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## Delayed density dependence and oscillatory population dynamics in overlapping-generation systems of a seed beetle *Callosobruchus chinensis*: matrix population model

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**Abstract** Long-term experimental systems with overlapping generations using a seed beetle, *Callosobruchus chinensis*, were maintained by providing 5 g of azuki beans (*Vigna angularis*) in two different renewal intervals: either 7 days or 10 days. The 7-day-renewal system (system 1) showed oscillatory dynamics with a constant periodic cycle of ca. 7 weeks. More stable population dynamics were seen in the 10-day-interval system (system 2). Short-term experiments showed that survivorship of adults increased with higher adult density, and that the survival rate of adults up to the age of 7 days was much higher than up to 10 days of age. In addition, the per capita production of hatched eggs by females which had survived for 7 days increased with increasing density experienced by the females. Females aged 10 days rarely laid eggs which hatched. We constructed a matrix population model based on either 1 week for system 1 or 10 days for system 2. The model included five stages in system 1: the hatched egg, the final instar larva, the pupa, the young adult and the old adult. Four stages were incorporated in the model for system 2: the young instar larva, the pupa, the young adult, and the old adult. Logistic-difference equations were applied to formulate both overcompensatory density dependence in the hatched-egg production by adults and undercompensatory response in the larval development up to the pupa. The survivorship of young adults to the old stage and the per capita hatched-egg productivity of the old females followed a linear regression against the young adult density. Inside-bean processes were adjusted to be equivalent in the two models, irrespective of the resource renewal intervals. The model predicted that system 1 would oscillate for a long time but that system 2 would rapidly converge to the equilibrium point. Multiplicative effects of both the delayed density dependence through interstage restraint effects and the overcompensatory density dependence in hatched-egg production generated various dynamic patterns ranging from a quickly disap-

pearing damped oscillation to stable limit cycles in system 1. The relationship between resource renewal cycles and delayed density dependence was discussed based on these simulations.

**Key words** Interstage density dependence · Delayed density dependence · Population oscillation · Projection matrix model · Resource renewal cycle

### Introduction

In single-species populations with overlapping generations, interstage density-dependent interactions, such as cannibalism of larvae/adults on eggs/pupae in a flour beetle *Tribolium castaneum* (Desharnais and Liu 1987; Caswell 1989), are ubiquitous. In addition, the density of one stage at a given time may often severely affect individuals at a later stage after a time delay, due to a developmental lag in stage-structured populations; for example, the blowfly, *Lucilia cuprina* (Nicholson 1954). Theoretical models incorporating such interstage and/or delayed density dependences have predicted a large variety of dynamical behaviors of a population (Gurney et al. 1980; Gurney et al. 1983; Gurney and Nisbet 1985; Liu and Cohen 1987; Caswell 1989). However, most of these models have been theory-oriented and their primary aims were theoretical analyses on population processes generating the oscillatory behaviors. There have been quite few studies, other than Desharnis and Liu (1987), modeling an actual overlapping-generation system with formulation and parameter estimations based on the data.

The seed beetle, *Callosobruchus chinensis* (L.) (Coleoptera: Bruchidae), is good laboratory material, with detailed information on its ecological characteristics (Utida 1941a, b; Fujii 1968; Bellows 1982a, b; Hassell et al. 1989; Shimada 1989, 1990; Tuda and Shimada 1993). In a discrete-generation system of *C. chinensis*, the two episodes of density dependence are completely separated in the life cycle; one occurring inside (larval growth) and the other outside the bean (adult's egg-deposition). The

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latter process shows overcompensation with a peaked density response curve (Utida 1941b; Bellows 1982b; Shimada 1989), but the non-linear effect is almost cancelled out by exact compensation of the saturated curve in the larval development. Therefore, those discrete-generation systems, both in experiments and models, soon converge to an equilibrium level with quickly disappearing damped oscillations due to no or weak effects of interstage and delayed density-dependences (Bellows 1982a, b; Shimada 1989).

On the other hand, in an overlapping-generation system of *C. chinensis*, the density-dependent egg-deposition process changes considerably from the discrete-generation system. *C. chinensis* females deposit most eggs in the first 5 days after emergence, although they survive for several days thereafter (Bellows 1982b; M. Shimada, unpublished data). These old surviving adults may decrease hatchability of eggs deposited by young, newly emerged adults, because the major cause of egg mortality at a high adult density is reported to be the mechanical damage of eggs by adult trampling (Utida 1941b; Bellows 1982b). Therefore, we can incorporate into a system interstage and delayed density-dependent effects of the old adults on the young adults' egg deposition.

In the present study, we looked at the effect of old adults as a new oscillation-promoting factor in *C. chinensis*. We altered the effect experimentally by means of changing the resource renewal intervals in long-term systems with overlapping generations. Next, we applied Leslie-type matrix population models (Leslie 1945, 1948), which incorporate density-dependent elements (for a review see Caswell 1989), to the experimental systems. The aims are (1) to examine if oscillatory dynamics occur in the overlapping-generation systems of *C. chinensis* with different resource renewal intervals, and (2) to analyze the dynamics of experimental systems using a matrix population model which includes the interstage and delayed density-dependent effects.

## Experimental systems

### Materials and methods

A laboratory strain, jC, of *C. chinensis*, which has been frequently studied since 1936 (Utida 1941a, b; Fujii 1968; Shimada 1989; Tuda and Shimada 1993), was used in the present study. Experiments were conducted at 30° C and 70% relative humidity without adult feeding. Under these conditions, basic life history characteristics, namely mean adult longevity and fecundity per female, of strain jC have been reported by those authors to be ca. 8.5 days and about 80 eggs (74 hatched eggs), respectively. Developmental period from egg to fully grown final (fourth) instar larva is ca. 14 days, and to the adult is ca. 22 days, on average.

Long-term systems with overlapping generations were established according to Fujii (1983). The resource for *C. chinensis* was 5 g of azuki beans (*Vigna angularis* c.v. *dainagon*) which was provided periodically. Two types of long-term system were set up, differing in their resource renewal cycles.

In the first type (system 1), 5 g of beans were added every 7 days. Each replicate of the system was set up in a four-compartment

Petri dish (90 mm in diameter and 15 mm in depth). In week 0, 1, and 2, we introduced the same number of newly emerged adults from stock cultures (either 8, 32, or 128 pairs) into the Petri dish. During each of these weeks, 5 g of azuki beans were added to one compartment of the dish, compartment I, II, and III in turn. In week 3, we provided only 5 g of beans to compartment IV, and thereafter the compartment of 4-week-old infected beans was constantly replaced with 5 g of new beans. At each resource renewal, we counted the numbers of living and dead adults in a Petri dish, and removed the dead insects. The population censuses were carried out until week 35. The number of emergent adults per week was calculated as (no. of living adults in week  $i$ ) + (no. of dead adults in week  $i$ ) - (no. of living adults in week  $i-1$ ).

In addition, we counted the numbers of hatched and unhatched eggs on five beans that were randomly chosen from the compartment of 1-week-old beans. These five beans were marked individually in the hilum with different color pencils after counting the eggs. These were returned to the system, and in the following week we counted the number of fourth instar larvae by dissecting the beans. The larvae were restored to the compartment, because fully grown final instar *C. chinensis* larvae can usually pupate and emerge as adults even after being removed from the beans. We estimated the total numbers of hatched eggs and the final instar larvae in a whole system as multiplied by the ratio of the total number of beans to five. The censuses of eggs and larvae were carried out until week 11.

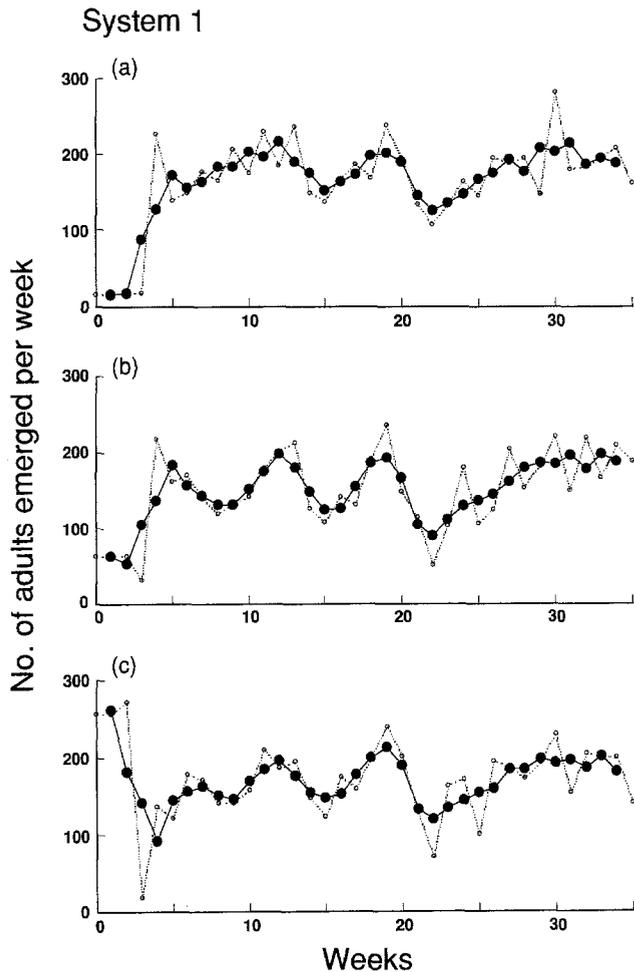
In the second type of long-term system (system 2), we renewed beans every 10 days and performed the same census of adults as in system 1 at each resource renewal. We set the same ambient conditions of 30° C and 70% relative humidity as in system 1 and founded three replicate dishes. Ten pairs of newly emerged adults from stock cultures were introduced into four-compartment Petri dishes on days 0, 10 and 20. On day 30 and thereafter we conducted only resource renewal and counts of live and dead adults. We continued the population censuses every 10 days until day 260. The number of adults to emerge over a 10-day period was calculated using the same method as system 1. Unfortunately, we could not set the same number of founders in both systems because the two long-term systems were established separately by each of us in different laboratories. The effect of initial founder density was examined in simulation analysis, as described later.

In addition, in short-term experiments conducted under the same ambient conditions, we examined whether density dependence is seen in the survival rate of adults and the reproductive ability of the old survivors. We introduced newly emerged adults from stock cultures at densities of 4, 8, 16, 32, 64 and 128 pairs into a four-compartment Petri dish containing 5 g of *V. angularis* beans. We counted the number of surviving adults at each density condition 7 and 10 days after the set-up. For survival rate up to 7 days of age, we established at least four replicates at densities lower than 64 pairs but three at the 128 pair condition. For the survival rate up to 10 days of age, we set three replicates at densities lower than 32 pairs, but two with 64 and 128 pairs.

To examine the reproductive ability of the surviving adults, we collected the surviving females of either 7-day or 10-day-old beetles and provided four grains of *V. angularis* to each female in a Petri dish. Four grains of *V. angularis* (ca. 190 mg per grain) were judged to be enough to receive more than 50 eggs in total (Utida 1941a; Tuda 1993). These females were allowed to lay eggs until they died. Five days after their death, we counted the number of hatched and unhatched eggs. We set ten replicates at each density condition with more than 8 pairs for 7-day-old adults and with more than 32 pairs for 10-day-old adults, respectively, though the small number of surviving adults 10-days-old prevented us from doing this at the 16 pair condition ( $n=3$ ).

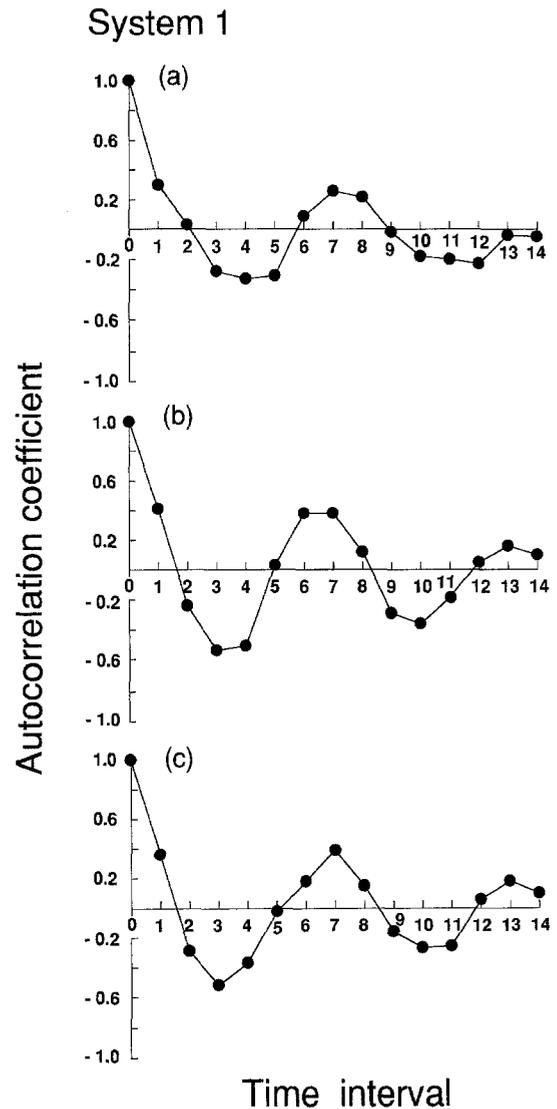
## Results

After fluctuations for about 5–6 weeks due to the initial set-up, the number of emergent adults per week reached



**Fig. 1a–c** Population dynamics of adults emerged per week in system 1 (7-day renewal system). **a** Replicate no. 1 with an 8 pair introduction; **b** no. 2 with a 32 pair introduction; **c** no. 3 with a 128 pair introduction. *Open circles and dotted lines* show the actual population size. *Closed circles and solid lines* are for the smoothing plot by three-point moving average

a similar average level in the long-term system 1 irrespective of the initial founder density. Population dynamics continued to fluctuate with a large magnitude in system 1 (Fig. 1). A three-point moving average curve is superimposed on each replicate system in Fig. 1. Replicate number 1 (where eight pairs were introduced) showed a gradual increase of emergent adults during the first 13 weeks, then oscillations emerged from week 13 to 28 with an amplitude of 70–80 and a cycle period of ca. 7 weeks in the moving average curve (Fig. 1a). Replicate number 2 (where 32 pairs were introduced) began to oscillate from just after the emergence of founders' offspring (Fig. 1b). The oscillations continued until week 25 with an amplitude of 80–90 and a cyclic period of 7 weeks. Replicate number 3 (where 128 pairs were introduced) also fluctuated strongly from week 7 to 23, and these oscillations had an amplitude of 60–90 and a cyclic period of ca. 7 weeks (Fig. 1c). Autocorrelations of the actual number of emerged adults per week (not the moving average curve) during the oscillating phase in Fig. 1

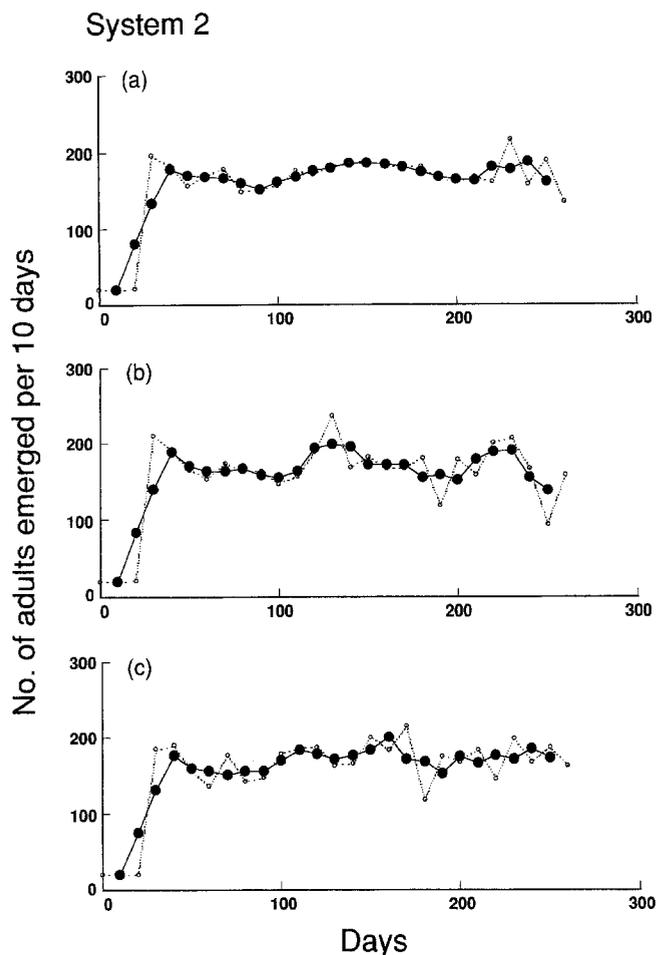


**Fig. 2a–c** Correlograms based on autocorrelations of the actual population size of emerged adults per week in system 1. Correlograms from week 12 to week 29 in replicate no. 1 are shown in **a**, and from week 6 to 24 in no. 2 and no. 3 in **b** and **c**, respectively

detected a cyclic period of 7 weeks in all the three replicates in system 1 (Fig. 2), though the correlations were not very strong.

In system 2, however, no oscillatory cycle was seen in the actual number nor in the smoothing curve using a three-point moving average, and highly stable dynamics were seen in the moving average curves (Fig. 3). No significant cyclic tendency was detected in autocorrelations in system 2.

The average numbers and the variability of live and dead adults at each census, and emergent adults during a census interval, are shown in Table 1. There were twice, or more than twice, as many living adults in all three replicates of system 1 as in system 2. Significantly larger variance of live adult density in system 1 may be ascribed to the higher average density but not to the population variability itself of the live adults, because the co-

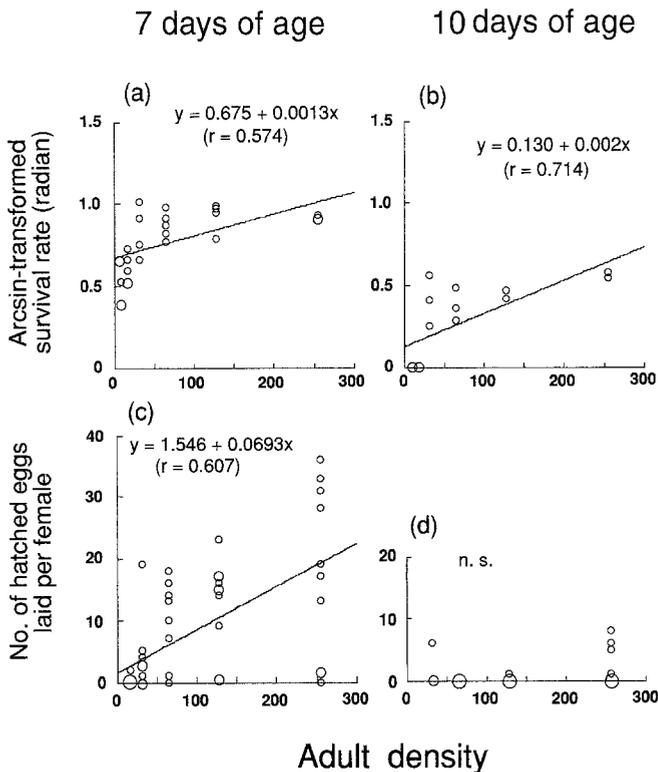


**Fig. 3a-c** Population dynamics of adults emerging over 10-day periods in system 2 (10-day renewal system). The number of founders were kept at ten pairs for all the three replicates **a**, **b** and **c**. Open circles and dotted lines show the actual population size. Closed circles and solid lines are for the smoothing plot by three-point moving average

efficient of variation did not differ between the two systems. The average numbers of dead adults did also not differ significantly between the two systems. On the other hand, although the average number of emergent adults was similar in the two systems, significant differences were detected by Bartlett's homogeneity test between the variance ( $\chi^2=21.5$ ,  $P<0.001$ ). This corresponds to the

**Table 1** The numbers of live and dead adults at each census, and emerged adults during a census interval. Statistical tests are shown at the bottom (n.s. non-significance at  $P=0.05$ )

System	Repl. no.	Average no. ( $\pm$ S.D.)		
		Living adults	Dead adults	Emerged adults
1	1	170.2 $\pm$ 33.2	179.0 $\pm$ 32.3	179.3 $\pm$ 36.7
	2	136.4 $\pm$ 43.9	157.8 $\pm$ 42.8	158.7 $\pm$ 43.4
	3	152.6 $\pm$ 38.6	170.4 $\pm$ 35.8	171.4 $\pm$ 36.8
2	1	62.6 $\pm$ 18.7	174.3 $\pm$ 20.6	171.4 $\pm$ 17.5
	2	67.8 $\pm$ 19.8	168.6 $\pm$ 35.0	166.0 $\pm$ 29.6
	3	63.7 $\pm$ 21.3	171.5 $\pm$ 23.3	169.0 $\pm$ 24.2
Nested ANOVA for mean		system: $F=285.8$	n.s.	n.s.
$P$		replicate: n.s.	n.s.	n.s.
		$P<0.0001$		



**Fig. 4 a, b** Survival rate of young adults to the old stage depending on their density when introduced into a dish with 5 g of beans. **a** Survival rate until 7 days of age, and **b** until 10 days of age. Fraction values are converted by arcsin transformation (radian). Note that the fraction 1.0 corresponds to 1.57 radian. **c**, **d** Number of hatched eggs produced by a surviving female. **c** Aged 7 days, **d** aged 10 days. The largest circle shows the number of observations greater than, or equal to, five, the medium circle the number from 2 to 4, and the smallest circle equals 1. The regression line and the correlation coefficient are shown in each panel

more fluctuating population dynamics of emergent adults in system 1 than in system 2 (Figs. 1 versus 3).

In the short-term experiment, the survival rate of adults increased with a higher introduced density of adults both 7 and 10 days after the set-up. We obtained significant positive linear regressions in both cases [ $F=16.9$ ,  $P<0.0001$  for 7 days of age (Fig. 4a);  $F=14.5$ ,  $P<0.002$  for 10 days of age (Fig. 4b)]. Average female ratio of individuals surviving until 7 days old was 0.62 (=496/799) at densities higher than 64 introduced pairs. All survivors up to 10 days of age were females.

Reproductive ability was measured as the number of hatched eggs deposited per female, because frequently none of the eggs laid by an old female hatch even if she has laid dozens of eggs (M. Shimada, unpublished data). Females that survived until 7 days old deposited significantly more hatched eggs as the adult density they had experienced increased [ $F=27.5$ ,  $P<0.0001$  (Fig. 4c)], though some females laid only unhatched eggs. On the other hand, females that survived until 10 days old deposited hardly any hatched eggs, and only five females out of 33 replicates laid even a small number of eggs (Fig. 4d). Neither regression nor correlation analysis could detect any significant effect.

**Model analysis**

Model formulation for system 1

Five life stages of *C. chinensis* were incorporated in the projection matrix for system 1 according to age: the hatched egg (up to 1 week), the final instar larva (up to 2 weeks), the pupa (up to 3 weeks), the young, actively reproductive adult (up to 4 weeks), and the old, less active adult (later than 4 weeks), whose population sizes were denoted as  $H_t$ ,  $L_t$ ,  $P_t$ ,  $A_t$ , and  $O_t$ , respectively. We constructed a 5x5 projection matrix with density-dependent elements:

$$\begin{bmatrix} H_{t+1} \\ L_{t+1} \\ P_{t+1} \\ A_{t+1} \\ O_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & m_A(A_t, O_t) & m_O(A_t, O_t) \\ p_H(H_t) & 0 & 0 & 0 & 0 \\ 0 & p_L(L_t) & 0 & 0 & 0 \\ 0 & 0 & p_P(P_t) & 0 & 0 \\ 0 & 0 & 0 & p_A(A_t) & 0 \end{bmatrix} \begin{bmatrix} H_t \\ L_t \\ P_t \\ A_t \\ O_t \end{bmatrix} \tag{1}$$

where  $t$  is the discrete time-step, and one unit corresponds to 1 week in system 1. Non-zero elements  $m$  and  $p$  are the fecundity per reproductive female and the survival rate through the particular stage denoted by the subscripts  $H$ ,  $L$ ,  $P$  and  $A$ , respectively. They are the following functions of the population size at each stage:

$$\begin{aligned} m_A(A_t, O_t) &= 0.5 r_{0A} / [1 + c_A(A_t + \alpha O_t)]_A^b & (2) \\ m_O(A_t, O_t) &= q r_{0O} / [1 + c_O(\beta A_t + O_t)]_O^b & (3) \\ p_H(H_t) &= h_0 / [1 + c_H H_t]_H^b & (4) \\ p_L(L_t) &= l_0 / [1 + c_L L_t]_L^b & (5) \\ p_P(P_t) &= s_P & (6) \\ p_A(A_t) &= s_0 + s_A A_t & (7) \end{aligned}$$

where

$$\begin{aligned} c_A &= \{ (0.5 r_{0A} K_A / H_{\max})_A^{1/b} - 1 \} / K_A \\ c_O &= \{ (q r_{0O} K_O / H_{\max})_O^{1/b} - 1 \} / K_O \\ c_H &= \{ (h_0 K_H / L_{\max})_H^{1/b} - 1 \} / K_H \\ c_L &= \{ (l_0 K_L / P_{\max})_L^{1/b} - 1 \} / K_L \end{aligned}$$

All parameters in Eqs. 2, 3, 4 and 5 are defined as a list in Table 2. Equations 2, 3, 4 and 5 followed a logistic-difference equation from Hassell (1975) modified by

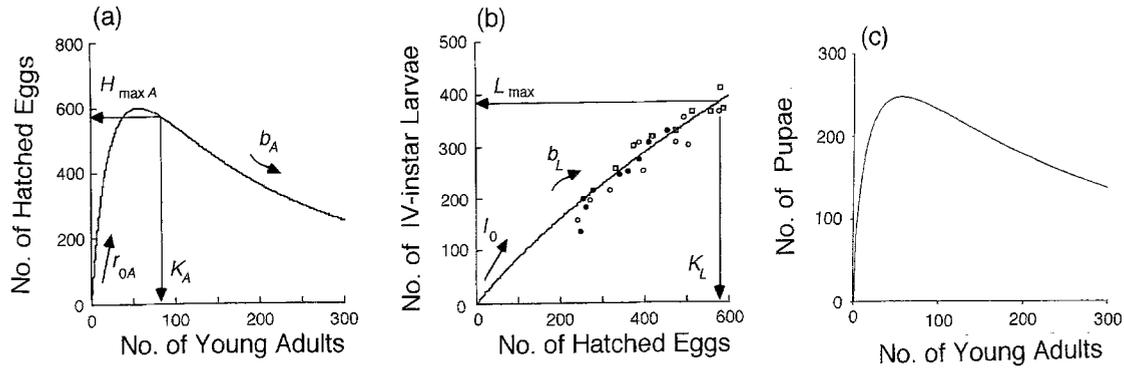
**Table 2** Definition of parameters in Eqs. 2, 3, 4 and 5. See Fig. 5a and b for Eqs. 2 and 4

Parameters	Definition
Eqs. 2 and 3	
$r_{0i}$	The number of hatched eggs produced per female at the stage $i$ ( $i=A$ or $O$ )
$H_{\max i}$	The observed maximum population size of hatched eggs produced by the stage $i$ ( $i=A$ or $O$ )
$K_i$	Density of stage $i$ producing $H_{\max i}$ ( $i=A$ or $O$ )
$b_i$	Degree of compensation in density dependence of $H$ against the stage $i$ ( $i=A$ or $O$ )
$\alpha$	Interstage competition coefficient expressing the per capita inhibitory effect from $O$ to $A$
$\beta$	As for $\alpha$ , but from $A$ to $O$ ( $\beta=1/\alpha$ )
$q$	Sex ratio of old, surviving adults
Eq. 4	
$h_0$	Per capita survival rate of a hatched egg to a final instar larvae
$L_{\max}$	The observed maximum population size of larvae
$K_H$	Density of $H$ producing $L_{\max}$
$b_H$	Degree of compensation in density dependence of $L$ against $H$
Eq. 5	
$l_0$	Per capita survival rate of a final instar larva to a pupa
$P_{\max}$	The observed maximum population size of pupae
$K_L$	Density of $L$ producing $P_{\max}$
$b_L$	Degree of compensation in density dependence of $P$ against $L$

Shimada (1989) (see Appendix 1). This equation can show various types of density-dependent population responses, from a peaked curve with a long tail to the right in overcompensatory production of hatched eggs outside beans (Fig. 5a), to a convex-upward saturated curve in exactly compensatory (or just undercompensatory) larval competition inside beans (Fig. 5b) (see also Shimada 1989; Shimada 1990; Tuda and Shimada 1993).

In Eqs. 2 and 3, we took into account that old, less-reproductive adults inhibit the egg-deposition by young actively reproducing adults and vice versa. Tramping by adults was suggested as the most severe mortality factor of eggs (Utida 1941b; Bellows 1982b). Therefore, the existence of old, surviving adults may cause a surplus density effect on the production of hatched eggs by young adults. The parameters  $\alpha$  and  $\beta$  are interstage competition coefficients which followed interspecific ones in May (1974) and Hassell (1978). Conveniently, we assumed  $\beta=1/\alpha$  (where  $0<\alpha<1$ ) because the negative density effect of young, active adults on old, less-active adults may be larger than the reverse. The parameter  $r_{0O}$  in Eq. 3 should be dependent on the previous population density when they were in the young adult stage,  $A_{t-1}$ , as seen in Fig. 4c. The regression line in Fig. 4c was applied to  $r_{0O}$ .

Equation 6 was set as a constant because intraspecific competition inside beans is most severe from younger instars to the final (fourth) instar larvae, and once they pupate they rarely die (Utida 1941b). A simple linear function was applied to Eq. 7, taken from a linear regression in



**Fig. 5a-c** Population response curve of the logistic-difference equation of Hassell (1975) modified by Shimada (1989) for the hatched-egg production by adults **a**, and the development from the hatched larvae to the final instar larvae **b**, where a *solid circle* is data from replicate no. 1, a *square* is data from no. 2, and an *open circle* is data from no. 3 in system 1. **c** Competition curves through all the processes inside the bean in the two systems. Note that the equivalent responses make two competition curves of the two systems look like one curve

Fig. 4a. Note that the linear density-dependent survival rate in Eq. 7 gives rise to a convex-downward quadratic curve of the actual number of survivors against the adult density.

Parameter values for system 1 were determined as in Appendix 2.

**Model for system 2**

In modeling system 2, we set a 4x4 projection matrix with four life stages which were separated by 10 day periods: the larvae in younger instars (up to 10 days), the pupa (up to 20 days), the young, active adults (up to 30 days), and the old, surviving adults (later than 30 days), whose population densities were denoted as  $J_t$ ,  $P_t$ ,  $A_t$ , and  $O_t$ . The 4x4 matrix was as follows:

$$\begin{bmatrix} J_{t+1} \\ P_{t+1} \\ A_{t+1} \\ O_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & m_A(A_t, O_t) & 0 \\ p_J(H_t) & 0 & 0 & 0 \\ 0 & p_P(L_t) & 0 & 0 \\ 0 & 0 & p_A(P_t) & 0 \end{bmatrix} \begin{bmatrix} J_t \\ P_t \\ A_t \\ O_t \end{bmatrix} \quad (8)$$

Old adults surviving to 10 days of age laid hardly any eggs which hatched (Fig. 4d), thus we ignored their hatched-egg production and replaced  $m_O(A_t, O_t)$  with 0 in the matrix of Eq. 8. The performance of old adults in this model was only the restraint effect of  $O_t$  on the hatched-egg production by young adults in  $m_A(A_t, O_t)$ . All the parameters in  $m_A(A_t, O_t)$  followed Eq. 2 for system 1 except the value of  $\alpha$ , which was set to 0.1, based on the reproductive activity, the movements and the remaining longevity in old adults aged 10 days.

We formulated the production of young instar larvae ( $J_{t+1}$ ) by adults based on the basic logistic-difference equation, Eq. 12, considering the density-dependent mortality from the hatched larvae to the larvae in younger instars up to 10 days old:

$$Y = m_A(A_t, O_t)A_t \quad (9)$$

$$\begin{aligned} J_{t+1} &= p_Y(Y)Y \\ &= y_0 Y / [1 + c_Y Y]^b \end{aligned} \quad (10)$$

where

$$c_Y = \{ (y_0 K_Y / J_{max})^{1/b} - 1 \} K_Y$$

$Y$  is the number of hatched larvae, and  $m_A(A_t, O_t)$  is as defined in Eq. 2 except for the value of  $\alpha$ . Note that the process from Eq. 9 to Eq. 10 occurs within one time-step. Then, the development of the young instar larvae to the pupae was:

$$\begin{aligned} P_{t+1} &= p_f(J_t)J_t \\ &= j_0 J_t / [1 + c_J J_t]^b \end{aligned} \quad (11)$$

where

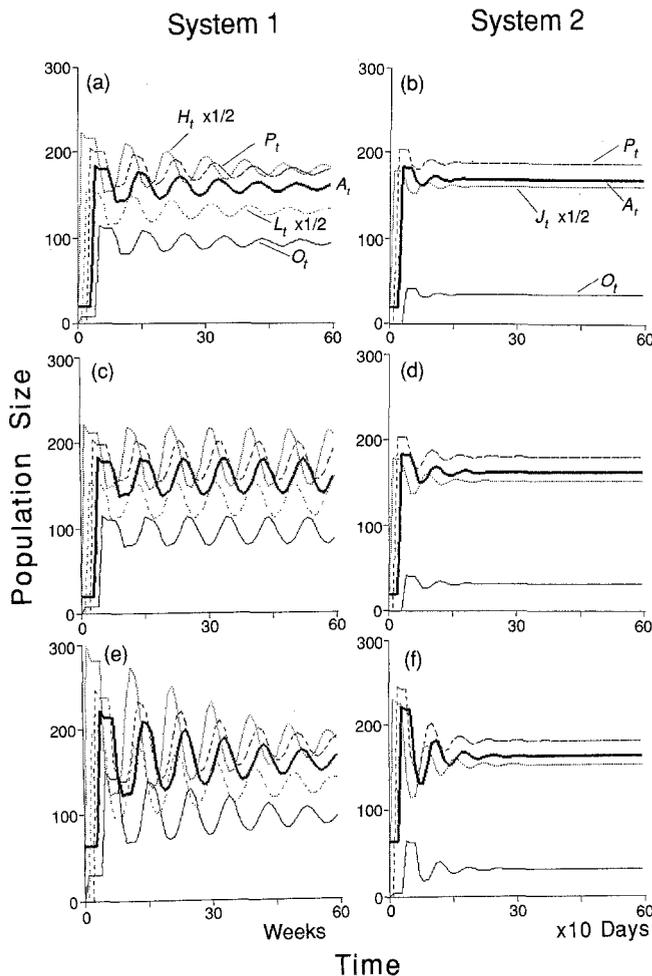
$$c_J = \{ (j_0 K_J / P_{max})^{1/b} - 1 \} / K_J$$

Larval development inside beans should be independent of the resource renewal interval, because only a maximum of the first 12 larvae to crawl into a bean can grow up to the emergent adult stage (Tuda 1993). This situation remains the same irrespective of the resource renewal interval. Therefore, we determined the parameter values in Eqs. 10 and 11 to generate the same number of pupae at a particular density of young adults in the two systems, as seen in Fig. 5c (see Appendix 2).

Thus, the model for system 2 was different from system 1 at only three points: (1)  $m_O(A_t, O_t)$  was replaced with 0, (2) the interstage competition coefficient  $\alpha$  was much smaller than in system 1, and (3) the density-dependent survival rate of young adults to the old stage was much lower, but the regression coefficient was somewhat higher, than in system 1, according to Fig. 4b.

**Model predictions for actual systems**

The model for system 1, when started from ten pairs with  $\alpha=0.3$ , showed damped but significant oscillations that persisted for more than 60 time-steps (60 weeks) (Fig. 6a). Setting  $\alpha=0.4$  resulted in quite long persistent oscillations continuing for more than 500 time-steps (Fig. 6c). A cyclic period was nine time-steps in both  $\alpha$  values and this was only just longer than the actual seven point (7 week) period in Figs. 1 and 2, though the pre-



**Fig. 6a–f** Model population dynamics. **a, c, and e** System 1; **b, d and f** system 2. **a** System 1 with  $\alpha=0.3$ ; **c** system 1 with  $\alpha=0.4$ ; **e** system 1 with  $\alpha=0.3$ , the initial founder density set to 32 pairs. **b** System 2 with  $\alpha=0.1$ ; **d** system 2 with  $\alpha=0.4$ ; **f** system 2 with  $\alpha=0.4$ , the initial founder density set to 32 pairs. The *fine dotted line* shows the density of hatched eggs ( $H_t$ ), the *rough dotted line* shows the final instar larvae ( $L_t$ ; note, these two densities are reduced to half-scale), the *dashed line* shows the pupal density ( $P_t$ ), the *thick solid line* shows young adults ( $A_t$ ), and the *thin solid line* shows old, surviving adults ( $O_t$ ) in system 1. The *fine dotted line* shows young instar larvae ( $J_t$ ) in system 2

dicted amplitudes were smaller (about a half, or less) than the actual ones. The population size of young adults ( $A_t$ ) converged to the equilibrium of 164.0 ( $\alpha=0.3$ ) and 161.5 ( $\alpha=0.4$ ), respectively, that accorded with the experimental average population size of emergent adults per interval (system 1 in Table 1).

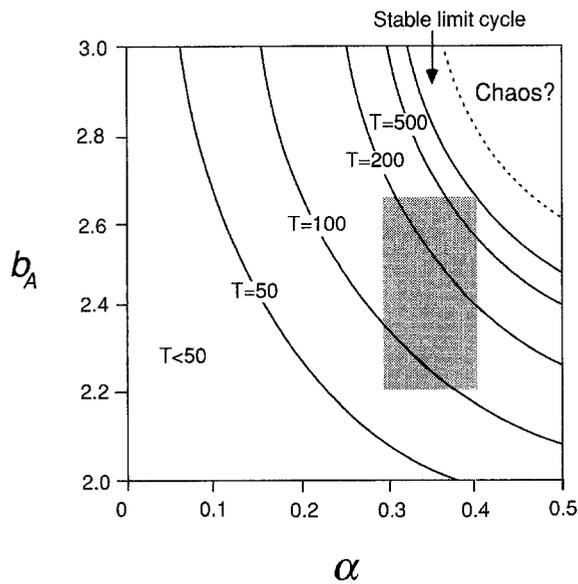
On the other hand, the model for system 2 showed quite stable dynamics with  $\alpha=0.1$ , in which oscillations quickly disappeared and converged to an equilibrium point (Fig. 6b). This was consistent with the actual, stable dynamics in Fig. 3. The convergent level of  $A_t$  was 170.5, just higher than the level of system 1, this being compatible with the actual mean population size of emergent adults (system 2 in Table 1). As a trial, we changed the value of  $\alpha$  to 0.4, but the model dynamics were not significantly altered (Fig. 6c).

Comparing the simulation results for the two systems, we can predict that the number of live adults at each census should be higher in system 1 than in system 2, because of the existence of far more  $O_t$  in the former (Fig. 6a versus 6b). The number of live adults in Table 1 corresponded to this prediction. A larger part of old, surviving adults should be included in the live adults at each census point in system 1 than in system 2.

Changing the initial founder density from 10 to 32 pairs with  $\alpha=0.3$  caused larger amplitudes, though they were damped (Fig. 6e). However, this increase in amplitude is not surprising, because a peaked return-map like Fig. 5c often generates large oscillations when the dynamics starts from an initial point close to the peak (Peitgen et al. 1992). Introduction of 128-pair founders gave a similar dynamics to the 32 pair introduction. Note that these changes in the initial founders never altered the nine point periods and the convergent population size (=164.0), as seen in Fig. 6e. Therefore, the oscillatory tendency of the actual system 1 cannot be ascribed only to this initial effect, though the initial founder density changed the amplitude of oscillations in the model. Replicate number 1 (the eight pair introduction) also showed similar oscillations to the other replicates in Fig. 1, and in addition, the numbers of live adults in all three replicates in system 1 were definitely distinguished from three replicates in system 2 in Table 1. Thus, we conclude that system 1 should be more likely to oscillate than system 2, even if we introduced the same number of founders into both systems.

Difference in the matrix structure itself (5×5 versus 4×4) should not cause the difference in dynamical properties between the two systems, because the inside-bean process of the three stages in system 1 was adjusted to be equivalent to that of two stages in system 2, as seen in Fig. 5c. Thus, the dynamical difference can be ascribed only to the outside-bean processes of the two adult stages which both two matrices included. Tentatively, we increased two factors simultaneously, which might cause larger fluctuations in the model for system 2:  $\alpha$  (to 0.4) and initial population size (to 64). In spite of these changes, however, oscillations did not last much longer (Fig. 6f).

For the trial, we incorporated  $m_O(A_t, O_t)$  of Eq. 3 into the matrix for system 2 in Eq. 8 and found that initial fluctuations still damped and disappeared quickly in system 2. In addition to this, by increasing the density-dependent survival rate of adults ( $\gamma$  intercept of the regression line in Fig. 4b) to 0.675, we at last found long persistent population cycles similar to Fig. 6b. Thus, we concluded that only the overcompensatory density-dependent response in hatched-egg production,  $m_A(A_t, O_t)$ , was not sufficient to maintain the oscillations and that the two processes of delayed density dependence, the adult survivorship in Fig. 4a and the egg-production by old adults,  $m_O(A_t, O_t)$ , in Fig. 4c, have important effects on generating and keeping oscillations in system 1.



**Fig. 7** The time periods ( $T$ ) until population oscillations were damped within  $\pm 0.6$  (for  $H_t$  and  $L_t$ , within  $\pm 1.2$ ) in system 1 with the various combinations of two parameters  $b_A$  in Eq. 2 and  $\alpha$  in Eqs. 2 and 3. The system was started from an initial founder density of ten pairs. The shaded area shows the actual  $b_A$  values in various strains of *C. chinensis* (Shimada 1990) and  $\alpha$  values used for calculation in Fig. 6a and c

#### Sensitivity of oscillations to parameters

Observing dynamical patterns by changing particular parameter values step by step, we can examine the sensitivity of population oscillations to the parameters in order to understand the major factors underlying the oscillatory tendencies in system 1. Though it was reported by Tuda and Shimada (1993) and M. Tuda and M. Shimada (submitted) that the level of equilibrium population size was highly sensitive to the maximum-density-setting parameters like  $H_{\max}$ ,  $L_{\max}$  and  $P_{\max}$  (see Fig. 5), the population fluctuation tendency should be directly related to parameters of non-linear, overcompensatory response and delayed density dependence outside beans. Hence, we focused on two parameters:  $b_A$  in Eq. 2 and  $\alpha$  in Eqs. 2 and 3.

Fig. 7 shows the number of time-steps (weeks) that oscillations continued in the model for system 1. Here, we consistently started the execution from ten pairs of founders and judged that the population dynamics reached an equilibrium point when the magnitudes of fluctuations in the last three stage classes were damped to within  $\pm 0.6$ ; for  $H_t$  and  $L_t$ , within  $\pm 1.2$ . The higher the values of either  $b_A$  or  $\alpha$ , the longer the oscillations persisted in Fig. 7. System 1 is likely to oscillate for a long time with the actual parameter ranges of *C. chinensis* (shaded area in Fig. 7). Multiplicative effects of simultaneous increases in both parameters kept oscillations longer, and finally generated stable limit cycles in which the magnitude of oscillations did not damp at all (Fig. 7). Further increases from this showed curious fluctuations resembling chaos.

## Discussion

### Biological process causing delayed density dependence

Delayed density dependence is associated with the performance of the old adults in the present system. The strain jC females usually deposit most eggs in the first 5 days after emergence, if they are provided with abundant beans. They begin to die from 5 days after emergence and the survival rate declines rapidly between 7 and 10 days (M. Shimada, unpublished data). If adult density is high, however, females cannot lay the full egg complement and males cannot copulate as many times due to frequent contacts among adults. The energy that was not used for reproduction is converted to the maintenance of adults themselves. Thus, the higher the density of adults, the more adults surviving to the next resource renewal (Fig. 4a, b). An increase in the number of young adults at a given time not only causes an immediate decrease in the hatchability of eggs deposited during the interval but also causes the surplus of restraint density effects and the additional reproduction by old adults at the next interval. This delayed density dependence may be characteristic of systems with overlapping generations.

### Delayed density dependence generating population cycles

The present results showed that relative length between resource renewal intervals and adult life span is an important factor governing whether oscillatory population dynamics are generated. Shimada (1989) reported a two-stage-class model separating the outside-bean and inside-bean processes. This model was made for his experimental *C. chinensis* system, where 5 g of *V. angularis* beans were renewed periodically every 21 days so that the period matched one generation cycle of *C. chinensis*. No inhibitory effect of old surviving adults occurred in this discrete-generation system. He showed considerably stable population dynamics that converged to this equilibrium point after a few, two-point damped cycles (Shimada 1989), which disappeared more quickly than in the present system 2 (Fig. 6b). The fairly stable tendency is similarly shown in Bellows' (1982a) two-stage-class model for *C. chinensis*. Thus, the more old surviving adults, the longer the oscillations last. Only the overcompensatory, non-linear density response in the hatched-egg production itself may not be sufficient to keep oscillations over a long time.

The relative importance of delayed density dependence in the present system with overlapping generations is also supported by the cyclic period. Gurney and Nisbet (1985) predicted that the period would be close to the developmental time ( $\tau$ ) from egg to adult with non-linear overcompensatory density dependence and close to  $2\tau$  with delayed density dependence. The period was 7 weeks in the actual system 1 (Fig. 2) and nine time-steps (i.e., 9 weeks) in simulation (Fig. 6a, b). These are ap-

proximately twice as long as the developmental time of strain jC (ca. 22 days), this being consistent with Gurney and Nisbet's (1985) prediction about oscillations caused by delayed density dependence.

Applying Liu and Cohen's (1987) model to the *Tribolium* system, Desharnais and Liu (1987) showed a stable limit cycle. Interstage cannibalistic interactions were important for generating population oscillations (Desharnais and Liu 1987; Caswell 1989). Even though *C. chinensis* does not have such antagonistic behaviors between stages, old surviving *C. chinensis* adults have inhibitory effects on young adults, this resulting in delayed density dependence in an overlapping-generation system. The present study shows important effects of resource renewal intervals on population oscillations through delayed density dependence in single-species systems. We should pay more attention to resource renewal patterns and interstage interactions that promote oscillatory tendencies in natural populations.

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## Appendix 1

### Basic equation

The basic equation is one of the logistic-difference equation family. This was modified from Hassell (1975) by Shimada (1989) for describing population dynamics of animals that consist of plural life stages:

$$z = \lambda x / [1 + cx]^b \quad (12)$$

where

$$c = \{(\lambda K_x / z_{\max})^{1/b} - 1\} / K_x \quad (c \geq 0)$$

The variable  $x$  is the population size at a stage,  $z$  is that at the next stage,  $\lambda$  is the per capita rate of density-independent change of a population,  $K_x$  is the population size of  $x$  that produces the maximum level of  $z$  (i.e.,  $z_{\max}$ ), and  $b$  is the degree of compensation in the density-dependent process. All these parameter values can be estimated from the competition curve experiment (the density-dependent population response from one stage to the next). In the basic equation,  $\lambda$  determines the increasing rate of the competition curve at low density,  $K_x$  and  $z_{\max}$  set the height of the curve, and  $b$  determines the curvilinearity (under-, exact, or overcompensation), as seen in Fig. 5a (hatched egg production) and 5b (larval development).

## Appendix 2

### Parameter values for system 1

To determine the parameters for system 1 in Eqs. 2, 3, 4 and 5, we followed Shimada (1989) and Tuda and Shimada (1993) who examined one-generation processes of *C. chinensis* based on compe-

titution curve experiments. The process of hatched-egg production in Eq. 2 showed a peaked curve. The parameter values are  $r_{0A}=74$ ,  $K_A=80$ ,  $H_{\max A}=580$  and  $b_A=2.65$  (Shimada 1989). Though we have no empirical data on  $\alpha$ , the interstage competition coefficient from an old surviving adult to a young active adult, it may be roughly inferred as less than 0.5, judging from the reproductive activity, the movements and the remaining longevity of old adults. Thus, we assumed two levels for  $\alpha$ : 0.3 and 0.4.

In Eq. 3, the regression line in Fig. 4c was applied to  $r_{0O}$ . We assumed  $H_{\max O}$  to have the same value (=580) as  $H_{\max A}$  in Eq. 2, because it is not the per capita reproductive ability but the density effect of adults that actually restrains  $H_{\max}$  (Shimada 1990). The parameter  $K_O$  was set at 120 which was higher than  $K_A$  (=80), because ca. 30% of old adults laid only a few, or no, hatchable eggs at densities at higher than the 64 pair condition (Fig. 4c). We assumed  $b_O$  to be the same value (=2.65) as in Eq. 2. The sex ratio of old adults,  $q$ , was set to the experimental data, 0.62.

In Eq. 4, we set  $h_0=0.95$ ,  $K_H=580$ ,  $L_{\max}=385$  and  $b_H=0.4$ , which showed a good fit to the data (Fig. 5b). In Eq. 5,  $l_0=0.95$ ,  $K_L=385$ ,  $P_{\max}=242$  and  $b_L=0.2$ . The parameter  $s_A$  was set to 0.9 in Eq. 6, based on 10% mortality in the adult emergence, so that  $P_{\max}$  (=242) may be 10% higher than the maximum level of the emerged adults (220 in Shimada 1989). We applied the regression line in Fig. 4a to Eq. 7.

### Parameter values for system 2

The parameter values for system 2 were determined as  $y_0=0.95$ ,  $K_E=580$ ,  $J_{\max}=450$  and  $b_Y=0.3$  in Eq. 10, and  $j_0=0.95$ ,  $K_J=450$ ,  $P_{\max}=242$  and  $b_J=0.3$  in Eq. 11. Note that, through the processes inside the bean, we got an equivalent density dependent response in the two systems, as shown in Fig. 5c. Equation 6 was applied to the survival probability,  $p_p$ , from  $P_t$  to  $A_{t+1}$ , and it was similarly set to 0.9. We applied the regression line in Fig. 4b to the survival rate of the young adults to the old stage,  $p_A$ , using Eq. 7.

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