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Evolutionarily Stable Seasonal Timing for Insects with Competition for Renewable Resource

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資源獲得競争による昆虫の孵化および蛹化のＥＳＳタイミング

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I study the evolutionarily stable seasonal patterns of hatching and pupation for herbivorous insects that engage in exploitative competition for a renewable resource. Longer larval feeding period enhances female fecundity, but also causes a higher mortality by predation and parasitism. Previously, it was shown that the evolutionarily stable population includes asynchronous starting and ending of larval feeding period in a model in which larval growth rate decreases with the total larval biomass in the population due presumably to interference competition. Here I study the case in which resource availability changes not only with environmental seasonality but also with the depletion by the feeding of larvae. If the environment for host plants changes fast, the ESS insect population may include synchronous timing of hatching and pupation. If the impact of the herbivory is strong compared with the speed of seasonal change of the environment, both hatching and pupation should occur asynchronously in the ESS. In addition, if the environmental variable changes as a symmetric function of time, the length of period in which hatching occurs tends to be much shorter than the period in which pupation occurs.

Introduction

Insects living in temperate regions have widely diverse life histories adapted to seasonality of the environment. Closely related species or even populations of the same species may sometimes show greatly different life history patterns, especially over latitudinal gradient (Danks 1987; Kidokoro & Masaki 1978; Masaki 1980; Furunishi & Masaki 1982; Sota 1987, 1998, 1994; Tauber *et al.* 1986). Diversity in phenology, or seasonality in life cycle, may partially attribute to the escape from the coldness during winter which may often require winter diapause. Phenology is also related with seasonally changing resource availability, as well as coldness in winter, possibly modified by seasonalily changing risk of predation and parasitism. Shapiro (1975) for example studied the phenology of eight univoltine oak-feeding lepidopterans in the New Jersey pine barrens and observed that all the eight species have their feeding larval stages in spring in spite of great differences among them in the adult season or in the overwintering stage.

In this paper, I study the evolutionarily stable insect life cycle under exploitative competition, in which the dynamics of resource availability are included explicitly. The resource (or host plant) availability increases by growth and decreases by herbivory. By mathematical and numerical analysis I show that whether hatching and pupation occur synchronously depends both on the intensity of herbivory and on the rate of seasonal change of the environment. Specifically both pupation and hatching occur synchronously in the ESS population if the feeding larval density is small and if the environment changes quickly, but they occur asynchronously if the impact of herbivory is strong compared with seasonal change of the environment. In addition, if both hatching and pupation occur asynchronously, the interval during which some pupation occur every day is likely to be much longer than a similar interval for hatching.

Model

Consider a population of herbivorous insects, the larvae of which feed on host plants with seasonal availability. Suppose that each larva in the population is indexed by i. The growth rate in the body weight W_i of a feeding larva i on day t is,

$$\frac{dW_i}{dt} = aR(t)W_i \quad , \qquad (1)$$

where a is a constant for growth efficiency. Function $R(t)$ is the abundance of host plants or resource availability. The initial size of larvae is assumed a constant w_0 which is given by the egg size.

Host plants expand their leaves and shoots for photosynthesis, which may be damaged by feeding larvae. Abundance of host plants $R(t)$ changes with time as follows:

$$\frac{dR}{dt} = \left\{ r\left(1 - \frac{R}{K(t)}\right) - bB \right\} R \quad , \qquad (2)$$

where $B(t)$ denotes total biomass of feeding larvae in the population. Equation 2 implies that, when there is no herbivory, resource level $R(t)$ follows a logistic equation with intrinsic reproductive rate r and carrying capacity $K(t)$.

In the model, a life history schedule of a larva is specified by its hatching date and pupation date, i.e. the start and the end of active feeding. To indicate the life cycle timing of an individual, I here introduce a feeding activity schedule instead of those two dates. The strategy of individual i is represented by function $\sigma_i = \sigma_i(t)$ such as σ_i is equal to unity when it is fully active in feeding on day t, zero when it is inactive, and takes a value between zero and unity for an intermediate level of feeding activity. A similar formulation was used for activity schedule of male frogs in the study on the seasonal pattern of sex ratio (Iwasa &

Odendaal, 1984), for mate searching activity for male butterflies within a day (Iwasa & Obara, 1989), for sex expression in discussing sex change evolution (Iwasa, 1991b), as well as for feeding activity of butterfly larvae (Iwasa, 1991a).

By using σ_i, Equation 1 can be rewritten as the following equation, which holds over the whole season [0, T]:

$$\frac{dW_i}{dt} = aR(t)W_i\sigma_i \quad , \qquad (3a)$$

together with the initial condition:

$$W_i(0) = w_0 \quad . \qquad (3b)$$

Since W_i does not change before hatching, W_i on the hatching day is the same as w_0 from Equation 3b.

Total biomass of feeding larvae $B(t)$ in the population is the sum of weight of all larvae multiplied by the survivorship to day t and the activity on that day $\sigma_i(t)$:

$$B(t) = \sum_i W_i(t)\sigma_i(t)\exp\left(-m\int_0^t \sigma_i(t)dt\right) \quad . \qquad (4)$$

Constant m is the daily mortality of an actively feeding larva. Note that the sum in Equation 4 needs to be calculated for all the individuals included in the initial population with population size N_0. I here assume that mortality in inactive stages is negligibly small relative to m.

I assume that fecundity, or the expected number of eggs which an adult female can lay, is proportional to its pupation size, the final body weight of larvae (for justification of this assumption, see Iwasa, 1991a; Iwasa *et al.*, 1992, 1994). In particular it is equal to $W_i(T)$ of the solution of Equation 3a, because W does not change with time after pupation date (i.e. during $\sigma_i(t) = 0$). The fecundity is equal to $QW_i(T)/w_0$, where w_0 is weight of an egg and Q is a proportionality constant.

This multiplied by the larval survivorship is the fitness of an individual adopting strategy σ_i:

$$\phi(\sigma_i) = Q\frac{W_i(T)}{w_0}\exp\left(-m\int_0^T \sigma_i(t)dt\right) \quad , \tag{5}$$

where ϕ is the functional of function $\sigma_i(\bullet)$. In the evolutionarily stable population, each individual chooses its own schedule of feeding activity σ_i so as to maximize its fitness $\phi(\sigma_i)$.

Calculating derivative of Equation 5 and using Equation 3a, I can derive

$$\phi(\sigma_i) = Q\exp\left[\int_0^T (aR(t)-m)\sigma_i(t)dt\right] \quad . \tag{6b}$$

When $R(t)$ is given, Equation 6b is maximized by choosing $\sigma_i(t)$ as follows:

$$aR(t)-m>0 \Leftrightarrow \sigma_i = 1 \tag{7a}$$

$$aR(t)-m<0 \Leftrightarrow \sigma_i = 0 \tag{7b}$$

$$aR(t)-m=0 \Leftrightarrow \quad \sigma_i \text{ may have any value between zero and one.} \tag{7c}$$

In the ESS population, each individual must have the fitness that is no smaller than the fitness for any mutants that invade in small abundance in the population. Hence I can conclude that all of the members in the population must satisfy Equations 7a, 7b, and 7c, which indicate that all the individuals must engage in active feeding when the resource availability $R(t)$ exceeds m/a, all should stay inactive when $R(t)$ is less than m/a, and actively feeding and inactive individuals can coexist simultaneously only when $R(t)$ equals to m/a. Then f_i is the same between individuals for all t, and I remove the suffix i of $f_i(t)$ in the following. It is followed that Equation 4 and Equation 6a are rewritten as

$$B(t) = N_0 f\overline{\sigma} \quad , \tag{8}$$

and

$$\phi(\sigma_i) = Q\exp\left[\int_0^T (aR(t) - m)\bar{\sigma}(t)dt\right] \quad , \qquad (9)$$

respectively. In Equation 8, N_0 denotes the initial population of eggs at the start of the season and $\bar{\sigma} = \bar{\sigma}(t)$ is the population average of σ_i, and I call it "average activity" on day t. Then Equation 2 can be rewritten as:

$$\frac{dR}{dt} = \left\{r\left(1 - \frac{R}{K(t)}\right) - bN_0 f\bar{\sigma}\right\}R \quad . \qquad (10)$$

Specifically I assume that a season favourable for growth of host plant lasts from the beginning (t=0) to date T_f (T_f<T), during which carrying capacity $K(t)$ has a single peak K_1>m/a. After T_f, $K(t)$ is a small value satisfying K_0<m/a. Specifically I choose

$$K(t) = \begin{cases} K_0 \quad , & t < 0, \quad \text{or} \quad t > T_f \\ K_0 + \dfrac{K_1 - K_0}{2}\left(1 - \cos\dfrac{2\pi t}{T}\right) \quad , & 0 < t < T_f \end{cases} \quad . \qquad (11)$$

The evolutionarily stable patterns for typical cases are shown in Fig. 1 and Fig. 2. Figure 1a illustrates the case in which the impact of herbivory by the larvae on host plants is large. The season is composed of five phases. In the beginning of the season, both carrying capacity $K(t)$ and the resource availability $R(t)$ are low. Then $K(t)$ starts increasing and resource level $R(t)$ increases following $K(t)$ with some time delay. When $R(t)$ reaches a critical level m/a, on day t_1, some fraction of eggs hatches on that day. However in this particular example, some fraction of eggs remains unhatched and they hatch asynchronously over a period from t_1 to t_2 , which I call "hatching interval". This is the second phase. On t_2 , all the eggs finish hatching and then engage in active feeding as larvae. This third phase of full growth ends on day t_3 , on which some fraction of surviving larvae enters pupation. However the others remain feeding larvae and they turn to pupae asynchronously over some period from t_3 to t_4, which I call "pupation interval".

During this fourth phase, resource availability $R(t)$ remain constant m/a. On t_4, all the larvae finish pupation and thereafter they experience non-feeding stages (pupa, adult, and egg), the timing of which is out of concern of our present model. In addition, this asynchronisation also occurs if the rate of change in carrying capacity $K(t)$ is fast compared with intrinsic growth rate r and growth efficiency of larva a.

In Fig. 1a hatching and pupation occur asynchronously. During hatching and pupation intervals, the resource availability remains constant ($R(t)=m/a$) and the biomass of actively feeding larvae $B(t)$ is equal to

$$B^*(t)=\frac{r}{b}\left(1-\frac{m}{aK(t)}\right) \quad , \tag{12}$$

which can be determined only by carrying capacity function $K(t)$. This curve is illustrated in Fig. 1a by a broken line. On the first date of hatching interval t_1, $K(t)$ is greater than $R(t)=m/a$, then $B(t)$ discontinuously changes from zero to $B^*(t_1)>0$. The last date of hatching interval t_2 is derived from $B^*(t_2)=N_0w_0$. Note that those individuals hatching early do not change its expected biomass during hatching intervals, because gain by growth and loss by mortality cancel with each other exactly. Similarly if the day for beginning of pupation t_3, $B(t)$ is greater than $B^*(t)$, $B(t)$ discontinuously goes down to $B^*(t_3)$. The last date of pupation interval t_4 is obtained from $B^*(t_4)=0$.

If the impact of herbivory by the larvae to host plants is not very strong, either hatching or pupation or both occur synchronously. Figure 1b is the phenology of the ESS population in which hatching occurs synchronously but pupation occurs asynchronously. When $R(t)$ reaches a critical level m/a on day t_1, the total biomass of the insect population may be smaller than the value given by Equation 12 on that day:

$$N_0 w_0 \le \frac{r}{b}\left(1-\frac{m}{aK(t_1)}\right) \quad . \qquad (13)$$

Then all the eggs hatch synchronously and hatching interval does not exist. Inequality 13 can be satisfied if the egg biomass of the insect $N_0 w_0$ is sufficiently small. This is likely to be the case if the rate of change in seasonal carrying capacity $K(t)$ is fast (Fig. 2b), because $K(t)$ becomes quite large on the day at which resource availability reaches the prescribed level m/a.

Figure 1c illustrates the case in which not only hatching but also pupation occurs synchronously. Whether or not the pupation occurs asynchronously in the ESS population should also depend on the impact of the herbivory on host plants. During the period in which all the individuals should engage in active feeding, the resource availability should be larger than m/a. After the peak season, the resource availability starts to decline with time. The date t_3 on which fully active feeding ends is determined as a date on which $R(t)$ becomes equal to m/a. If the impact of the insect feeding on the resource is very small, $R(t)$ is larger than $K(t)$, as the resource availability decreases following the decline of carrying capacity $K(t)$ with some time delay. Hence, we have

$$K(t_3) \le \frac{m}{a} \quad , \qquad (14)$$

then $B^*(t_3)$ is negative. Consequently t_3 is later than the date t_4 on which Equation 14 becomes zero. This implies that all the larvae should pupate on the same day synchronously (Fig. 1c). If instead the impact of feeding larvae on the food plant is strong, resource availability is smaller than the carrying capacity on day t_3, and then there is a pupation interval, as is the case for Fig. 1a and 1b. Whether or not pupation occurs asynchronously is determined by the relative magnitude of $R(t_3)$ and $K(t_3)$, which in turn reflects the impact of herbivory relative to the rate of change in seasonal environment.

Discussion

In this paper I studied the evolutionarily stable pattern of hatching and pupation within a population of insects which engage in intraspecific exploitative competition for seasonally changing resource. I found that the hatching and pupation timing are synchronous in the evolutionarily stable population if seasonal environment changes rapidly and if the impact of herbivory by the insects on host plants is small.

Previously, Iwasa (1991a) and Iwasa *et al.* (1994) studied the evolutionarily stable seasonal timing of hatching and pupation by theoretical models in which the larval growth rate is simply assumed as a decreasing function of the biomass of feeding larvae at that time. They concluded that the phenological timing of insects is always asynchronous. In contrast the analysis in the present paper in which the resource dynamics are traced explicitly shows that both pupation and hatching can be synchronous if the impact of herbivory to the host plant population is small or if the environmental change very rapidly. It also supports the conclusion of the previous works that the pupation is more likely to occur asynchronously than hatching.

A similar idea of evolutionarily stable timing under competition for resource has been developed for modelling seasonality in leaf expanding activity for terrestrial plants. Harada & Takada (1988) studied optimal timing of leaf expansion and shedding of deciduous trees with competition by shading in a model with two layers of leaves, and found that the optimal schedule is different between the two layers, which engage in asymmetric competition. Sakai (1992) studied the evolutionarily stable timing of leaf expansion for equivalent competitors, and found that the schedule of leaf expansion and shedding is synchronous when their competition is not very strong, but both leaf expansion

and shedding can be asynchronous under strong competition for light. This conclusion is qualitatively similar to the one in this paper, although Sakai dealt with the case in which no reproduction or growth of consumers (i.e. tree leaves) is considered.

In this paper, I adopted several simplifying assumptions, some of which may be removed in the future theoretical works. First, I assumed that daily growth rate is proportional to the larval body weight in Equation 1 and that the number of eggs female can lay is also proportional to its pupation weight in Equation 4. However it is more plausible that female fecundity increases with her body weight but saturates for a very large body weight. Second, the growth rate is assumed to be proportional to the resource availability in Equation 1. In reality it is more likely that the growth rate would saturate for very large resource availability, and also that the saturation level would increase with the larval body weight because larger larva is more mobile and is able to sequester more resource. This effect was considered in Iwasa *et al.* (1992, 1994) in a model without resource dynamics. Third, the competitors may be sibs or half-sibs from the same clutch laid by a single mother. Then we need the analysis including kin selection. These modifications would be important future theoretical study of insect life cycle from the view point of evolutionary ecology.

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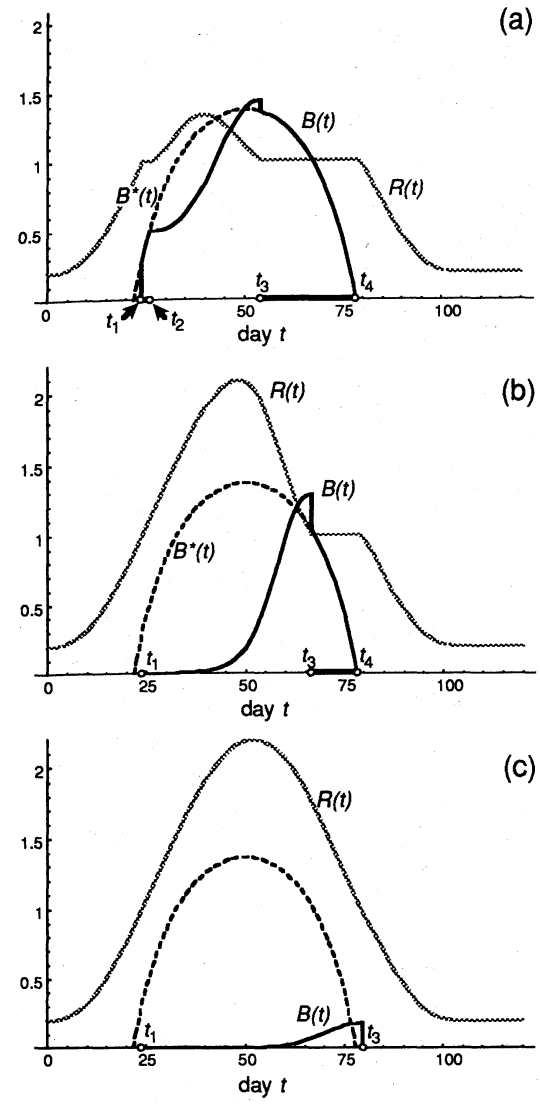

Figure 1 ESS growth schedule for different initial population size N_0. (a) N_0=10x10^6, (b) N_0=10000, and (c) N_0=100. Other parameters are: T_f=100, r=0.5, a=0.2, m=0.2, b=1, w_0=5.0x10-7, K_1=2.2, K_0=0.2.

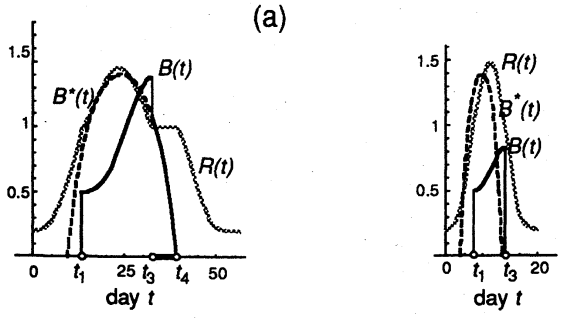

Figure 2 ESS growth schedule for shorter lengths of favorable season for the host plant T_f. Parameters are the same as in Fig. 1a except (a) T_f=50, and (b) T_f=20.