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A SIMPLE EVOLUTIONARY MODEL OF DORMANCY AND DISPERSAL IN HETEROGENEOUS PATCHES WITH SPECIAL REFERENCE TO PHYTOPHAGOUS LADY BEETLES: I. STABLE ENVIRONMENTS

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SUMMARY

A simple evolutionary model of dormancy and dispersal is presented with special reference to phytophagous lady beetles. In order to investigate spatially heterogeneous environments, we assume the simplest patch structure, that is, there are only two patches, main and sub. Environments are also assumed to be temporally constant. The main patch is superior to the sub patch, but density effect at the main patch is higher than at the sub patch. Optimal dormancy and dispersal are obtained at the same time by the method of evolutionarily stable strategy (ESS). In the univoltine life cycle, dormancy strategy vanishes because dormant individuals do not reproduce at all but suffer from a certain mortality rate during winter hibernation. In the bivoltine life cycle, the dormancy and dispersal rates constitute a trade-off: the rates change together with a negative correlation when the mortality rate during dispersal or during winter hibernation changes. When suitability of the main patch gradually deteriorates, the optimal strategy changes as follows: neither dormancy nor dispersal is adopted at the most suitable condition, the dispersal rate is increased without dormancy in the intermediate condition, and then the dormancy rate is increased with a constant dispersal rate. We discuss the field observation data of lady beetles in the light of results of our model.

KEYWORDS: dormancy, dispersion, lady beetle, heterogeneous patches, stable environments, evolutionary model.

INTRODUCTION

Phytophagous 28-spotted lady beetles, *Henosepilachna vigintioctopunculata* complex, are comprised of *H. vigintioctomaculata* (*Hvm*, hereafter), *H. vigintioctopunctata* (*Hvp*, hereafter), *H. niponica* (*Hn*, hereafter) among others, and the host plants are cultivated potatoes and cultivated egg plants for *Hvm* and *Hvp*, and wild thistles for *Hn*. *Hvp* is bivoltine, and *Hvm* and *Hn* are univoltine, and these species overwinter in the phase of adults (Nakamura, 1983).

There are many insect species in which the number of individuals widely varies from year to year, as is typical in locusts. However, *Hvp* and *Hn* are almost constant in this respect. This stability is caused by density-dependent dispersal and density-dependent oviposition in *Hvp* and *Hn* (Nakamura and Ohgushi, 1979, 1981; Ohgushi and Sawada, 1985; Hirano, 1984).

Nakamura (1976a) observed on bivoltine *Hvp* in the field that first generation adults may overwinter as well as the second generation adults. Nakamura (1976b) also reported in a cage experiment on the same species that there is a positive correlation between dormancy rates and densities of different cages. Ohgushi and Sawada (1985) found in *Hn* that females reabsorb their eggs under a high-density condition. Ito et al. (1990) suggested that dormant individuals which have reabsorbed their eggs may improve their survival rate during winter. Accordingly, we assume that the lady beetles can take two strategies to escape from locally unfavorable environments: dispersal to other patches for reproduction or dormancy with egg absorption.

In general, either dormancy or dispersal can reduce a reproductive risk due to spatial and temporal variability of natural environments, and dispersal reduces selection for dormancy, while dormancy reduces selection for dispersal (Cohen and Levin, 1987). A central question here is what is the optimal combination of dispersion and dormancy (or how the dispersal and dormancy rates evolve) in a given heterogeneous environment.

Models of dispersion and dormancy have been analyzed mainly as adaptation for spatially and temporally fluctuating environments (Levin et al., 1984; Ellener, 1985 a, b; Cohen and Levin, 1987, 1991). Hamilton and May (1977), however, showed that dispersal can evolve even when environments are completely constant. Sota (1988) also showed that partial bivoltism (i.e., a mixture of univoltine and bivoltine individuals) may evolve in a stable environment. Although almost all the models of dispersal have assumed that there are several equivalent patches, we treat a case where patches are not equivalent in order to make clear the effect of spatially heterogeneous environments. For simplicity, our model has only two patches: a superior main patch and an inferior sub patch. As the first step, we investigate here the case where environmental conditions are temporally constant. Temporally fluctuating environments will be studied in another paper.

ASSUMPTIONS AND ANALYSIS

We model two types of lady beetles, univoltine and bivoltine. As we consider the population dynamics of only females, the number of individuals here means the number of females.

Univoltine Case

First, we discuss univoltines (see Fig. 1). The main patch is assumed to be superior: high survival rate and high fecundity. But the density effect is also assumed to be high. Many sub patches are assumed to be located around the main patch. We shall treat the sub patches as one non-main patch, which is taken to be inferior: low survival rate and low fecundity. But the density effect is low because there are many inferior sub patches.

All overwintering adults at a certain year $t(x_t)$ come to the main patch first. They may remain at the main patch or disperse to the sub patch. The number of individuals (d_t) that can reach the sub patch is denoted by

$$d_t = D_i x_t V \tag{1}$$

where D_i is a dispersal rate to the sub patch and V a survival rate when they disperse. The dispersed individuals reproduce the next generation (q_t) at the sub patch:

$$q_t = \frac{s_2 F_2 d_t}{1 + a_2 F_2 d_t} \tag{2}$$

where a is the coefficient of density effect, s the survival rate from egg to adult, F the number of eggs per female, and the suffix "2" means the sub patch.

On the other hand, individuals that remain at the main patch, i.e.,

$$y_t = (1 - D_i) x_t \tag{3}$$

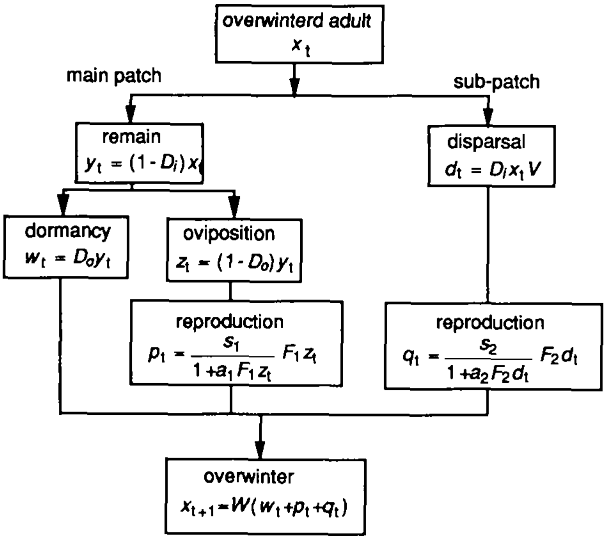

Fig. 1. Model assumptions in the univoltine case. Patches are comprised of a main patch and a sub patch. D_i and D_o are dispersal rate and dormancy rate at the main patch, respectively. Here a is the coefficient of density effect, s survival rate from egg to adult, and F the number of eggs per female, and suffixes 1 and 2 mean the main and sub patches, respectively. V and W are the survival rates during dispersal and overwintering, respectively. For the bivoltine case, one more reproduction process is added to the top of the figure.

may oviposit or enter dormancy without ovipositing. When D_o is a dormancy rate, the number of individuals

$$z_t = (1 - D_o) y_t \tag{4}$$

reproduce the next generation (p_t) at the main patch. Namely,

$$p_t = \frac{s_1 F_1 z_t}{1 + a_1 F_1 z_t}, \tag{5}$$

where a, s and F are the same as in Eq. (2) and the suffix "1" means the main patch. The number of individuals directly entering dormancy at the main patch is

$$w_t = D_o y_t. \tag{6}$$

According to the assumption that the main patch is superior to the sub patch and has a more severe density-dependent effect, we put

$$s_1 > s_2,\ F_1 > F_2, \text{ and } a_1 > a_2. \tag{7}$$

The number of individuals in the next year (x_{t+1}) is

$$x_{t+1} = W(w_t + p_t + q_t) \tag{8}$$

Here, W is a survival rate during overwintering ($W < 1$). We assume that iteration of Eqs. (1) through (8) makes x_t reach a stationary value.

There are three paths for individuals to choose, i.e., dispersing to the sub patch and reproduce, remaining at the main patch and reproduce, or remaining at the main patch and enter dormancy without reproduction. We will determine the optimal dispersal rate and the optimal dormancy rate at the same time by the method of the evolutionarily stable strategy (ESS) (Maynard Smith, 1982). We can analytically obtain the optimal values as follows.

Let us assume that all individuals (wild type) take a dormancy rate, D_o^*, and a dispersal rate, D_i^*. From the assumption of "stationarity", the reproductive rate per year (x_{t+1}^*/x_t^*) becomes 1 in the population with D_o^* and D_i^*:

$$\Phi^* = \frac{x_{t+1}^*}{x_t^*} = \frac{W(w^* + p^* + q^*)}{x^*} = 1. \tag{9}$$

Where, "*" represents the stationary value of the wild type. Applying Eqs. (1) through (6) to Eq. (9), we have

$$W\left[(1 - D_i^*)\left\{D_o^* + (1 - D_o^*)\frac{s_1 F_1}{1 + a_1 F_1 z^*}\right\} + D_i^* V \frac{s_2 F_2}{1 + a_2 F_2 d^*}\right] = 1. \tag{10}$$

Suppose that a few mutants take a certain dormancy rate $\hat{D}_o$, not equal to D_o^*, and a certain dispersal rate $\hat{D}_i$, not equal to D_i^*. The reproductive rate per year of the mutants is

$$\hat{\Phi}=\frac{W(\hat{w}+\hat{p}+\hat{q})}{\hat{x}}, \tag{11}$$

where "^" represents the value of the mutants. Using again eqs. (1) through (6) for the mutants, we obtain

$$\hat{\Phi}=W\left[(1-\hat{D}_i)\left\{\hat{D}_o+(1-\hat{D}_o)\frac{s_1F_1}{1+a_1F_1(z^*+\hat{z})}\right\}+\hat{D}_iV\frac{s_2F_2}{1+a_2F_2(d^*+\hat{d})}\right]. \tag{12}$$

Note that the density effects on reproduction appear with the total densities $z^*+\hat{z}$ and $d^*+\hat{d}$. However, we can neglect $\hat{z}$ and $\hat{d}$ in the denominators in Eq. (12) as we assume that the numbers of mutants $\hat{z}$ and $\hat{d}$ are much smaller than z^* and d^*, respectively.

When $D_o{}^*$ and $D_i{}^*$ are between 0 and 1, the necessary conditions for $D_o{}^*$ and $D_i{}^*$ to be ESS's are

$$\left.\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}\right|_{(\hat{D}_o=D_o{}^*,\ \hat{D}_i=D_i{}^*)}=0 \tag{13}$$

and

$$\left.\frac{\partial\hat{\Phi}}{\partial\hat{D}_i}\right|_{(\hat{D}_o=D_o{}^*,\ \hat{D}_i=D_i{}^*)}=0 \tag{14}$$

because $\hat{\Phi}$ should take the highest value when $\hat{D}_i=D_i{}^*$ and $\hat{D}_o=D_o{}^*$. $D_o{}^*$ and $D_i{}^*$ also satisfy the stationary condition in Eq. (10).

From Eqs. (12), (13) and (14), we have

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}=W(1-D_i{}^*)\left(1-\frac{s_1F_1}{1+a_1F_1z^*}\right)=0 \tag{15}$$

and

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_i}=-W\left\{\frac{s_1F_1}{1+a_1F_1z^*}(1-D_o{}^*)-\frac{s_2F_2V}{1+a_2F_2d^*}+D_o{}^*\right\}=0. \tag{16}$$

From Eq. (15),

$$\frac{s_1F_1}{1+a_1F_1z^*}=1. \tag{17}$$

From Eqs. (10), (16) and (17), we get $W=1$. This contradicts the assumption that $W<1$.

$s_1F_1/(1+a_1F_1z^*)$ in Eq. (17) is the stationary reproductive rate per capita at the main patch. Considering that the reproductive rate per year is exactly 1 in the stationary population, the reproductive rate per individual at the main patch should be grater than 1 because the overwintering survival rate (W) is less than 1. Therefore, the value of Eq. (15) should be negative:

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}<0. \tag{18}$$

This means that the optimal dormancy rate (D_o^*) is 0 in the univoltine case. Thus, $z^*=y^*$ from Eq. (4).

From Eqs. (10) and (16) with $D_o^*=0$, we obtain

$$W\frac{s_1F_1}{1+a_1F_1y^*}=1 \tag{19}$$

and

$$W\frac{s_2F_2V}{1+a_2F_2d^*}=1. \tag{20}$$

Eqs.(19) and (20) mean that the reproductive rates per year through paths of the main and sub patches are equal to 1, respectively. The optimal dispersal rate (D_i^*), and the stationary numbers of the remaining individuals (y^*) and dispersal individuals (d^*/V) are

$$D_i^*=\frac{d^*/V}{y^*+d^*/V}, \tag{21}$$

$$y^*=\frac{s_1F_1W-1}{a_1F_1} \tag{22}$$

and

$$d^*/V=\frac{s_2F_2WV-1}{a_2F_2V}, \tag{23}$$

respectively. From these equations, we can see that the optimal dispersal rate (D_i^*) becomes large when V is large, the main patch is inferior (larger a_1, smaller F_1 or smaller s_1), the sub patch is superior (smaller a_2, larger F_2 or larger s_2), or else W is large since $s_1F_1>s_2F_2V$ (see Eq. (7)).

Bivoltine Case

All overwintering adults in a certain year $t(u_t)$ reproduce the first generation (x_t):

$$x_t=\frac{s_0F_0u_t}{1+a_0F_0u_t}, \tag{24}$$

where a, s and F are the same definitions as in Eq. (2) and the suffix "0" means the first generation. In the first reproduction, we assume that the main patch is so suitable that individuals need neither to disperse to the sub patch nor to enter dormancy. After this reproduction, females of the first generation take the same paths as univoltines (refer to Fig. 1).

In this case, the reproductive rate per year of wild type individuals is

$$\Phi^*=\frac{x^*_{t+1}}{x^*_t}=\frac{u^*_{t+1}}{x^*_t}\frac{x^*_{t+1}}{u^*_{t+1}}=\frac{s_0F_0}{1+a_0F_0u^*}W(w^*+p^*+q^*)=1. \tag{25}$$

On the other hand, the reproductive rate per year of mutants is one that is Eq. (12) multiplied by $s_0F_0/(1+a_0F_0u^*)$. Applying Eqs. (13) and (14) for this modified mutant fitness, and using Eq. (25), we can reduce the following relations in the stationary population of individuals adopting ESS's satisfying $0<D_i^*<1$ and $0<D_o^*<1$.

$$W\frac{s_0F_0}{1+a_0F_0u^*}=1, \tag{26}$$

$$\frac{s_1F_1}{1+a_1F_1z^*}=1 \tag{27}$$

and

$$V\frac{s_2F_2}{1+a_2F_2d^*}=1. \tag{28}$$

Eq. (26) means that the overwinter survival rate times the reproductive rate of the first generation equals 1; Eq. (27) means the reproductive rate of the second generation at the main patch equals 1; and Eq. (28) means the dispersal survival rate times the reproductive rate of the generation at the sub patch equals 1. The reproductive rate of individuals that enter dormancy is naturally 1. We also say from the above relations that the mortality during the overwinter period (1-W) is exactly compensated by the reproduction by the overwintering generation, and the stationary numbers of adults in the first generation, both in the main and sub patches, are independently determined.

Explicit forms of the optimal rates (D_i^* and D_o^*) and the stationary values are given as

$$D_i^*=\frac{d^*/V}{x^*}, \tag{29}$$

$$D_o^*=\frac{y^*-z^*}{y^*}, \tag{30}$$

$$y^*=x^*-d^*/V, \tag{31}$$

$$x^*=\frac{s_0F_0W-1}{a_0F_0W}, \tag{32}$$

$$z^*=\frac{s_1F_1-1}{a_1F_1}, \tag{33}$$

$$d^*/V=\frac{s_2F_2V-1}{a_2F_2V}. \tag{34}$$

We can see that the optimal dispersal rate (D_i^*) becomes large when W is small, V is large, the patch for the first generation is inferior (smaller s_0, smaller F_0 or larger a_0), or the sub patch for the second generation is superior (larger s_2, larger F_2 or smaller a_2). D_i^* is independent of the main patch parameters. The conditions for the optimal dormancy rate (D_o^*) to be large are that the reverses of the above conditions to be the case, and the main patch is inferior.

Let us consider the relation between the optimal rates and W or V. When W is larger, D_i^* decreases while D_o^* increases. When V increases, D_i^* increases while D_o^* decreases. We thus show the relation in Fig. 2 where the increase in the dispersal rate corresponds to the decrease in the dormancy rate and vice versa. We may regard this relation between D_i^* and D_o^* as a trade-off of strategies where one compensates for the other.

We have obtained the conditions in the case where both D_i^* and D_o^* exist between 0 and 1 ($0<D_i^*<1$ and $0<D_o^*<1$). We can get the conditions in other cases where $D_o^*=1$ and $0<D_i^*<1$, $D_o^*=0$ and $0<D_i^*<1$, and $D_o^*=0$ and $D_i^*=0$ are ESS's (see Appendix). These ESS's, with the first case, can be represented as a function of the suitability of the main patch (s_1) as shown in Fig. 3. The interesting dependency of D_i^* and D_o^* on s_1 can be explained in biological contexts. When s_1 is sufficiently large, the individuals in the main patch neither disperse nor enter dormancy. If s_1 takes a smaller value, individuals first begin to disperse without dormancy. The dispersal rate (D_i^*) increases as s_1 decreases. At a certain value of s_1, where the dispersal rate does not increase any further because of the density-effect of the sub patch, it becomes constant and the remaining individuals at the main patch begin to enter dormancy. When s_1 is at the worst value, individuals do not reproduce at the main patch and they disperse or enter dormancy. As shown in Appendix, the threshold value of s_1 at which the dispersal rate begins to increase from 0 is smaller as a_1 is smaller, F_1 larger, V smaller, s_2 smaller or F_2 smaller. The critical value of s_1 at which the dormancy rate begins to increase is smaller as a_1 is smaller, F_1 larger, V larger or the sub patch is better (large s_2, large F_2 or small a_2). The other parameters (a_1 or F_1) representing the suitability in the main patch also have the same effect on D_i^* and D_o^* as s_1.

Parameter-dependent Strategies

We have derived the optimal dispersal and dormancy rates assuming that the rates are independent of any other parameters. We call them constant rate strategies. The dispersal and dormancy rates may depend on a certain parameter, for example, density (density-dependent) or survival rate from egg to adult in the main patch (patch-quality-dependent). Let us assume that these rates are density-dependent, such that

$$D_i=\frac{1}{1+\alpha x_t} \tag{35}$$

and

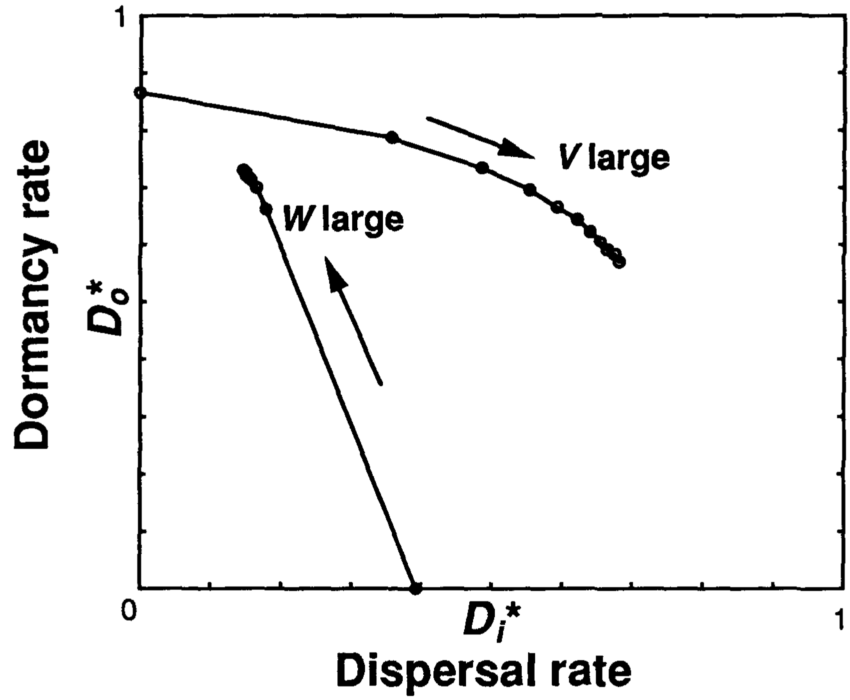

Fig. 2. Two examples of the trade-off between optimal dispersal (D_i^*) and dormancy (D_o^*) rates. As the survival rate during dispersal (V) increases, D_i^* increases and D_o^* decreases. Where $s_0=0.7$, $a_0=0.01$, $F_0=50$, $s_1=0.5$, $a_1=0.05$, $F_1=20$, $s_2=0.5$, $a_2=0.01$, $F_2=20$ and $W=0.5$. As the survival rate during overwintering (W) increases, D_i^* decreases and D_o^* increases. Where $s_0=0.7$, $a_0=0.01$, $F_0=50$, $s_1=0.5$, $a_1=0.03$, $F_1=30$, $s_2=0.2$, $a_2=0.01$, $F_2=20$ and $V=0.5$.

$$D_o=\frac{1}{1+\beta y_t}. \tag{36}$$

In this case, we should derive the optimal values, α^* and β^*. The ESS condition that the reproductive rate per year is 1 regardless of the path that the individual takes should also hold in this case. The condition leads a result that the stationary numbers of individuals are the same as those when the constant strategies were investigated. Then, α^* and β^* satisfy next equations:

$$D_i^*=\frac{1}{1+\alpha^* x^*} \tag{37}$$

and

$$D_o^*=\frac{1}{1+\beta^* y^*}. \tag{38}$$

These equations mean that the optimal dispersal and dormancy rates are essentially the same in temporally constant environments even if D_i and D_o are dependent on

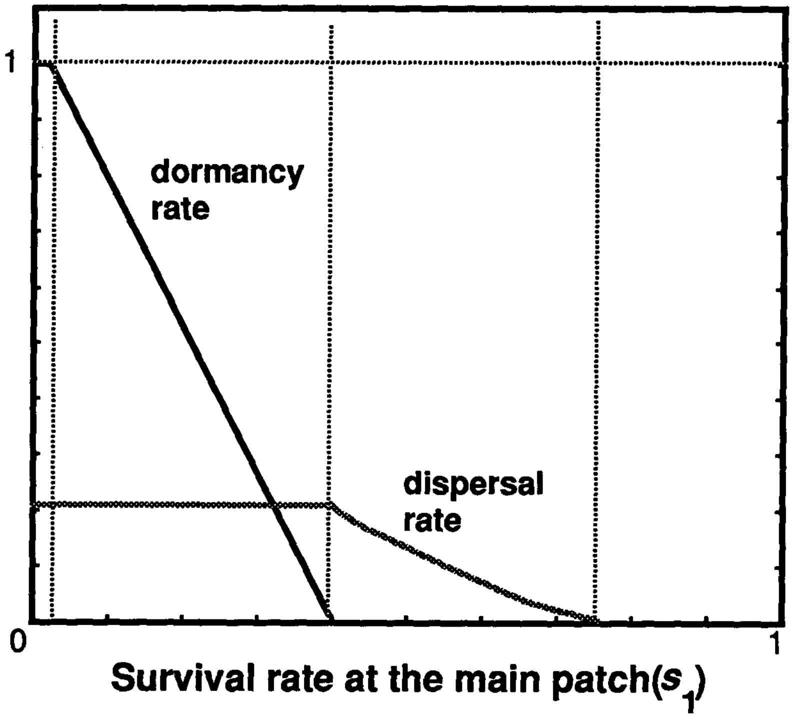

Fig. 3. The relationship of optimal dispersal rate (D_i*) and optimal dormancy rate (D_o*) with the survival rate at the main patch (s_1). In case of gradual deterioration of the main patch, individuals should primarily disperse to the sub patch without dormancy and only secondarily enter dormancy with a constant dispersal rate. Parameters values are $s_0=0.5$, $a_0=0.01$, $F_0=100$, $a_1=0.01$, $F_1=50$, $s_2=0.3$, $a_2=0.01$, $F_2=10$, $V=0.5$ and $W=0.5$.

other parameters. We can easily expand this result to general cases where the rates are arbitrary functions of any given set of parameters.

DISCUSSION

In the bivoltine case, we have shown that dormancy and dispersal may be complementary to each other to escape from locally unfavorable environments (see Fig. 2). Although this property has been confirmed for adaptation for unpredictable fluctuating environments (Cohen and Levin, 1987), it can be said that the trade-off between dormancy and dispersal may evolve under stable environments.

Under the stationary condition, we found the interesting relationship between the optimal dormancy rate (D_o*), the optimal dispersal rate (D_i*), and the survival rate at the main patch (s_1) in bivoltines (Fig. 3). Individuals neither disperse nor enter dormancy if the main patch is superior. They disperse to the sub patch without dormancy, and then enter dormancy with a constant dispersal rate, as the main patch becomes inferior. This pattern of the optimal strategy suggests that individuals may respond to changes in the suitability of patches in seasonally changeable environments in real life. At present we cannot find actual data showing this pattern in the bivoltine cases, but we will show later the similar trend in a univoltine case.

In our model, the individuals taking the dormancy strategy eventually vanish in the univoltine case when the environmental parameters are constant. Since some of the individuals die during hibernation as stated before, the overwintered individuals should compensate somewhere for that loss. Nakamura and Ohgushi (1979) and Ohgushi and Sawada (1985) reported the existence of individuals taking dormancy in the univoltine lady beetle, *Henosepilachn niponica* (*Hn*). In actual fields, environments are no doubt temporally fluctuating. In another paper (Tsuji and Yamamura, in preparation), we will show by numerical calculation that the optimal dormancy rate may not be 0 in univoltines when the environment is fluctuating, and that the optimal strategy changes in the similar way as shown in Fig. 3.

Actually, the univoltine lady beetle (*Hn*) ceases oviposition when the percentage of thistle leaf damage is about 50 % in a cage experiment, and they resume oviposition after they are transferred to another cage with a fresh thistle (Ohgushi and Sawada, 1985). This response may be regarded as a strategy by which to avoid a derogated patch and disperse to another patch for oviposition. Ohgushi and Sawada (1985) also reported the observational results on *Hn* as follows. Lady beetles in the field gradually increase the intensity of movement from May to the middle of June, and gradually decrease the intensity of movement after late June. The proportion of individuals with reabsorbed oocytes rapidly increased after late June. In the laboratory experiment, females in high density cages reabsorb oocytes at the end of the experiment when most of the thistles are highly exploited. It is expected that food is superior in early May because there are few active overwintering adults and the thistles are not severely exploited, and that food condition gradually deteriorates because active overwintering adults increase as well as newly emerged adults in the first generation. This observation on the response to deterioration of the main patch corresponds to the tendency of the theoretical results in constant environments, i.e., dispersal to be primary and dormancy to be secondary.

We have not fully analyzed cases where dispersal and dormancy rates (D_i and D_o) are direct functions of some parameters, such as density or a survival rate. In another paper we shall present such cases under fluctuating environments, and compare differences among the constant strategy, the density-dependent strategy and the patch-quality-dependent strategies (Tsuji and Yamamura, in preparation).

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特に植食性テントウムシに関連した空間的に不均一なパッチにおける休眠と分散のモデル
Ⅰ．環境が時間的に一定の場合

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特に植食性テントウムシに関連した，休眠・分散の簡単なモデルを作った．環境が空間的に不均一な場合を考えるために，メインとサブの二つのパッチより構成され，環境は時間的に一定であると仮定した．また，メインパッチはサブパッチより生存率，産卵数は高く，密度効果もサブパッチより高いと仮定した．進化的に安定な戦略の手法で，最適な休眠率・分散率を，同時に求めた．年一化においては，休眠のみの個体は全く増殖せずに越冬中に死ぬので，休眠は進化しない．年二化においては，分散や越冬の際の死亡率が変るときに，休眠と分散の間には，トレードオフの関係がある．年二化においてまた，メインパッチの環境がしだいに悪くなるにつれて，二つの最適戦略は次のように変る．メインパッチが良いときは休眠も分散もしない．メインパッチの質が中くらいのときは，分散のみを行い，休眠はしない．最悪のときは，分散は一定で休眠を増す．我々は，モデルの結果と，テントウムシの観察データを比較して，モデルの有効性を検討した．

Appendix

D_i^* and D_o^* when s_1 changes. There are 4 ESS conditions depending on whether D_o^* or D_i^* takes 0, 1, or an intermediate value.

(i) When $D_o^*=1$ and $0<D_i^*<1$, the conditions are

$$\left.\frac{\partial\hat{\Phi}}{\partial\hat{D}_i}\right|_{(\hat{D}_i=D_i^*,\ D_o^*=1)}=0, \tag{A1}$$

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}>0 \tag{A2}$$

and

$$\hat{\Phi}(\hat{D}_i=D_i^*,\ D_o^*=1)=1. \tag{A3}$$

From the above equations, we have

$$s_1<1/F_1. \tag{A4}$$

(ii) When $0<D_o^*<1$ and $0<D_i^*<1$,

$$\frac{1}{F_1}<s_1<a_1\left(\frac{s_0F_0W-1}{a_0F_0W}-\frac{s_2F_2V-1}{a_2F_2V}\right)+\frac{1}{F_1} \tag{A5}$$

as analyzed in the text.

(iii) When $Do^*=0$ and $0<Di^*<1$,

$$\left.\frac{\partial\hat{\Phi}}{\partial\hat{D}_i}\right|_{(\hat{D}_i=D_i^*,\ D_o^*=0)}=0, \tag{A6}$$

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}<0 \tag{A7}$$

and

$$\hat{\Phi}(\hat{D}_i=D_i^*,\ D_o^*=0)=1. \tag{A8}$$

From Eqs. (A6)–(A8), we have

$$d^*/V=\frac{s_2F_2VW(a_0F_0+s_0F_0a_1F_1)-(a_0F_0Ws_1F_1+a_1F_1)}{a_0F_0VW(s_1F_1a_2F_2+a_1F_1s_2F_2)+a_2F_2a_1F_1V}. \tag{A9}$$

From $0<D_i^*<1$, we obtain

$$a_1\left(\frac{s_0F_0W-1}{a_0F_0W}-\frac{s_2F_2V-1}{a_2F_2V}\right)+\frac{1}{F_1}<s_1<\frac{s_2F_2V}{F_1}+\frac{s_2F_2Vs_0a_1}{a_0}-\frac{a_1}{a_0F_0W}. \tag{A10}$$

(iv) When $D_o^*=0$ and $D_i^*=0$,

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_i}<0, \tag{A11}$$

$$\frac{\partial\hat{\Phi}}{\partial\hat{D}_o}<0 \tag{A12}$$

and

$$\hat{\Phi}(D_i^*=0,\ D_o^*=0)=1. \tag{A13}$$

The condition is

$$\frac{s_2F_2V}{F_1}+\frac{s_2F_2Vs_0a_1}{a_0}-\frac{a_1}{a_0F_0W}<s_1<1. \tag{A14}$$