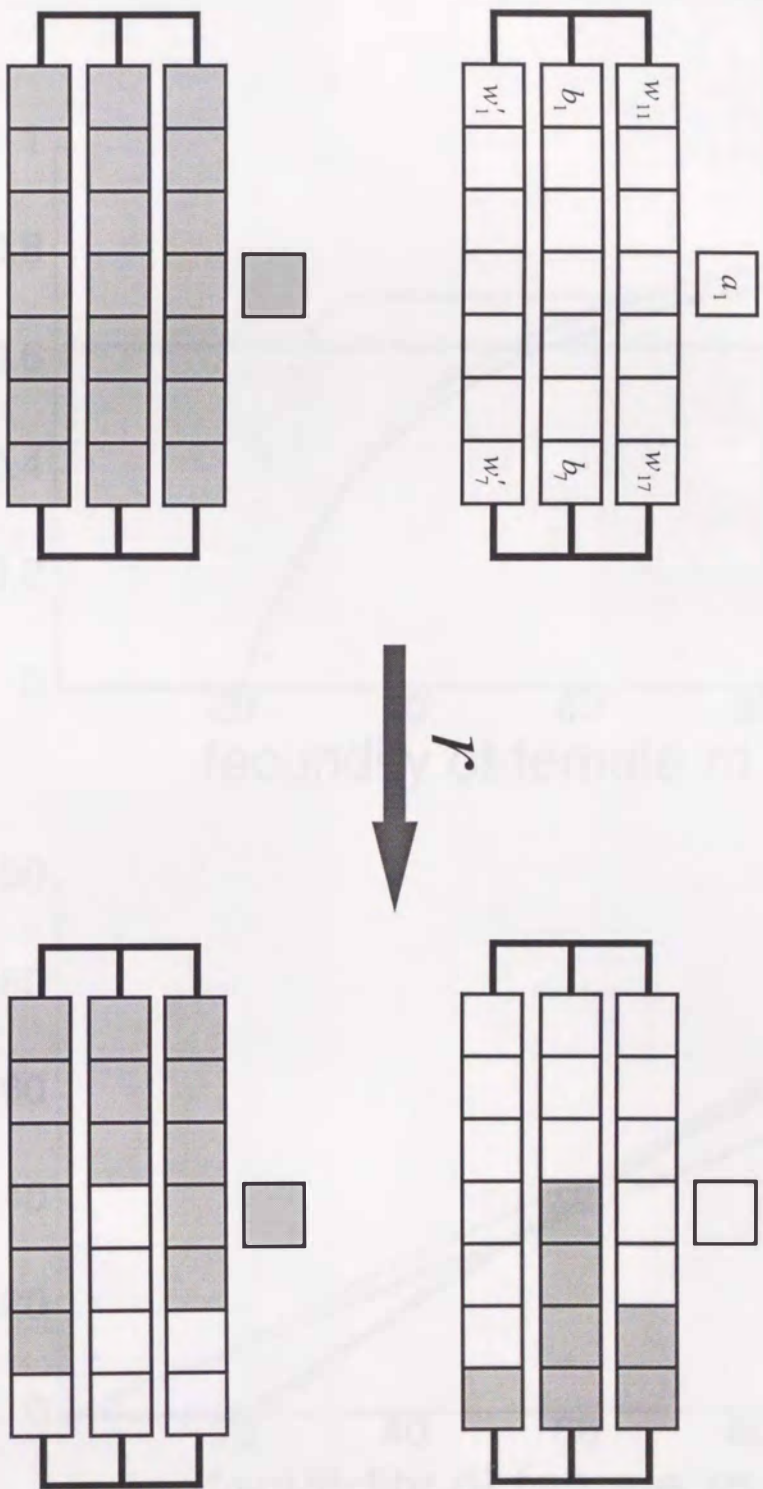


Fig.3

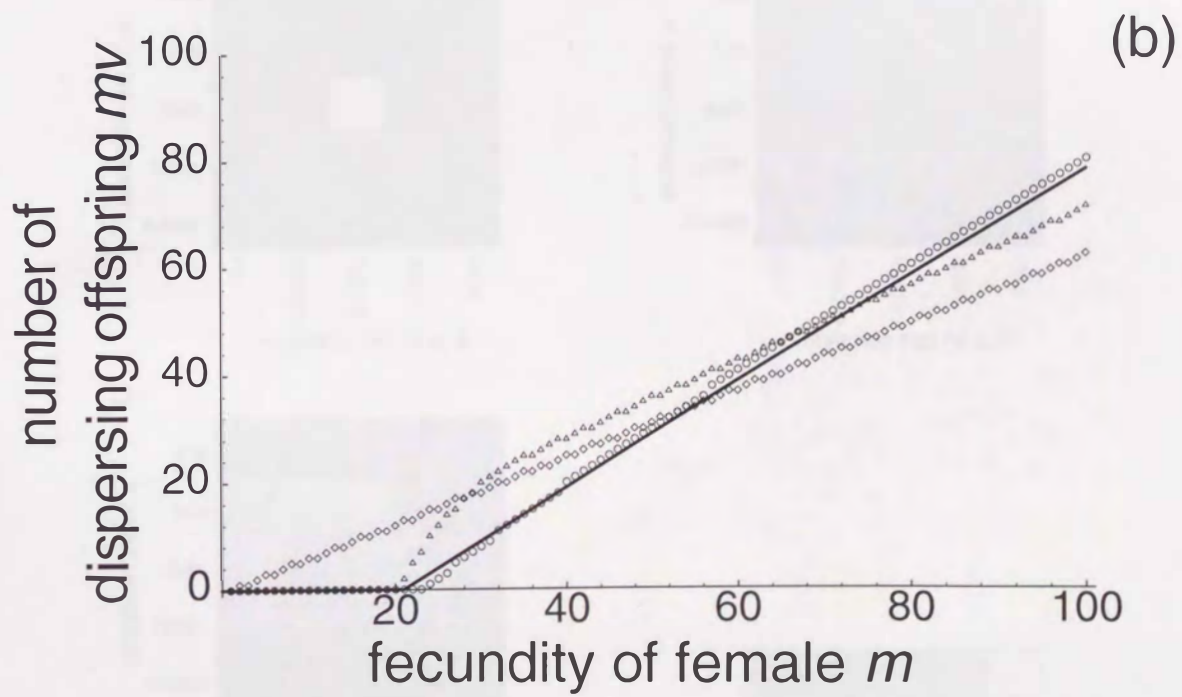
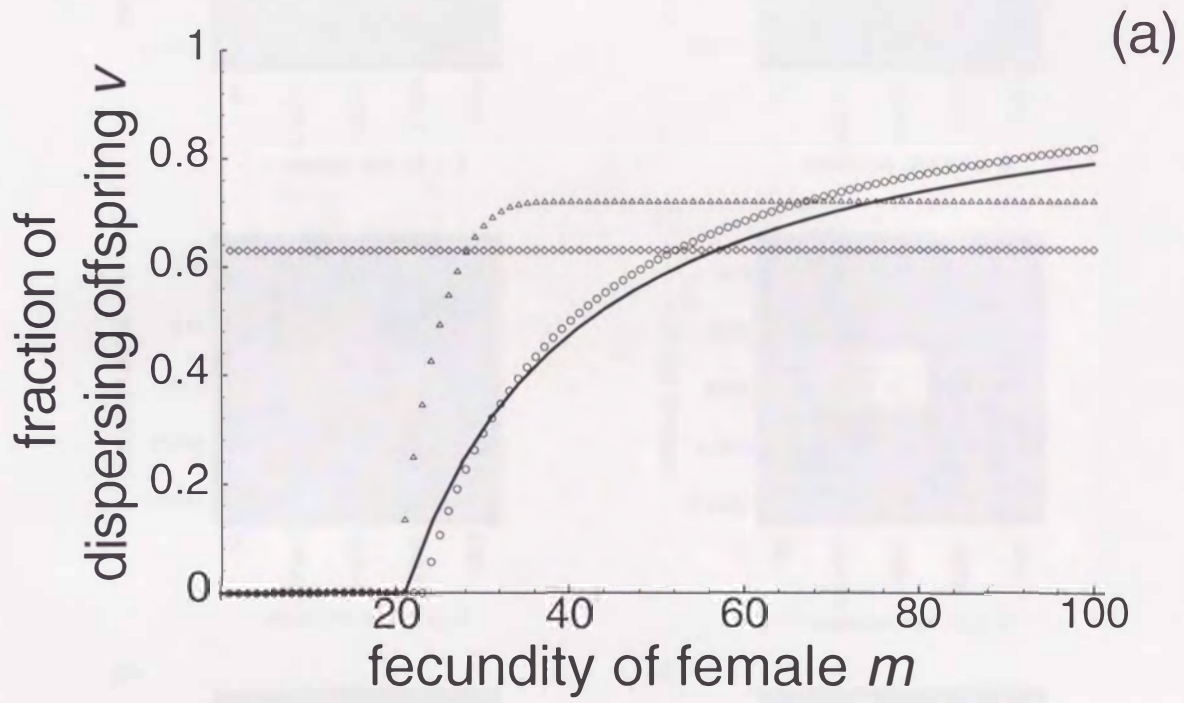


Fig.4

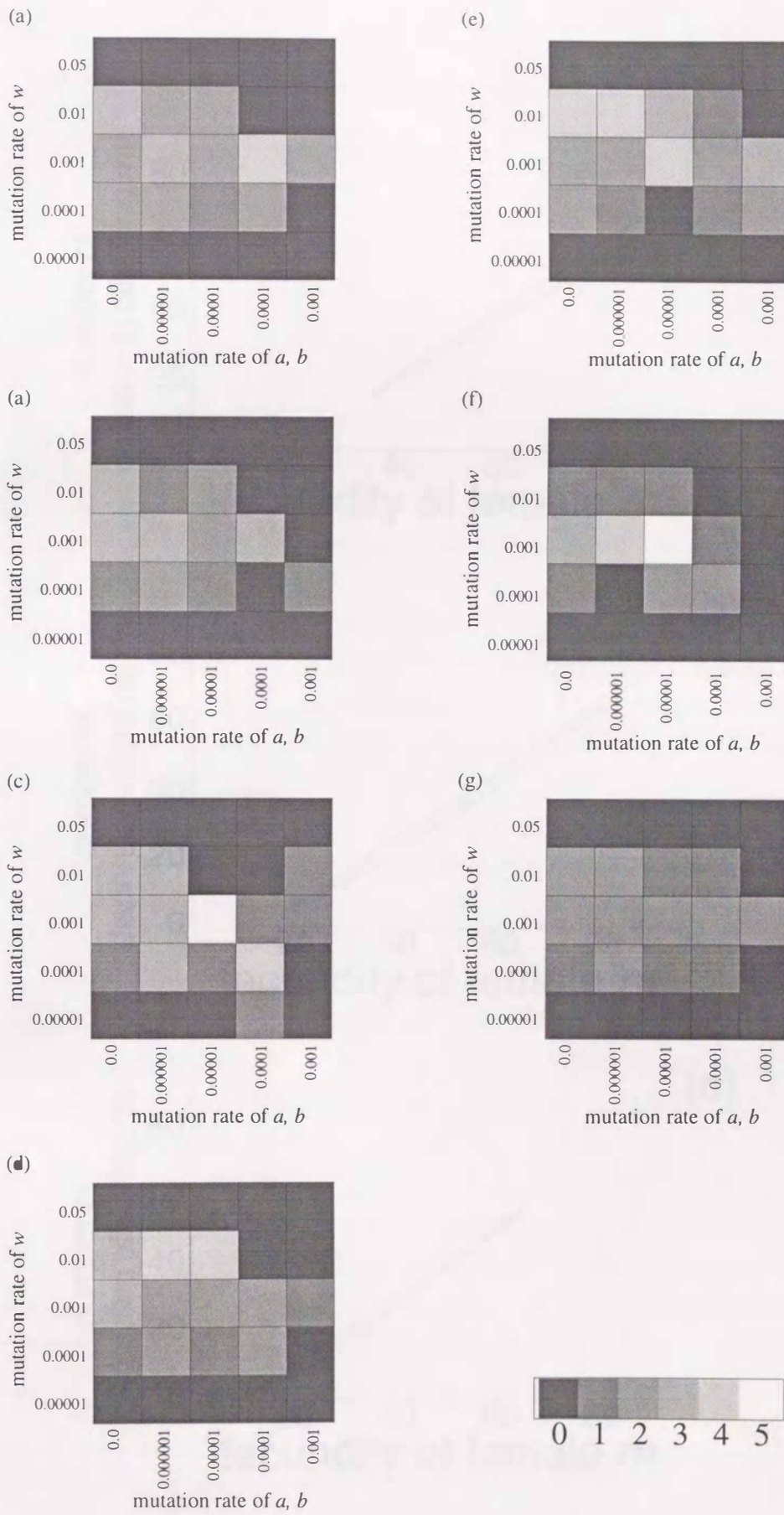
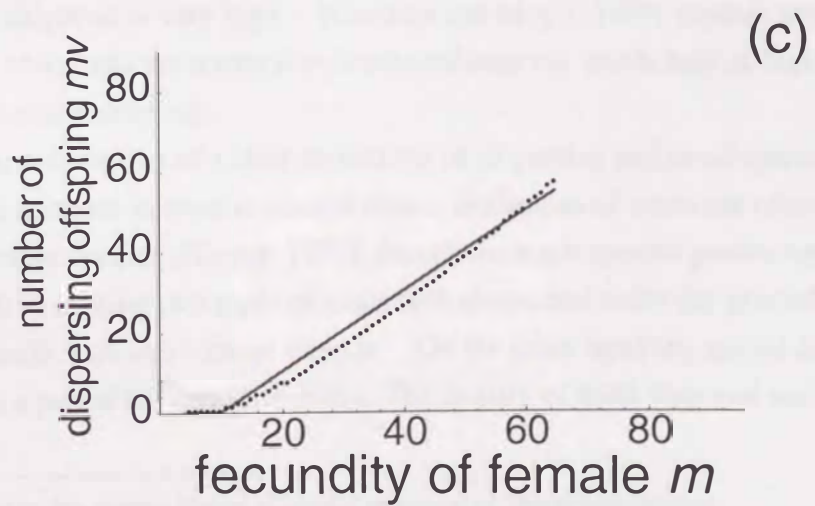
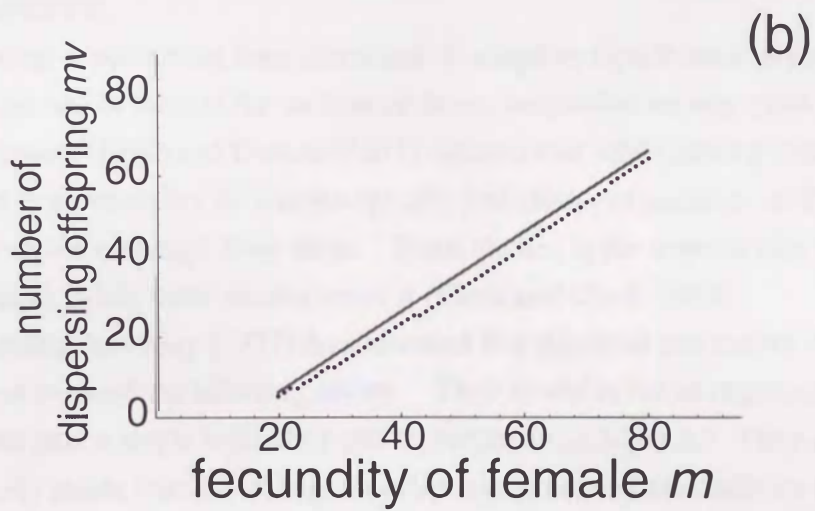
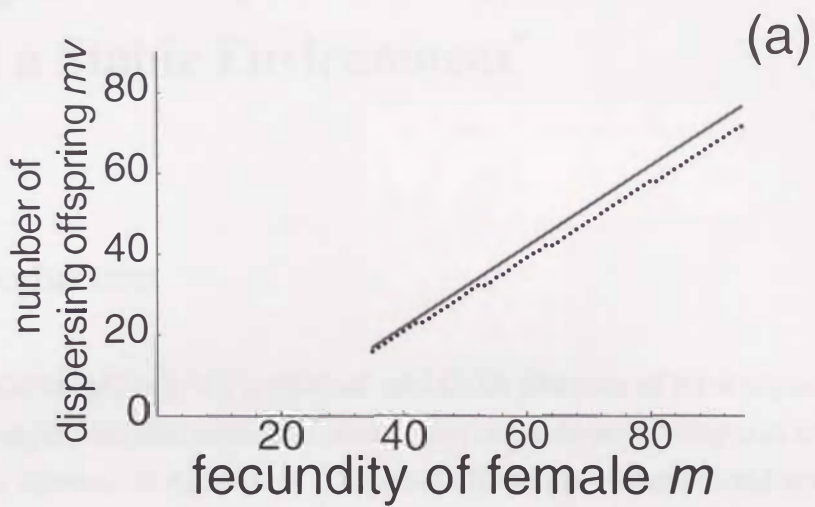


Fig.5



Chapter 2

Optimal Dispersal Range and Seed Size in a Stable Environment*

2.1 Introduction

Dispersal plays a very important role in life histories of most organisms. Sedentary organisms like terrestrial plants have some dispersal stages as seeds, propagules, runners, or rhizomes. Dispersal affects the numerical and genetic dynamics of the population. On the other hand, dispersal traits evolve as an adaptation to the environment.

Several aspects have been discussed on adaptive significance of seed dispersal. An important one of them is the avoidance from competition among close relatives such as sibs. Janzen (1970) and Cornell (1971) claimed that seeds landing near the parent suffer from extra mortality by species-specific predators and parasites so that seed dispersal evolved to escape from them. Some studies in the tropical rain forest support this hypothesis, while other studies reject it (Clark and Clark, 1984).

Hamilton and May (1977) demonstrated that dispersal can evolve in a stable environment to avoid the sib-competition. Their model is for an organism in patchy habitats, and only a single individual can reproduce in each patch. They calculated the evolutionarily stable fraction of migrant offsprings produced asexually by each mother. They show that in the ESS at least half of daughters are migrant even if the mortality cost of the dispersal is very high. Hamilton and May's (1977) models assumed that dispersing offsprings are uniformly distributed over the whole habitat regardless of the distance from the natal one.

The assumption of a clear dichotomy of dispersing and nondispersing offsprings may not be accurate in most terrestrial plants, as the size of seeds are often relatively uniform within species (Harper, 1977), though there are species producing dimorphic seeds, such as making two types of seeds both above and under the ground (Zeide, 1978) or seeds with and without puppus. On the other hand the spatial distribution of seeds from a parent is far from uniform. The density of wind dispersal seeds is the

* The content in this chapter is now submitted to Journal of Theoretical Biology.

highest near the parent and decreases with the distance from the parent (e.g. Okubo and Levin, 1989; Portnoy and Willson, 1993). Seeds which happen to land near the maternal plant suffer severe sibling competition, while in sites distant from the parent sibling competition is milder (Cheplink, 1993).

In this paper, I develop a mathematical model on the evolution of dispersal distance of seeds when the dispersal ability of seeds are dependent on the seed size which also affects competitive ability and the cost of seed production. A negative correlation between seed size and seed dispersal range are often reported (e.g. Green and Johnson, 1993). I examine the effect of size-dependent seed dispersal on ESS seed size and dispersal range.

The shape of the spatial distribution of seed dispersal is assumed to be a two-dimensional normal distribution with dispersal variance small for large seeds and large for small seeds. Seed size also affects the probability of settlement and the number of seeds produced by an individual. Larger seeds are often more tolerant for severe environments, and likely to enjoy an advantage in competition among individuals landed on the same site (e.g. Geritz, 1995; Sakai *et al.*, 1997). On the other hand, larger seeds require more resources to produce, reducing the number of seeds produced by a mother. Many arguments on the seed size has been developed considering the last two aspects, and the optimal seed size has been considered as the one that maximizes the product of seed survivability and seed number (e.g. Smith and Fretwell, 1974). In the model studied in this paper considering the dependence of the dispersal range on seed size, the ESS seed size w^* is always smaller than \tilde{w} , the optimal size neglecting size-dependent seed dispersal. The difference between the two seed sizes can be regarded as "the cost of dispersal" indicating the relative importance of seed dispersal.

The ESS seed size can be calculated theoretically under the simplification of neglecting the accumulated clumping of relatives. In the environment unfavorable for seed dispersal, the ESS seed size w^* is much smaller than \tilde{w} , but there is a lower limit for the ESS dispersal range even in the extremely sticky environment. On the other hand, if the dependency of seed survivability on the seed size is so weak that the cost of seed dispersal is small, the ESS seed dispersal range cannot become very large. I also analyze the model by individual-based computer simulation in a more realistic situation considering the spatial clumping of non-sub relatives, and confirm the accuracy of theoretical results.

2.2 Model

I consider a population of annual plants which reproduces only by self-fertilized seeds or by parthenogenetic seeds in a homogeneous habitat. The population is assumed at the equilibrium with the density of the mature individuals, a constant D . At the end of seasons, each individual produces seeds of size w . Since the amount of resource for an adult to use for reproduction is limited, the number of seeds to be produced, denoted by n , is a decreasing function of seed size w .

Seeds are dispersed with the density following the two-dimensional normal distribution with a peak at the place of the maternal plant. The standard deviation of this normal distribution, denoted by $\sigma(w)$, decreases with the seed size w . Let $d(w, r)$ be the density of seeds landed in the distance r from the parent for a plant producing seeds of size w . It is a product of the number of seeds and a normal distribution:

$$d(w, r) = n(w) \delta(w, r) \quad , \quad (1)$$

where

$$\delta(w, r) = \frac{1}{\pi \sigma(w)} \exp\left(-\frac{r^2}{\sigma(w)^2}\right) \quad . \quad (2)$$

Variable r is the distance from the maternal plant and $\sigma(w)$ is the standard deviation of $\delta(w)$. I assume that a single plant produces seeds of the same size w , and that the number of seeds $n(w)$ is sufficiently large. I also assume that the standard deviation of dispersal is inversely proportional to the seed size: $\sigma(w) = 1/(hw)$, where h is the parameter indicating the difficulty of dispersal in the environment. It may depend on many factors including wind velocity, height of plants, soil conditions, topography, and so on.

At the beginning of the next season, only seeds that successfully landed in vacant sites can germinate and start to grow. For simplicity I do not consider seed dormancy. As juveniles grow, they compete among themselves for the site and self-

thinning occurs. I assume that the final density of individuals D after the competition stage is not dependent on the initial density of seeds. The probability that one of seeds dispersed from a maternal plant wins a particular site is proportional to the product of the number of the seeds arrived at the site and the competitive advantage. Let $a(w)$ be the competitive advantage, an increasing function of seed size w , indicating that juveniles growing from larger seeds are likely to be more advantageous in competition. The probability with which a seed wins a particular site is:

$$\frac{Dad}{\sum ad} = \frac{Dan\delta}{\sum an\delta} \quad (3)$$

In Eq. 3 the sum in the denominator is over all the maternal individuals dispersing seeds to the site. A similar formulation of competitive advantage has been adopted in previous studies (e.g. Sakai, 1997).

In the following analysis the competitive advantage of seeds $a(w)$ and the number $n(w)$ appear only as the product $a(w)n(w)$, then it is convenient to replace them by a single function with respect to seed size w . Since the monumental work by Smith and Fretwell (1974), there assumed to be a trade-off between the number of seeds that an individual produces and the seed size that increases the survivability of the offsprings. Now I assume that the product $a(w)n(w)$ is a function of seed size having a single peak. I denote this product by $\rho(w)$ and assume that it is of the following form:

$$\rho(w) = a(w)n(w) \propto \frac{w}{m+w^2} + k \quad (4)$$

When k is small, $\rho(w)$ depends sharply on the seed size w . As k becomes larger, the dependence on w becomes weaker. The value of w attaining the maximum $\rho(w)$, which I denote by \tilde{w} , is the optimal seed size without consideration of the seed dispersal ability depending on the size. Note that this optimal seed size is independent of k . Hence I call k as "flatness" of the fitness landscape. The parameter m indicates the location at which $\rho(w)$ attains its maximum. In reality I solve $d\rho/dw = 0$ to find the optimal size \tilde{w} equal to the square root of m .

It is assumed that individuals who win the competition are distributed uniformly over the habitat, and they disperse their descendant by seeds in the successive season.

The problem to solve is the strategy (the seed size and the dispersal range) that they should evolve.

2.3 Evolutionarily Stable Dispersal Strategy

I examine the evolutionarily stable strategy (ESS) of seed dispersal range. Assume that a mutant with seed size w invades in a population dominated by the resident type of seed size \bar{w} . In the end of a season adults of both mutant and wildtype disperse their seeds. The density of the mutant's seed is $n(w)\delta(w, r)$, as there are unlikely to exist other mutants that are rare. In contrast, the density of wild-type seeds is $n(\bar{w})(D - \delta(\bar{w}, r))$, because in the absence of mutant wildtype's seed would distribute uniformly with density $Dn(\bar{w})$. Following Eq. 3, the expected fitness of the mutant can be obtained by integrating the probability for her seeds to win vacant sites over the habitat Ω :

$$f(w|\bar{w}) = \int_{\Omega} \frac{Dan\delta}{an\delta + \bar{a}\bar{n}(D - \bar{\delta})} d\Omega = \int_0^{\infty} \frac{D\rho\delta}{\rho\delta + \bar{\rho}(D - \bar{\delta})} 2\pi r dr \quad (5)$$

where integration is over all of the sites in the habitat. In Eq. 5, \bar{a} , \bar{n} , $\bar{\rho}$ and $\bar{\delta}$ are abbreviated as $a(\bar{w})$, $n(\bar{w})$, $\rho(\bar{w})$ and $\delta(\bar{w}, r)$ respectively. The coefficient $2\pi r$ is required for integrating with respect to the radius r . Differentiating Eq. 5 with respect to w and then setting \bar{w} equal to w , I have the ESS condition for w :

$$\left. \frac{\partial f}{\partial w} \right|_{\bar{w}=w} = \frac{D}{\bar{\rho}^2} \int_0^{\infty} (\bar{\rho}\bar{\delta})' (D - \bar{\delta}) 2\pi r dr = 0 \quad (6)$$

Applying Eqs. 2 and 4 to Eq. 6, I obtain

$$\frac{1}{k+1} \left[\left(D - \frac{h^2 w^2}{2\pi} \right) \frac{m-w^2}{(m+w^2)^2} - \frac{h^2 w}{2\pi} \left(k + \frac{w}{m+w^2} \right) \right] = 0 \quad (7)$$

When k equals to zero, Eq. 7 becomes very simple, and the ESS seed size w^* is:

$$w^* = \sqrt{\frac{\pi m D}{h^2 m + \pi D}} \quad (8)$$

When k is positive, Eq. 7 can also be solved algebraically using Mathematica, but the explicit solution of w^* is much more complex than Eq. 8.

I show the dependency of ESS seed size w^* and dispersal range $\sigma(w^*)$ on two parameters, h and k , in Figs. 1a, 1b, 2a and 2b. The solid lines are the theoretical result of w^* and $\sigma(w^*)$ and the broken ones are of \tilde{w} and $\sigma(\tilde{w})$, the latter two being for the optimal when the size-dependent dispersal is neglected. The dots are the results by computer simulations, which will be explained below (and in Appendix).

First, I examine various cases with different environmental parameter h , which indicates the difficulty of seed dispersal. As shown in Fig. 1a, the ESS seed size w^* is always smaller than \tilde{w} , the optimal when the size-dependency of dispersal is neglected. However when h is small seeds are easy to disperse so that the difference between w^* and \tilde{w} is small. As h increases, w^* gets much smaller than \tilde{w} because they must disperse to reduce sib competition at the expense of its survivability. In Fig. 1b as h increases, $\sigma(w^*)$ also decreases, but does not converge to zero. Instead, there is a lower limit of the ESS dispersal range even if the cost of dispersal is infinitely large. From Eq. 8 and the definition of $\sigma(w)$, it is equal to square root of πD , which is independent of m , a parameter controlling the ESS seed size when h is small. This result that dispersal must evolve even when dispersal is highly costly can be thought to correspond to the result of Hamilton and May (1977), who show that in the ESS population at least a half of the offsprings are produced as migrant type, although the mathematically exact relationship between the both results is too complicated.

Second, the dependency of seed survivability on the seed size k is examined. In Figs 2a and 2b it is found that as k becomes larger, the ESS seed size w^* gets smaller and the dispersal range $\sigma(w^*)$ larger, because the survival disadvantage against smaller

seed size become weaker for larger k . The magnitude of $\sigma(w^*)$ when k is equal to 100 is, however, less than twice as large as when k is zero and at most several times as large as the square root of the area that a individual occupies $\sqrt{1/D}$. This result is reasonable because, if the cost of seed dispersal is very small, the plant need not disperse their seeds very far.

The theoretical analysis above assumes that the seeds produced by different adult individuals are not related at all. However offsprings of a plant may produce clumped distribution, and genetically similar individuals may exist close to each other, forming clumps of relatives. This effect is especially important in clonal plants (see Harada and Iwasa, 1996). Although I neglected clonal reproduction in the present paper, limited seed dispersal may also produce clumping of relatives. Since I assumed the self-fertilization, the relatedness between parent and offspring are equal to unity, so all of the relatives are genetically identical. Then, it may be important to consider the effect of competition among non-sib relatives to the evolution of seed dispersal and seed size. If there is a tendency for neighbors to tend to be genetically related, then mutants would find other mutants in its neighborhood with a significant probability even if the overall frequency of mutants is very low.

To confirm the accuracy of the theoretical results above, I also analyzed the model by an individual-based computer simulation (See Appendix). Five trials independent from each other were carried out for each value of parameters h and k . The results are plotted in Fig. 1a, 1b, 2a, and 2b. Each dot represents the mode (the most frequent type) of the population at the last generation in each trial of the simulation. The results of computer simulation are close to the prediction of theoretical analysis.

2.4 Discussion

In this paper, I studied the ESS seed size and the ESS dispersal range, taking into account a trade-off between the two as dispersal range is reduced for large seed size. First, I examined the effect of the environmental difficulty for seed dispersal and found that, as the environment becomes less favorable for seed dispersal, both the ESS seed size and the corresponding dispersal range decrease. However, there is a lower-limit of the seed dispersal range to evolve even in an environment where a high dispersal is very costly in terms of seed survivability. This result is closely related to the

conclusion of Hamilton and May (1977), who showed that in a stable patchy environment a high fraction of migrant offsprings are produced just to avoid the competition among sibs, and more than a half of offspring is migrant type if mortality cost is extremely high. Instead of the fraction of dispersing seeds, I expressed a similar idea in terms of dispersal range of seeds.

Second I examined the dependency of seed survivability on the seed size and observed that the ESS seed dispersal range cannot become very large even when the trade-off is extremely weak. That result implies that in general the evolution of the long-range seed dispersal of plants cannot be only because of the relaxation of competition for sites among relatives, although the present model is simple so that I neglect some more realistic factors as I remark below.

In analyzing the model, I assumed the unique ESS seed size. But it is not often the case in considering the evolutionary stable seed size with competition within species. Geritz *et al.* (1988) and Geritz (1995) showed that assuming the extreme asymmetric competition in favor of larger seeds, any unique seed size can be unstable and the ESS population becomes polymorphic with respect to the seed size, because the spatial variation of the density of larger and fewer seeds allows the invasion by the individual producing seeds of smaller size and larger number. Their models are similar to the present model in showing that it is more adaptive for individuals to disperse seeds more uniformly, while they assumed an extremely asymmetric competition among seedlings within the same site in which an individual from the largest seeds in the site exclusively dominate over others.

In the analytical calculation, I neglected the likelihood that neighbors can be of the same type. Since the seed dispersal range is limited, the spatial correlation that neighbors of a individual are its close relatives should not be negligible. Enhancement of relatedness among neighbors is characteristic of models in which spatial structure is explicitly considered and the dispersal range is limited. The simplest modeling is lattice population dynamics (e.g. Matsuda *et al.*, 1987; Durrett and Levin, 1994; Harada and Iwasa, 1996; Kubo *et al.*, 1996; Nakamaru *et al.*, 1997), which was adopted in the computer simulation in the present paper. Harada and Iwasa (1996) examined lattice models of limited dispersal range for plants reproduce asexually as well as sexually. By calculating the "clone identity probability" defined as the probability for a randomly chosen pair of sites to belong to the same clone, for a spatial genetic patterns, and then calculating the rate at which clonal identity probability decreases with the distance of sampled plants, we can estimate the relative success of clonal and seed production in the population.

In the model studied in the present paper, I might think that the evolution of less competitive behavior, i.e. larger dispersal range, is automatically favored if neighbors are close relatives than if they are completely unrelated. However, many theoretical studies of lattice structured models suggest that such a casual conclusion may not be correct, and the effect of relatedness between close neighbors should be carefully examined.

There are theoretical studies of the evolution of social or ecological interaction on lattice populations, such as behavior modifying the mortality or fertility of neighboring individuals (Matsuda *et al.*, 1987; Wilson *et al.*, 1992; Taylor, 1992; Durrett and Levin, 1997; Nakamaru *et al.*, 1997). The spatial structure causes that the interaction between neighbor individuals is more frequent than that between two random samples from the entire population. Contrary to what casual thinking might suggest, all of these studies conclude that it is not always the case that spatial structure favor the evolution of more altruistic and less spiteful behavior. The reason is that close relatives must compete for space among themselves that give the advantage of spiteful or more aggressive behavior toward neighbors.

The observation that the computer simulation in the present paper was close to the prediction of analysis based on neglecting relatedness of neighbors suggests that the effect of spatial structure may not be very large in the evolution of dispersal range. However more careful and detailed analysis is required.

For simplicity of argument, I neglected the anatomical structures of seeds such as wings or feathers that enhance the seed dispersal ability. The essential assumption in the present paper is that there is some trade-off between the dispersal range and the survivability of seeds. When the amount of resources which maternal plants invest to seed production is limited, making larger structures and enjoying better dispersal efficiency results in allocating smaller resource to produce seed that suffers higher mortality. The present model can be modified easily to considering seed structures highly efficient for dispersal but reducing the viability of seeds. Sakai *et al.* (1997) developed a mathematical model of optimal resource allocation between seed embryo and structure for dispersal.

For future studies I may consider several additional factors. First, soil or other physical condition is likely to be spatially heterogeneous, which leads the difference among the fecundity of individuals. Modifications of Hamilton and May's (1977) model to the cases in which the habitat quality varies have been examined (Crespi and Taylor, 1990; Ozaki, 1995). The results are that each individual produces a constant number of nondispersing offspring, while the number of dispersing offsprings is varied with the fecundity of individuals. In the present model I assume monomorphic adult

size. However in the case that the fecundity is different among reproductive individuals, those with high fecundity may well produce smaller seeds and disperse them in a wider spatial range than the ones with poor fecundity, otherwise the seedlings emerging from their seeds suffer from stronger competition among the sibling. Second, spatial heterogeneity also affects the settling probability of individuals. The gap formation rate in the tropical seasonal forest was found to be proportional to the fraction of gaps in the nearest neighbors of the site (Kubo *et al.*, 1996). This heterogeneity tends to cause the positive spatial autocorrelation in the suitability of sites and favoring smaller seed dispersal range. Third, herbivores and seed predators specific to the host species suggests that the seedling emerging near their parents suffer higher mortality (Clark and Clark, 1984), which might work for genotypes within the same species as well. This would favor higher seed dispersal range.

Although the present model is quite simplified, I think it is a new trial to deal with the effect of seed dispersal range explicitly. Considering the possible factors remarked above and constructing more realistic models, we will be able to estimate quantitatively their relative importance on the evolution of seed dispersal for a particular plant, which might be impossible without quantitative theoretical models. I hope this paper would serve as the first step toward the understanding of the evolution of plant seed dispersal.

2.5 Appendix: Individual-Based Computer Simulation

To examine how much deviation can be produced by simplifications adopted in the analysis in the text, I did a more realistic computer simulation of the model. In this simulation, I adopted the simplification concerning the competition procedure. Note that in competition between adults for producing offsprings that succeed in occupying sites, a number of seeds $n(w)$ and competitive ability of each seeds $a(w)$ always appear together as their product $\rho(w)$, as shown by Eq. 4. Hence, instead of producing different number of seeds each with different competitive ability, I treat them in the computer simulation that all the parents produce the same number of seeds irrespective of seed size, then the whole number of seeds per generation is constant, but offspring's competitive ability is a function of seed size given by "combined competitive ability" $\rho(w)$. This is a very efficient way of calculating the competition of seeds of vastly different sizes in individual based modeling, because small seeds requires to follow

numerous individual seeds, while the total number cannot be very small because the number of large seeds becomes then very small and stochasticity causes unreliable results in the computation of ESS (Geritz, 1995; Geritz *et al.* 1988).

The procedures are as follows:

- (i) In the initial population, seeds with different sizes are put in the habitat of sixty by sixty squares. Each site contains one and only one seed. The coordinate of a seed in the square is randomly chosen. In the initial stage there is no competition, and all the seeds grow into adults.
- (ii) Each adult produces thirty seeds. The weight of each seed is the same as its parent. The seeds are dispersed around the parents, which the probability distribution is radially symmetric and is given by Eq. 2 with respect to the distance.
- (iii) Among the juveniles in the same site, only one individual is randomly chosen to win and to become adult. The probability that an individual is chosen is weighted by Eq. 4.
- (iv) The procedure (ii) and (iii) are iterated for 20,000 generations.

I executed five trials independent from each other for each value of parameters h and k . In each trial the distribution of seed size of the population at the final generation shows a single sharp peak, which indicates the ESS population is monomorphic. The result of simulation supports the prediction of the theoretical analysis in the former section very well (Fig. 1a, 1b, 2a, and 2b). Each dot represents the mode of the population at the last generation in each trial. The result of the simulation implies that the neglect of the competition with non-sib relatives does not cause much error in predicting the ESS dispersal range and the ESS seed size.

In the right side of Figs. 2a and 2b the results of simulation show fluctuation in the mean seed size. The population mean seed size converged quickly to a single ESS seed size and then fluctuated around it. The fluctuation was caused by the genetic drift caused by the finiteness of the lattice size.

2.6 Figures

Figure 1 The ESS seed size (a) and the ESS seed dispersal range (b). Horizontal axis is for h , a parameter indicating difficulty of dispersal in the environment.

Parameter k , m , and D are fixed to 0, 0.1, and 1 respectively. Solid curves show the result of theoretical analysis. Dots are the result of the individual-based computer simulation, each of which represents the mode of the final population in each trial. The broken lines show the optimal seed size not considering the effect of seed dispersal range \tilde{w} . When the environment is favorable for seed dispersal (h is small), the ESS seed size is close to \tilde{w} . As the environment becomes less favorable for dispersal (h increases), the ESS seed size decreases, but the ESS seed dispersal range $\sigma(w^*)$ converges to a lower limit greater than zero.

Figure 2 The ESS seed size (a) and the ESS seed dispersal range (b). Horizontal axis is for the "flatness" parameter k of seed survivability on the size. Parameter h , m , and D are fixed to 1, 0.1, and 1 respectively. Solid curves show the result of theoretical analysis, and dots are of the computer simulation. The broken lines show \tilde{w} , optimal seed size of the size-dependency of dispersal range is neglected. When the seed survivability strongly depends on the size (k is small), the ESS seed size is close to \tilde{w} . As the survivability depends on the size less strongly (k is large), the ESS seed size is larger, but its dispersal range $\sigma(w^*)$ remains at most several times as large as $\sqrt{1/D}$ ($=1$).

Fig.1

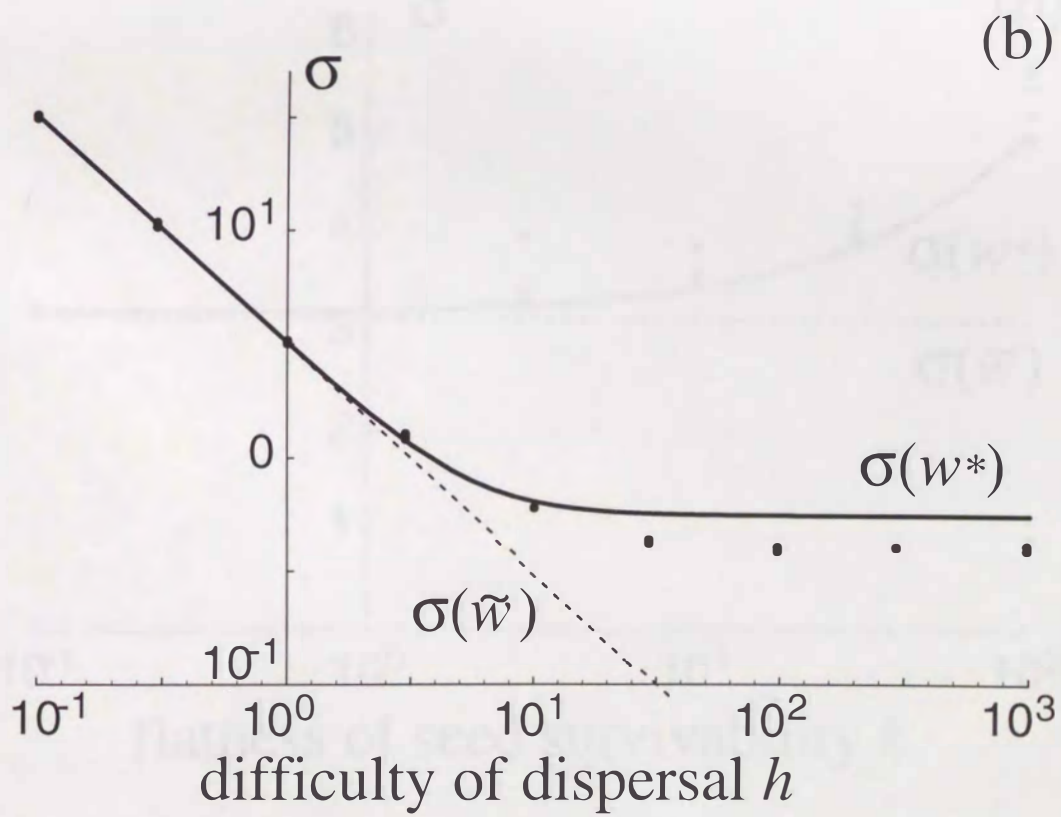
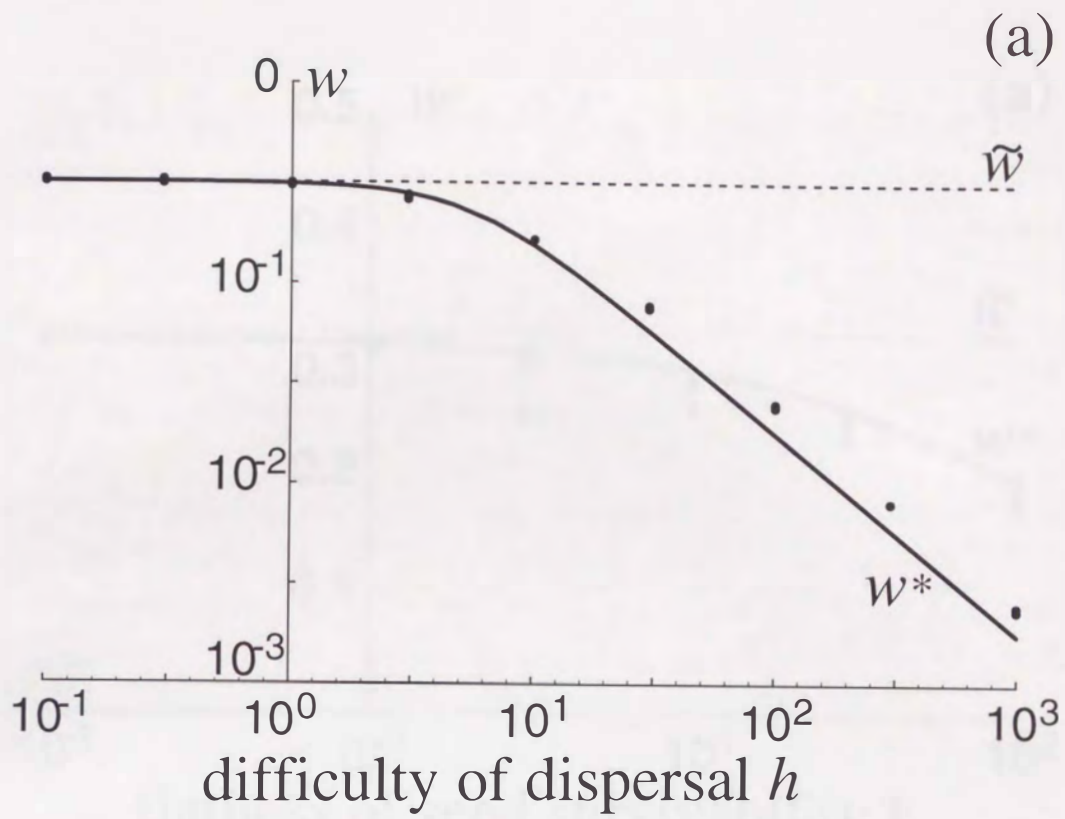
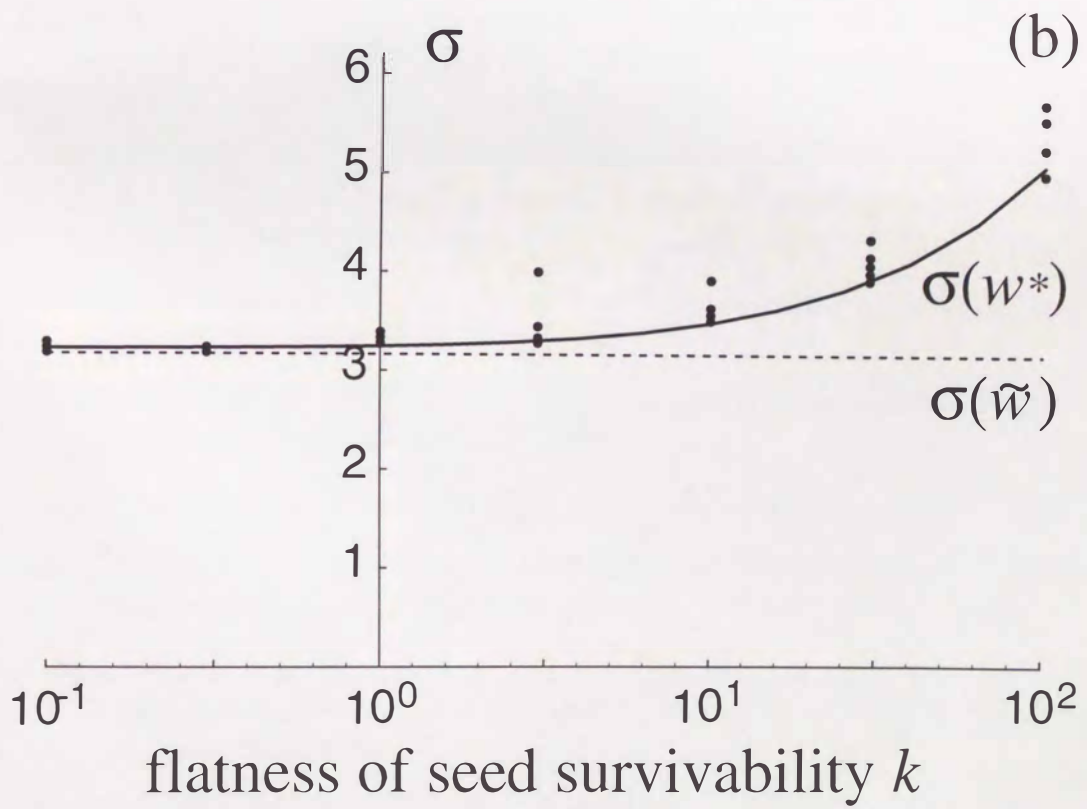
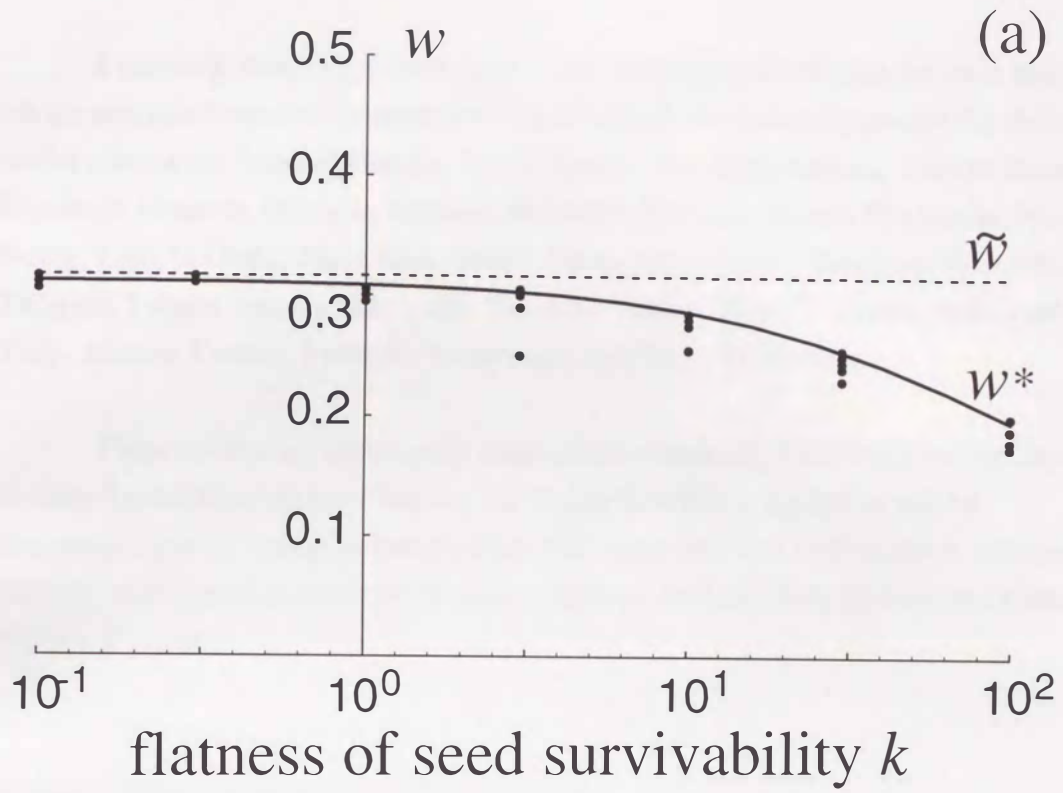


Fig.2



Acknowledgments

I sincerely thank Professors Yoh Iwasa and Toshiyuki Namba for their helpful advice and continuous encouragement. I also thank the following people for their useful comments: Yasushi Harada, Yuko Harada, Masakado Kawata, Takuya Kubo, Hirotsugu Matsuda, Hiroyuki Matsuda, Nobuhiro Minaka, Atsushi Mochizuki, Naohiko Noma, Kenichi Ozaki, Mark Rees, Satoki Sakai, Akira Sasaki, Masakazu Shimada, Takenori Takada, Satoshi Takahashi, Yasuhiko Takeda, Peter D. Taylor, Nobuyuni Tsuji, Masaru Tomita, Yukihiko Toquenaga, and Norio Yamamura.

These studies are done partly supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists, a grant-in-aid for Encouragement of Young Scientists from The Japan Ministry of Education, Science and Culture, and a grant-in-aid from the Japan Ministry of Education, Science and Culture to Prof. Y. Iwasa.

References

- Arak, A and Enquist, M. (1993) Hidden preferences and the evolution of signals. *Philosophical Transactions of Royal Society of London, Series B* **340**: 207-213.
- Aukema, B. (1995) Evolutionary significance of wing dimorphism in Carabid beetles (Coleoptera: Carabidae). *Researches on Population Ecology* **37**: 105-110.
- Cheplick, G. P. (1993) Reproductive systems and sibling competition in plants. *Plant Species Biology* **8**: 131-139
- Clark, D. A. and Clark, D. B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen - Connell model. *American Naturalist* **124**: 769-788.
- Cohen, S. A. and Motro, U. (1989) More on optimal rates of dispersal: taking into account the cost of the dispersal mechanism. *American Naturalist* **134**: 659-653.
- Comins, H. N., Hamilton, W. D. and May, R. M. (1980) Evolutionarily stable dispersal strategies. *Journal of Theoretical Biology* **82**: 205-230.
- Crespi, B. J. and Taylor, P. D. (1990) Dispersal rates under variable patch density. *American Naturalist* **135**: 48-62.
- Davis L. (1990) *Handbook of genetic algorithms*. van Nostrand Reinhold, New York.
- Denno, R.F. (1994) The evolution of dispersal polymorphisms in insects: the influence of habitats, host plants and mates. *Researches on Population Ecology* **36**: 127-135.
- Durrett, R. and Levin, S. A. (1994) Stochastic spatial models - a user's guide to ecological applications. *Philosophical Transactions of Royal Society of London, Series B* **343**: 329-350.
- Durrett, R. and Levin, S. A. (1997) Allelopathy in spatially distributed populations. *Journal of Theoretical Biology* (in press).
- Enquist, M. and Arak, A. (1993) Selection of exaggerated male traits by female aesthetic senses. *Nature* **361**: 446-448.
- Enquist, M. and Arak, A. (1994) Symmetry, beauty and evolution. *Nature* **372**: 169-172.
- Ezoe, H. (1995) Evolutionarily stable seasonal timing for insects with competition for renewable resource. *Evolutionary Ecology* **9**: 328-339
- Fairbairn, D.J. (1994) Wing dimorphism and the migratory syndrome: correlated traits for migratory tendency in wing dimorphic insects. *Researches on Population Ecology* **36**: 157-163.

- Gatehouse, A.G. (1994) Insect migration - variability and success in a capricious environment. *Researches on Population Ecology* **36**: 165-171.
- Geritz, S. A. H., Metz, J. A. J., Klinkhamer, P. G. L. and De Jong, T. J. (1988) Competition in safe sites. *Theoretical Population Biology* **33**: 161-180.
- Geritz, S. A. H. (1995) Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *American Naturalist* **146**: 685-707.
- Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology* **144**: 517-546.
- Greene, D. F. and Johnson, E. A. (1993) Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos* **67**: 69-74.
- Hamilton, W. D. and May, R. M. (1977) Dispersal in stable habitats. *Nature* **269**: 578-581.
- Hamilton, W. D. (1996) *Narrow Roads of Gene Land I*. pp.369-385. W.H.Freeman Spektrum, Oxford.
- Hanski, I. A. (1983) Coexistence of competitors in patchy environment. *Ecology* **64**: 493-500
- Hanski, I. A. and Gilpin, M.E. (eds.) (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, San Diego.
- Hanski, I. A. and Gilpin, M.E. (eds.) (1997) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego.
- Harada, Y., Ezoe, H., Iwasa, Y., Matsuda, H. and Sato, K. (1995) Population persistence and spatially limited social interaction. *Theoretical Population Biology* **48**: 65-91.
- Harada, Y. and Iwasa, Y. (1996) Analyses of spatial patterns and population processes of clonal plants. *Researches on Population Ecology* **38**: 153-164.
- Harper, L. D. (1977) *Population Biology of Plants*. pp.892. Academic Press, London.
- Holland, J. (1985) *Adaptation in Natural and Artificial World*. MIT Press, Boston.
- Huffaker, C. B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**: 343-383.
- Ishikawa, M. (1990) An adaptive structural learning of connectionist models using forgetting. *Journal of Japanese Society for Artificial Intelligence* **5**: 595-603.
- Iwasa, Y. (1991) Sex change evolution and cost of reproduction. *Behavioral Ecology* **2**: 56-68.
- Iwasa, Y. and Pomiankowski, A. (1994) Evolution of mate preferences for multiple sexual ornaments. *Evolution* **48**: 853-867.

- Iwasa, Y., Pomiankowski, A. and Nee, S. (1991) The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution* **45**: 1431-1442.
- Johnstone, R. A. (1994) Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature* **371**: 172-175.
- Johnstone, R. A. (1995) Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology* **177**: 87-94.
- Johnston, V.S. and Franklin, M. (1993) Is the beauty in the eye of the beholder? *Ethology and Sociobiology* **14**: 183-199.
- Kamo, M., Kubo, T. and Iwasa, Y. (1997) Neural network for female mate preference, trained by a genetic algorithm. *Philosophical Transactions of Royal Society of London, Series B* (in press).
- Kawada, K. (1987) Polymorphism and morph determination. pp. 255-268. In A. K. Minks and P. Harrewijn (eds.) *Aphids: their biology, natural enemies and control*. vol. A. Elsevier, Amsterdam.
- Kubo, T., Iwasa, Y. and Furumoto, N. (1996) Forest spatial dynamics with gap expansion: total gap area and gap size distribution. *Journal of Theoretical Biology* **180**: 229-246.
- Lande, R. (1981) Models of speciation by sexual selection of polygenic traits. *Proceeding of National Academy of Science USA* **78**: 3721-3725.
- Liu, S-S. (1994) Production of alatae in response to low temperature in aphids: a trait of seasonal adaptation. pp. 245-261. In H. V. Danks (ed.) *Insect life-cycle polymorphism*. Kluwer Academic Publishers, Dordrecht.
- Masaki, S. and Shimizu, T. (1995) Variability in wing form of crickets. *Researches on Population Ecology* **37**: 119-128.
- Matsuda, H., Tamachi, N. Ogita and Sasaki, A. (1987) A lattice model for population biology. In: *Mathematical topics in biology: Lecture Notes in Biomathematics* **71** (Teramoto, E. and Yamaguti, M., eds), pp.154-161. Springer-Verlag, New York.
- Maynard Smith, J. (1982) *Evolution and the Theory of Game*. Cambridge University Press, Cambridge.
- Michalewicz, Z. (1994) *Genetic Algorithms + Data Structure = Evolution Programs*. (2nd. ed.) Springer-Verlag, New York.
- Nakamaru, M., Matsuda, H. and Iwasa, Y. (1997) The evolution of cooperation in the lattice-structured population. *Journal of Theoretical Biology* **184**: 65-81.
- Nee, S. and May, R. M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* **61**: 37-40.

- Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York.
- Okubo, A. and Levin, S. A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**: 329-38.
- Olivieri, I., Michalakis, Y. and Gouyon, P-H. (1995) Metapopulation genetics and the evolution of dispersal. *American Naturalist* **146**: 202-228.
- Ozaki, K. (1995) Intergall migration in aphids; a model and a test of ESS dispersal rate. *Evolutionary Ecology* **9**: 542-549.
- Pomiankowski, A. and Iwasa, Y. (1993) Evolution of multiple sexual ornaments by Fisher's process of sexual selection. *Proceedings of Royal Society of London, Series B* **253**: 173-181.
- Pomiankowski, A., Iwasa, Y. and Nee, S. (1991) The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* **45**: 1422-1430.
- Portnoy, S. and Willson, M. F. (1993) Seed dispersal curves: behavior of the tail of the distribution. *Evolutionary Ecology* **7**: 25-44.
- Roff, D.A. (1994a) Why is there so much genetic variation for wing dimorphism? *Researches on Population Ecology* **36**: 145-150.
- Roff, D. A. (1994b) Habitat persistence and the evolution of wing dimorphism in insects. *American Naturalist* **144**: 772-798.
- Roff, D.A. and Fairbairn, D.J. (1991) Wing dimorphisms and the evolution of migratory polymorphisms among the insecta. *American Zoology* **31**: 243-251.
- Sakai, S. (1995) A model for seed size variation among plants. *Evolutionary Ecology* **9**: 495-507.
- Sakai, S., Kikuzawa, K. and Umeki, K. (1997) Evolutionarily stable resource allocation for production of wind-dispersed seeds. *Evolutionary Ecology* (in press).
- Shigesada, N., Kawasaki, K. and Teramoto, E. (1986) Traveling periodic waves in heterogeneous environments. *Theoretical Population Biology* **30**: 143-160.
- Shigesada, N. and Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Smith, C. and Fretwell, S. D. (1974) The optimal balance between size and number of offsprings. *American Naturalist* **108**: 499-406.
- Solbreck, C. (1995) Variable fortunes in a patchy landscape--the habitat templet of an insect migrant. *Researches on Population Ecology* **37**: 129-134.
- Sumida, B. H., Houston, A. I., McNamara, J. M. and Hamilton, W.D. (1990) Genetic algorithms and evolution. *Journal of Theoretical Biology* **147**: 59-84.

- Takeda, Y. (1993). A new analytical method for developmental system and its application to *Drosophila* dorso-ventral axis formation. *Forma* **8**: 211-232.
- Takeda, Y. and Iwasa, Y. (1997) A neural network modeling for concentration-dependent pair-rule gene expression. *Forma* (in press).
- Tanaka, S. (1994) Evolution and physiological consequences of de-alation in crickets. *Research on Population Ecology* **36**: 137-143.
- Taylor, P. D. (1992) Altruism in viscous populations -- an inclusive fitness model. *Evolutionary Ecology* **6**: 352-356.
- Toquenaga, Y., Kajitani, I. and Hoshino, T. (1994) Egret of a feather flock together. pp. 140-151. In R. A. Brooks and P. Maes (eds.) *Artificial life. IV*. MIT Press, London.
- Wilson, D. S., Pollock, G. B. and Dugatkin, L. A. (1992) Can Altruism evolve purely viscous populations. *Evolutionary Ecology* **6**: 331-341
- Zeide, B. (1978) Reproductive behavior of plants in time. *American Naturalist* **112**: 636-639.
- Zera, A.J. and Mole, S. (1994) The physiological costs of flight capability in wing-dimorphic crickets. *Researches on Population Ecology* **36**: 151-156.
- Zera, A.J. and Denno, R.F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* **42**: 207-230.

