

Evolution of Semelparous and Iteroparous Perennial Plants: Comparison between the Density-independent and Density-dependent Dynamics

TAKENORI TAKADA

*Department of International Cultural Relations, Hokkaido Tokai University,
Sapporo 005, Japan*

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The evolution of the frequency of reproduction in perennial plants is analyzed using the Lefkovich matrix model. The model describes a population dynamics with a stage-specific pattern of reproduction and mortality of plants. Both the density-independent and density-dependent models are analyzed, and the results of the two models are compared. In the density-independent model, the invincible condition depends on the survival rate at juvenile stage, the emergence rate of seeds and the trade-off curve between the number of seeds and the survival rate of mature plants. The result is qualitatively similar to the studies by Schaffer & Gadgil (1975, in: *Ecology and Evolution of Communities*. Cambridge, MA: Belknap Press.) and Pianka (1976, *Am. Zool.* **16**, 775–784). However, in the density-dependent model, the invincible condition does not depend on those parameters, but on only the trade-off curve. Therefore, the trade-off between the number of seeds and the adult survival rate, and the density-dependence of the dynamics, play an important role in the evolution of the frequency of reproduction. However, there is no significant difference between the results derived from the stage- and the age-structured population models.

1. Introduction

Since Cole (1954) discussed the evolutionary significance of semelparous species, many authors have attempted to explain on what conditions semelparity or iteroparity is favored (Gadgil & Bossert, 1970; Charnov & Schaffer, 1973; Schaffer & Gadgil, 1975; Pianka, 1976; Charlesworth, 1980; Bulmer, 1985). In order to obtain the life-history optimal strategy, they used life-table analysis, which is based on two life-table parameters, i.e. the age-specific fecundity (m_x) and age-specific survival rate (l_x). When these life table parameters are used, it is implicitly assumed that fecundity and/or survival rate strongly depend on the age of individuals. However, as Werner & Caswell (1977) pointed out, most perennial plants show size-dependent life history. For example, in perennial plants, individuals with the same age may have markedly different sizes because of intraspecific competition and because they reproduce sexually when they exceed a certain size threshold. It is also well known that the survival rate of perennial plants depends

on their size (Bierzychudek, 1982; Kinoshita, 1987; Kawano *et al.*, 1987). Therefore, evolution of the frequency of reproduction in perennial plants should be analyzed using size-dependent or stage-dependent parameters.

Moreover, the studies cited above—except Charlesworth (1980) and Bulmer (1985)—have disregarded the density-dependent factor. They used the intrinsic growth rate (r) or Fisher's reproductive value (V_x) as a criterion of the evolution, i.e. they assumed that species with the largest r or V_x would be favored under natural selection. However, small individuals of perennial plants are usually suppressed by surrounding individuals due to their immobility and the demographic process of perennial plants is basically density-dependent (Schellner *et al.*, 1982; S. Kawano *et al.*, unpublished data). Therefore, when we discuss the life-history evolution in perennial plants, we should employ the density-dependent model.

In order to analyze the evolution of the frequency of reproduction in perennial plants, I use the Lefkovich

matrix model that describes the population dynamics with stage-specific reproduction and survival. I analyze both the density-independent and density-dependent models (hereafter, these models are referred to as the DI and DD models, respectively), and compare the results derived from the two models. Moreover, the age-structured model is compared with the stage-structured one. As a result, it is concluded that the trade-off between fecundity and adult survival, and the density-dependence of the dynamics, play an important role in the evolution of the frequency of reproduction.

2. The Density-independent Model

For simplicity, only two stage classes are considered, i.e. the juvenile stage (including seedlings) and the mature stage. The Lefkovitch matrix of a hypothetical perennial plant is

$$\mathbf{L} = \begin{array}{c} \text{Juvenile} \\ \text{Mature} \end{array} \begin{array}{cc} \begin{array}{c} \text{Juvenile} \\ \text{Mature} \end{array} & \begin{array}{c} \text{Mature} \end{array} \\ \left[\begin{array}{cc} S_{JJ} & fS_0 \\ S_{MJ} & S_{MM} \end{array} \right] \end{array}$$

where S_0 represents the emergence rate of seeds ($0 \leq S_0 \leq 1$) and f is the number of seeds per plant. S_{JJ} represents the probability that the individuals at juvenile stage remain at the same stage next year and S_{MJ} represents the probability that the individuals at juvenile stage grow up to mature stage next year. Thus, $S_{JJ} + S_{MJ}$ represents the survival rate at juvenile stage ($0 \leq S_{JJ} + S_{MJ} \leq 1$). S_{MM} represents the survival rate at mature stage ($0 \leq S_{MM} \leq 1$). Therefore, if S_{MM} is equal to zero, then \mathbf{L} represents the life history of semelparous perennial plants because individuals at mature stage always disappear next year.

By the definition of the Lefkovitch matrix model (Lefkovitch, 1965), the dynamics of population with the stage-structure can be written as:

$$\mathbf{n}_{t+1} = \mathbf{L}\mathbf{n}_t, \quad (1)$$

where $\mathbf{n}_t = (n_{J,t}, n_{M,t})^T$ and $n_{i,t}$ represent the stage-class vector at time t and the population density of stage-class i at time t , respectively. Since the elements of Lefkovitch matrix are constant, the population density of each stage and thus the total population size, $N_t (= n_{J,t} + n_{M,t})$, grow exponentially by the rate λ per year as the time elapsed sufficiently. λ is the dominant eigenvalue of matrix \mathbf{L} and

$$\lambda = \frac{S_{MM} + S_{JJ} + \sqrt{(S_{MM} - S_{JJ})^2 + 4fS_0S_{MJ}}}{2}. \quad (2)$$

When a mutation occurs in the habitat of a wild-type population, the mutant-type with larger λ than the wild-type will be favored. Therefore, the invisable condition is

$$\delta\lambda > 0. \quad (3)$$

It means that the optimal solution has maximum value of λ .

Since large consumption of assimilating products due to seed production causes the increase of mortality risk of individuals, there is a trade-off between the number of seeds, f , and the survival rate of mature individuals, S_{MM} ($f \equiv g(S_{MM})$ and $g' < 0$, Fig. 1). Therefore, mutation occurs only along the trade-off curve and the set of (S_{MM}, f) with the largest λ is the optimal solution. From eqns (2) and (3), the optimal solution of this model depends both on parameters such as S_{JJ} , S_{MJ} and S_0 and on the shape of the trade-off curve.

Below, cases of three typical trade-off curves are analyzed, where the second derivatives are $g'' = 0$, $g'' > 0$ and $g'' < 0$ (Fig. 1).

CASE (I)

When $g'' = 0$, only a boundary solution exists (see Appendix A). If

$$g'(0) \leq \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}},$$

the optimal solution is $(0, g(0))$. Monocarpic perennial plants are favored in this case [Fig. 2(a)].

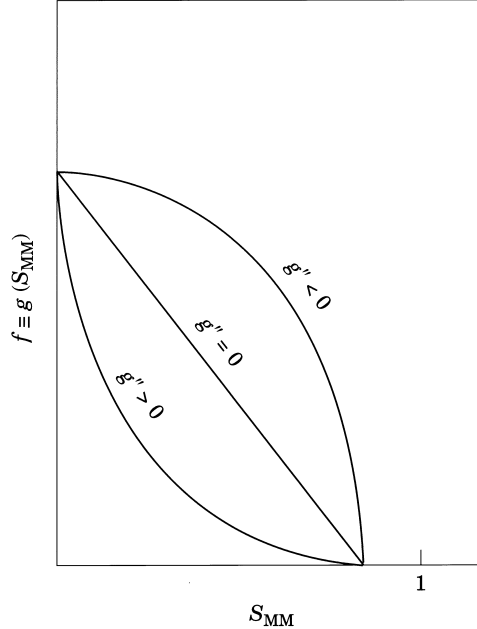


FIG. 1. The trade-off curves between the number of seeds per plant (f) and the survival rate of mature individuals (S_{MM}). Mutation occurs only along the trade-off curve ($f \equiv g(S_{MM})$ and $g' < 0$). This is because copious consumption of assimilating products due to seed production causes the increase of mortality risk of individuals. For simplicity, we consider three types of trade-off curves, i.e. $g'' = 0$, $g'' > 0$ and $g'' < 0$.

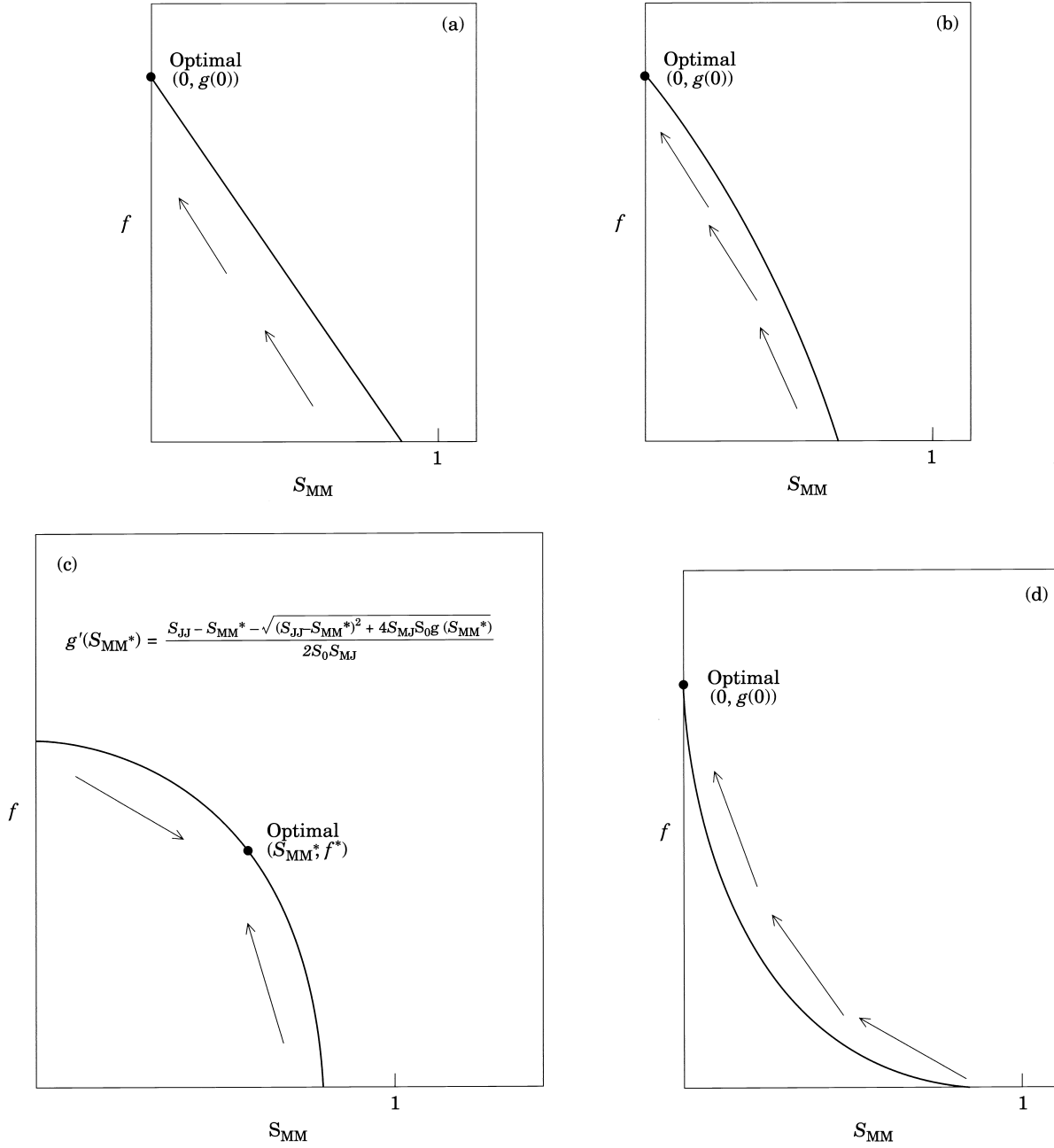


FIG. 2. Results of the density-independent model. (a) When the trade-off curve is linear ($g'' = 0$), $(0, g(0))$ is the optimal solution. In this case, semelparous perennial plants are favored. (b) (c) When the trade-off curve is convex upward ($g'' < 0$), there are two cases, depending on the values of $g'(0)$, $g(0)$, S_0 , S_{JJ} and S_{MJ} . (d) When the trade-off curve is convex downward ($g'' > 0$), $(0, g(0))$ is the optimal solution. Details are discussed in the text.

TABLE 1
Results for the density-independent model

To be favored	Conditions of parameters
Semelparous perennials	$g'' \leq 0$ and $g'(0) \leq \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}}$ $g'' > 0$
Iteroparous perennials	$g'' < 0$ and $g'(0) > \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}}$

CASE (II)

When $g'' < 0$, there are two cases, depending on the value of $g'(0)$, $g(0)$, S_0 , S_{JJ} and S_{MJ} (see Appendix A). If

$$g'(0) \leq \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}},$$

then λ has the highest value at $(0, g(0))$. Monocarpic perennial plants are favored in this case [Fig. 2(b)]. If

$$g'(0) > \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}},$$

then λ has the highest value at $S_{MM}^* > 0$. S_{MM}^* satisfies the equation

$$\begin{aligned} g'(S_{MM}^*) \\ = \frac{S_{JJ} - S_{MM}^* - \sqrt{(S_{JJ} - S_{MM}^*)^2 + 4S_{MJ}S_0g(S_{MM}^*)}}{2S_0S_{MJ}}. \end{aligned} \quad (4)$$

Polycarpic perennial plants are favored in this case [Fig. 2(c)].

CASE (III)

When $g'' > 0$, λ is the largest at $S_{MM} = 0$ [see Appendix A; Fig. 2(d)]. It does not depend on other parameters, such as S_0 , S_{MJ} and so on. Therefore, semelparous perennial plants are always favored when $g'' > 0$.

The results of this section are summarized in Table 1. The shape of the trade-off curve plays an important role in the DI model. $g'' < 0$ is the necessary condition for the iteroparity of perennial plants. $g'' < 0$ means that the decrease of the number of seeds does not lead to the linear increase of the survival of mature plants and gives a load for increasing the adult survival rate. Moreover, $g'' > 0$ is the sufficient condition for the semelparity. $g'' > 0$ means that the decrease of the survival of mature plants gives an accelerating effect on the increase of the number of seeds. Therefore, the single bout of producing seeds is favored. The second important factor affecting the optimal solution is the values of $g'(0)$ and other parameters. When $g'(0)$ is small, the semelparity is likely to be favored. These results, of course, coincide with the results of the studies by Charnov & Schaffer (1973), Schaffer & Gadgil (1975) and Pianka (1976).

3. The Density-dependent Model

Here the DD model is analyzed; the Lefkovitch matrix is the same apart from the emergence rate of

seeds (S_0). While the emergence rate of seeds is constant in the DI model, the emergence rate in this model is a monotonically decreasing function of the population size, N_t ($=n_{J,t} + n_{M,t}$). Thus $dS_0(N_t)/dN_t < 0$. This is because the survival rate at seedling or earlier stages is strongly affected by surrounding individuals due to the intraspecific competition. Some authors have noted that the density-dependence of seedling mortality is significant for the dynamics of perennial plant populations (Schellner *et al.*, 1982; Solbrig *et al.*, 1988; Allen, 1989; S. Kawano *et al.*, unpublished data). The density-dependent matrix of a hypothetical perennial plant is

$$\mathbf{L}(N_t) = \begin{array}{cc} & \begin{array}{cc} \text{Juvenile} & \text{Mature} \end{array} \\ \begin{array}{c} \text{Juvenile} \\ \text{Mature} \end{array} & \begin{bmatrix} S_{JJ} & fS_0(N_t) \\ S_{MJ} & S_{MM} \end{bmatrix} \end{array}$$

The dynamics of the population with stage-structure can be written as:

$$\mathbf{n}_{t+1} = \mathbf{L}(N_t)\mathbf{n}_t. \quad (5)$$

This dynamical system has only one non-trivial equilibrium (see Appendix B). At the equilibrium,

$$\mathbf{n}^* = \mathbf{L}(N^*)\mathbf{n}^* \quad (6)$$

is satisfied. N^* can be obtained from

$$\det[\mathbf{L}(N^*) - \mathbf{I}] = 0$$

or

$$(1 - S_{JJ})(1 - S_{MM}) = fS_{MJ}S_0(N^*). \quad (7)$$

Equation (7) is the eigenvalue equation with $\lambda = 1$ of the matrix $\mathbf{L}(N^*)$.

Suppose that there is a population composed of wild-type individuals whose Lefkovitch matrix is $\mathbf{L}(N_t)$. When the population is at the equilibrium state, a small number of mutant individuals invade their habitat. The Lefkovitch matrix of the mutants is

$$\mathbf{L}'(N_t) = \begin{array}{cc} & \begin{array}{cc} \text{Juvenile} & \text{Mature} \end{array} \\ \begin{array}{c} \text{Juvenile} \\ \text{Mature} \end{array} & \begin{bmatrix} S_{JJ} & (f + \delta f)S_0(N_t) \\ S_{MJ} & (S_{MM} + \delta S_{MM}) \end{bmatrix} \end{array}$$

where δf and δS_{MM} are sufficiently small because mutation changes the life-history parameters slightly. The invasible condition of a mutant in the DD projection matrix model is given in Takada & Nakajima (1992). Their result is divided into two parts as follows

RESULT 1

When the elements of $\delta \mathbf{L}(N^*)$ are sufficiently small, the sufficient condition such that a mutant can invade the wild-type population is

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0,$$

where \mathbf{u} and \mathbf{v}^T are the right and left eigenvectors of $\mathbf{L}(N^*)$ corresponding to the eigenvalue 1, respectively, satisfying the normalization condition

$$\mathbf{v}^T \mathbf{u} = 1 \quad \text{and} \quad \delta \mathbf{L}(N^*) = \mathbf{L}'(N^*) - \mathbf{L}(N^*).$$

RESULT 2

When the elements of $\delta \mathbf{L}(N^*)$ are sufficiently small, if $d l_{ij}(N^*)/d N^* \leq 0$ for all i, j and $d l_{ij}(N^*)/d N^* < 0$ for at least one set of (i, j) , then the invincible condition is $\delta N^* > 0$.

δN^* is the difference in equilibrium population sizes between the mutant and the wild-type. The second result means that, if at least one of the elements of Lefkovich matrix is a decreasing function of N_i and others are constant, then the mutant with the larger population size at the equilibrium can invade the wild-type population. Charlesworth (1971, 1980) and Roughgarden (1971) demonstrated that selection tends to maximize the number of individuals at the equilibrium in a negatively density-dependent population with age-structure. Since the matrix representing the dynamics of age-structured populations corresponds to a special case of the matrix on stage-structured populations, the second result is the extended version of their result.

Since $\mathbf{L}(N_i)$ and $\mathbf{L}'(N_i)$ satisfy the assumption of the second result, we can obtain the invincible condition in terms of the second result. From eqn (7),

$$\frac{1 - S_{JJ}}{S_{MJ} S_0(N^*)} = \frac{f}{1 - S_{MM}}. \quad (8)$$

Since the equilibrium population size, N^* , increases in the course of evolution of (S_{MM}, f) for a given S_{JJ} , S_{MJ} and $S_0(N_i)$, the left-hand side of eqn (8) increases as the invasions of invadable mutants are iterated. Therefore, the right-hand side of eqn (8) also increases in the course of evolution. Thus, the invincible condition of the mutant is as follows:

$$\delta \left(\frac{f}{1 - S_{MM}} \right) > 0. \quad (9)$$

$f/(1 - S_{MM})$ is a measure of fitness in this model and is also exactly the same as the reproductive value, i.e. the expected number of offspring to be produced in future by a single mature individual because

$$\frac{f}{1 - S_{MM}} = f + f S_{MM} + f S_{MM}^2 + f S_{MM}^3 + f S_{MM}^4 + \cdots,$$

where S_{MM}^n represents the probability that individuals at maturing stage can survive during n years.

ESSs were obtained in the cases of three typical trade-off curves, where the second derivatives are $g'' = 0$, $g'' > 0$ and $g'' < 0$ (Fig. 1).

CASE (IV)

When $g'' = 0$, we can obtain the ESS graphically [Fig. 3(a)]. The value of $f/(1 - S_{MM})$ represents the absolute value of the slope of the line drawn from $(1, 0)$ to a point on the trade-off curve. Therefore, the slope is maximum at $(0, g(0))$. Monocarpic perennial plants are favored when $g'' = 0$.

CASE (V)

When $g'' < 0$, there are two cases, depending on the values of $g'(0)$ and $g(0)$ (see Appendices A and C). If $g'(0) \leq -g(0)$, then the ESS, (S_{MM}^*, f^*) , is $(0, g(0))$. Monocarpic perennial plants are favored in this case [Fig. 3(b)]. If $g'(0) > -g(0)$, then an interior ESS is favored. This means that iteroparous perennial plants are favored in this case [Fig. 3(c)]. The following equation is satisfied at the ESS (S_{MM}^*, f^*) :

$$g'(S_{MM}^*) = \frac{g(S_{MM}^*)}{1 - S_{MM}^*}. \quad (10)$$

CASE (VI)

When $g'' > 0$, $f/(1 - S_{MM})$ is largest at $S_{MM} = 0$ [Fig. 3(d)]. It does not depend on other parameters such as S_0 , S_{MJ} and so on, but does not only on the shape of the trade-off curve. Therefore, semelparous perennial plants are always favored when $g'' > 0$.

The results of this section are summarized in Table 2. The shape of the trade-off curve again plays an important role in the evolution on the frequency of reproduction. $g'' < 0$ is the necessary condition for iteroparity and $g'' > 0$ is the sufficient condition for semelparity. The second factor is the values of $g'(0)$ and $g(0)$. Therefore, in the DD case, only the characters of the trade-off curve control the evolution on the frequency of reproduction.

4. Comparison between the Two Models

4.1. INVINCIBLE CONDITIONS

The invincible conditions in those two models are significantly different as follows:

$$\delta \left(\frac{S_{MM} + S_{JJ} + \sqrt{(S_{MM} - S_{JJ})^2 + 4fS_0S_{MJ}}}{2} \right) > 0,$$

[eqn (3)]

and

$$\delta\left(\frac{f}{1-S_{MM}}\right) > 0,$$

[eqn (9)]. While inequality (3) includes parameters such as S_{JJ} , S_{MJ} and S_0 , inequality (10) does not include those parameters (Table 3). That is, the invulnerable condition in the DD model does not depend on the parameters in younger stages. The ESS of DD model depends only on the trade-off curve between

the number of seeds and the survival rate at mature stage. In contrast, the invulnerable condition in the DI model is affected by those parameters and the shape of the trade-off curve.

4.2. ESS AND THE SHAPE OF THE TRADE-OFF CURVE

When the trade-off curve between the number of seeds and the survival rate at mature stage is linear or concave ($g'' \geq 0$), the ESSs in the two models are the same despite the discrepancy in the invulnerable

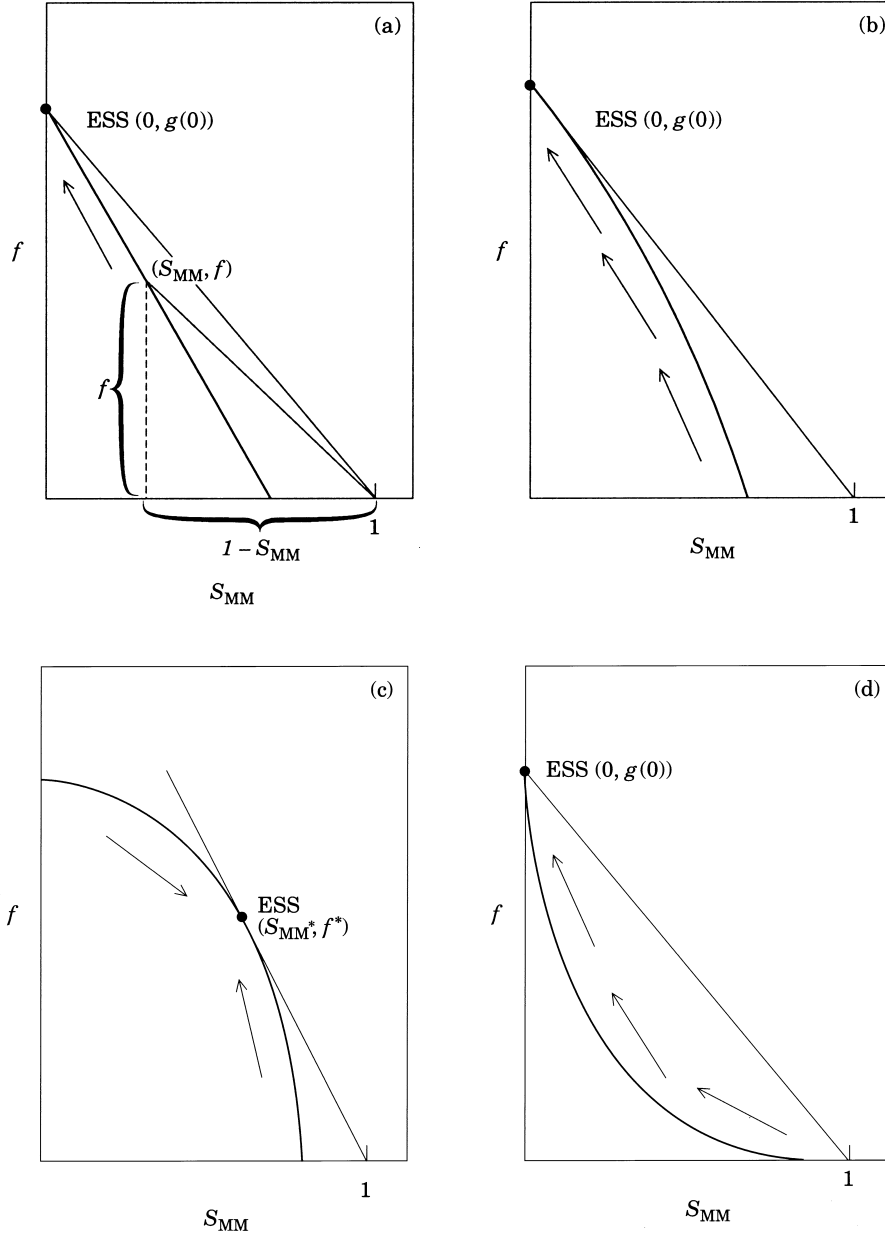


FIG. 3. Results of the density-dependent model. (a) When the trade-off curve is linear ($g'' = 0$), $(0, g(0))$ is an ESS because the slope of the line drawn from $(1, 0)$ to a point on the trade-off curve is maximum at $(0, g(0))$. In this case, semelparous perennial plants are favored. (b) (c) When the trade-off curve is convex upward ($g'' < 0$), there are two cases, depending on the values of $g'(0)$ and $g(0)$. (d) When the trade-off curve is convex downward ($g'' > 0$), $(0, g(0))$ is an ESS. Details are discussed in the text.

TABLE 2
Results for the density-dependent model

To be favored	Conditions of parameters
Semelparous perennials	$g'' = 0$ $g'' < 0$ and $g'(0) \leq -g(0)$ $g'' > 0$
Iteroparous perennials	$g'' < 0$ and $g'(0) > -g(0)$

condition (Table 3). Semelparous perennial plants are favored in both the DI and DD models. It means that the shape of the trade-off curve ($g'' > 0$) has a larger effect on the evolution of the frequency of reproduction than the density-dependence of the models. When the trade-off curve is convex ($g'' < 0$), semelparity or iteroparity is favored (Table 3), depending on the parameters in the juvenile and seed stages and on the values of $g(0)$ and $g'(0)$ (Tables 1 and 2). $g'' < 0$ is the necessary condition for iteroparity to be favored. The shape of the trade-off curve governs the evolution of the frequency of reproduction in both the DI and DD models.

4.3. ESS AND LIFE-HISTORY PARAMETERS

When $g'' < 0$, the ESSs of these models depend on the life-history parameters. While the ESS in the DD model depends on $g(0)$ and $g'(0)$ (Table 1), the optimal solution in the DI model depends on S_0 , S_{JJ} , S_{MJ} , $g(0)$ and $g'(0)$ (Table 2). This is a large difference between the two models. The ESS in the DD model is affected only by the parameters at mature stage (for example, $g(0)$ is the number of seeds when the total amount of assimilating products is invested in seeds). However, the optimal solution in the DI model is affected by the parameters at younger stages. From the conditions in Table 1, the decrease of $S_0 S_{MJ}$ and S_{JJ} causes the evolution of iteroparous perennial plants in the DI model because

$$\frac{\partial \left(\frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_0 S_{MJ} g(0)}}{2S_0 S_{MJ}} \right)}{\partial (S_0 S_{MJ})} = \frac{\{S_{JJ}^2 + 2S_0 S_{MJ} g(0)\} - \sqrt{S_{JJ}^4 + 4S_{JJ}^2 S_0 S_{MJ} g(0)}}{2\{S_0 S_{MJ}\}^2 \sqrt{S_{JJ}^2 + 4S_0 S_{MJ} g(0)}} > 0$$

and

$$\frac{\partial \left(\frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_0 S_{MJ} g(0)}}{2S_0 S_{MJ}} \right)}{\partial (S_{JJ})} = \frac{\sqrt{S_{JJ}^2 + 4S_0 S_{MJ} g(0)} - S_{JJ}}{2S_0 S_{MJ} \sqrt{S_{JJ}^2 + 4S_0 S_{MJ} g(0)}} > 0.$$

That is, in the DI model, iteroparous perennial plants would be favored due to the deterioration of environment at younger stages.

From the conditions in Table 1 and 2, large $g'(0)$ (i.e. small $|g'(0)|$) is a cause of the evolution of iteroparous perennial plants in both models. $|g'(0)|$ represents the increasing rate of the number of seeds when the survival rate of mature plants decreases. It is small when the cost of producing a seed is high. Then, iterative reproduction would be favored due to the high cost of producing a seed.

5. Discussion

The evolution of the frequency of reproduction is a classic subject in studies on the evolution of life history (Stearns, 1992). Over the last 20 years, many authors have attempted to explain on what conditions semelparity or iteroparity is favored (Gadgil & Bossert, 1970; Charnov & Schaffer, 1973; Schaffer & Gadgil, 1975; Pianka, 1976; Charlesworth, 1980; Bulmer, 1985). Several authors have examined whether plants should be semelparity (annual) or iteroparity (perennial). Charnov & Schaffer (1973) analyzed a simple model without the trade-off between fecundity and adult survival, and suggested that iteroparity is favored when the ratio of the survival rate at adult stage to that at juvenile stage is high. Bulmer (1985) incorporated the density-dependence into Charnov and Schaffer's model in two ways—the lottery model and the exponential model. In the lottery model, he obtained a similar result as Charnov and Schaffer's in that the ratio of the survival rate at adult stage to that at juvenile stage is a key factor in the evolution of the frequency of reproduction.

TABLE 3
Comparison between the DI and DD models

	Density-independent model	Density-dependent model
Invisible condition	Depend on the trade-off curve and S_0 , S_{MJ} , S_{JJ}	Depend on the trade-off curve
When $g'' \geq 0$	Semelparity	Semelparity
When $g'' < 0$	Semelparity or iteroparity	Semelparity or iteroparity

Schaffer & Gadgil (1975) and Pianka (1976) used an age-structured population model, taking into account for the trade-off between the current fecundity and the residual reproductive value. They concluded that the shape of the trade-off curve is a critical factor and that semelparity would be favored when the trade-off curve is concave. Since the residual reproductive value is strongly associated with the survival rate of mature stage, their conclusion coincides with that of this paper, derived from the DI model, although their models are based on the age-specific parameters. Therefore, the conclusion that semelparity would be selected when the trade-off curve is concave, is common irrespective of whether parameters are age-dependent or stage-dependent.

Charlesworth (1980: 227) analyzed the density-dependent dynamics model of an age-structured population and concluded that semelparity is favored when the adult survival is low. While his result depends on the adult survival, my result in the density-dependent model does not depend on it. This discrepancy arises from the fact that he does not assume the trade-off between the fecundity and the adult survival. The common conclusion in both models is that the ESS does not depend on the parameters at younger stages.

Comparing Tables 1 and 2, the difference between the DI and DD models appears only when the trade-off curve is convex. When $g'' < 0$, the ESS in the DD model does not depend on the parameters at younger stages. For example, suppose that the environment is too severe or the herbivory is too strong at the juvenile stage (i.e. the mortality at juvenile stage is high). Then, the values of S_{MJ} and S_{JJ} are low. However, the harshness of the environment or herbivory does not affect the consequence of evolution in the DD model. This is due to the density-dependence in the emergence rate of seeds. In summary, the trade-off between fecundity and survival and the density-dependence are important for the evolution of the frequency of reproduction, but the size-structure is not.

The density-dependence is an important factor affecting the population dynamics, and thus the evolution of life history, especially in perennial herbs, which often live in a stable and predictable environment such as a woodland. The density-dependence might be strong in the environment and K -selection is expected to operate there. Therefore, as Charlesworth (1980) and Takada & Nakajima (1992) pointed out, the population size at equilibrium increases in the course of evolution as long as the density-dependence has a negative effect on the fecundity and survival rate. On the contrary, in an

unstable environment, the density-dependence is too weak and r -selection is expected to operate there. Therefore, the evolution of life history would be strongly affected by the survival rate at younger stages. The present paper supports the above intuitive discussion on r - and K -selection.

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APPENDIX A

The Density-independent Model

In order to obtain S_{MM}^* with the largest λ , we examine the sign of $d\lambda/dS_{MM}$ for $0 \leq S_{MM} \leq S_{MMmax}$, where $g(S_{MMmax}) = 0$. Differentiating eqn (2) in the main text with respect to S_{MM} , we obtain

$$\frac{d\lambda(S_{MM})}{dS_{MM}} = \frac{\lambda - S_{JJ} + S_0 S_{MJ} g'(S_{MM})}{\sqrt{(S_{MM} - S_{JJ})^2 + 4fS_0 S_{MJ}}}. \quad (A.1)$$

Since the denominator of the right-hand side of eqn (A.1) is always positive, we put $Q(S_{MM}) = \lambda(S_{MM}) - S_{JJ} + S_0 S_{MJ} g'(S_{MM})$ and examine the sign of Q . The first derivative of Q with respect to S_{MM} is

$$\frac{dQ(S_{MM})}{dS_{MM}} = \frac{d\lambda(S_{MM})}{dS_{MM}} + S_0 S_{MJ} g''(S_{MM}). \quad (A.2)$$

When $g'' = 0$, if $d\lambda/dS_{MM} < 0$ (i.e. $Q < 0$) at $S_{MM} = 0$, then $dQ/dS_{MM} < 0$ at $S_{MM} = 0$ from eqn (A.2). If $d\lambda/dS_{MM} > 0$ (i.e. $Q > 0$) at $S_{MM} = 0$, then $dQ/dS_{MM} > 0$ at $S_{MM} = 0$. Thus, there are two cases as follows:

CASE (I.1)

$$\frac{d\lambda}{dS_{MM}} \text{ is negative for } 0 \leq S_{MM} \leq S_{MMmax}$$

(i.e. λ is the highest at $S_{MM} = 0$).

CASE (I.2)

$$\frac{d\lambda}{dS_{MM}} \text{ is positive for } 0 \leq S_{MM} \leq S_{MMmax}$$

(i.e. λ is the highest at $S_{MM} = S_{MMmax}$).

Since $\lambda(S_{MMmax}) = \max\{S_{JJ}, S_{MMmax}\} < 1$ from eqn (2) in the text, $\lambda < 1$ for $0 \leq S_{MM} \leq S_{MMmax}$ in Case (I.2). Case (I.2) cannot be favored under natural selection. Therefore, we have the following result:

Case (I.1)

When

$$g'(0) \leq \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}},$$

the ESS is $(0, g(0))$.

When $g'' < 0$, if $d\lambda/dS_{MM} = 0$ (i.e. $Q = 0$) at a certain S_{MM}^* , then $dQ/dS_{MM} < 0$ at $S_{MM} = S_{MM}^*$ from

eqn (A.2). Therefore, $d\lambda/dS_{MM} < 0$ and $dQ/dS_{MM} < 0$ at $S_{MM}^* < S_{MM} < S_{MMmax}$ from eqns (A.1) and (A.2). Thus, there are three cases as follows:

CASE (II.1)

$d\lambda/dS_{MM}$ is negative for $0 \leq S_{MM} \leq S_{MMmax}$ and $dQ/dS_{MM} \leq 0$ at $S_{MM} = 0$.

CASE (II.2)

$d\lambda/dS_{MM}$ is positive for $0 \leq S_{MM} < S_{MM}^*$ and $d\lambda/dS_{MM}$ is negative for $S_{MM}^* < S_{MM} \leq S_{MMmax}$.

CASE (II.3)

$d\lambda/dS_{MM}$ is positive for $0 \leq S_{MM} \leq S_{MMmax}$.

Since $\lambda(S_{MMmax}) = \max\{S_{JJ}, S_{MMmax}\} < 1$ from eqn (2) in the main text, $\lambda < 1$ for $0 \leq S_{MM} \leq S_{MMmax}$ in Case (II.3). We need not examine Case (II.3) because the population with $\lambda < 1$ would go extinct. Thus, we have the following results:

Case (II.1)

When

$$g'(0) \leq \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}}$$

(i.e. $Q \leq 0$ at $S_{MM} = 0$), λ is a decreasing function of S_{MM} for $0 \leq S_{MM} \leq S_{MMmax}$. Thus λ has the highest value at $(0, g(0))$.

Case (II.2)

When

$$g'(0) > \frac{S_{JJ} - \sqrt{S_{JJ}^2 + 4S_{MJ}S_0g(0)}}{2S_0S_{MJ}}$$

(i.e. $Q > 0$ at $S_{MM} = 0$), λ has the highest value at $S_{MM}^* > 0$. S_{MM}^* satisfies

$$g'(S_{MM}^*) = \frac{S_{JJ} - S_{MM}^* - \sqrt{(S_{JJ} - S_{MM}^*)^2 + 4S_{MJ}S_0g(S_{MM}^*)}}{2S_0S_{MJ}},$$

which is eqn (4) in the main text.

When $g'' > 0$, we can also analyze the sign of $d\lambda/dS_{MM}$ similarly. As a result, there are three cases as follows:

CASE (III.1)

$d\lambda/dS_{MM}$ is negative for $0 \leq S_{MM} \leq S_{MMmax}$ and $dQ/dS_{MM} \leq 0$ at $S_{MM} = 0$.

CASE (III.2)

$d\lambda/dS_{MM}$ is negative for $0 \leq S_{MM} < S_{MM}^*$ and $d\lambda/dS_{MM}$ is positive for $S_{MM}^* < S_{MM} \leq S_{MMmax}$.

CASE (III.3)

$d\lambda/dS_{MM}$ is positive for $0 \leq S_{MM} \leq S_{MM\max}$. Case (III.3) can be disregarded for the same reason in Case (II.3). (Q.E.D.)

APPENDIX B

The Local Stability Condition at Equilibrium

Equation (6) in the main text has two equilibria, i.e. $\mathbf{n}^* = (0, 0)$ or (n_J^*, n_M^*) . The second equilibrium is proportional to the right eigenvector of eqn (6) and satisfies eqn (7), i.e.

$$(1 - S_{JJ})(1 - S_{MM}) = fS_{MJ}S_0(n_J^* + n_M^*). \quad (\text{B.1})$$

Since $S_0(n_J^* + n_M^*)$ is a monotonically decreasing function, the solution which satisfies eqn (B.1) is unique when

$$(1 - S_{JJ})(1 - S_{MM}) < fS_{MJ}S_0(0). \quad (\text{B.2})$$

The stability condition of $(0, 0)$ is that the absolute value of all the eigenvalues of the following Jacobian matrix is less than 1 (Caswell, 1989; 237–242):

$$\begin{bmatrix} S_{JJ} & fS_0(0) \\ S_{MJ} & S_{MM} \end{bmatrix}.$$

That is, the stability condition of $(0, 0)$ is

$$2 > 1 + S_{JJ}S_{MM} - fS_0(0)S_{MJ} > S_{JJ} + S_{MM}.$$

or

$$(1 - S_{JJ})(1 - S_{MM}) > fS_0(0)S_{MJ}. \quad (\text{B.3})$$

Therefore, if $(0, 0)$ is stable, there is no non-trivial solution because of (B.2). (B.3) corresponds to the mathematical condition that $\lambda < 1$.

Similarly, the stability condition of (n_J^*, n_M^*) can be obtained as follows (Caswell, 1989; 237–242):

$$\begin{aligned} 2 &> S_{JJ} + S_{MM} - (S_{MM} - S_{MJ})fS'_0(N^*)n_M^* \\ &> |S_{JJ} + S_{MM} + fS'_0(N^*)n_M^*|. \end{aligned} \quad (\text{B.4})$$

Therefore, if $(0, 0)$ is unstable, (n_J^*, n_M^*) is stable and there is no strange attractor in the dynamical system of eqn (5), the population density at each stage and the population size reach the equilibrium after the time has elapsed sufficiently (Guckenheimer *et al.*, 1977).

APPENDIX C

The Density-dependent Model

In order to obtain S_{MM}^* with the largest $f/(1 - S_{MM})$ ($=W$), we can similarly examine the sign of dW/dS_{MM} as in the DI model (see Appendix A).