

Temporal/Spatial Structure and the Dynamical Property of Laboratory Host-Parasitoid Systems

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Abstract. The effects of spatial structure in terms of local capacity, or the maximum number of larvae surviving competition at resource patches, and temporal structure in terms of the period vulnerable to parasitoid attack in host populations on the persistence of host-parasitoid systems were quantitatively evaluated by laboratory experiments and well-parameterized model analyses. One of two bruchid beetles, *Callosobruchus maculatus* and *C. phaseoli*, were used as a host with *Heterospilus prosopidis* used as the parasitoid. *C. maculatus*, in which few larvae survive competition to become adults in each bean, and *C. phaseoli*, in which many larvae become adults in each bean, along with two kinds of beans, the mung and the azuki, were combined to construct four (2×2) resource-herbivorous host-parasitoid systems that differed in local capacity and vulnerable period. The mung-*C. maculatus* system with the parasitoid was the most persistent, i.e., took the longest time for extinction of either the host or parasitoid to occur. Since this resource-herbivorous host combination exhibited the lowest local capacity and the shortest vulnerable period, these two conditions possibly promoted the persistence of the system. A model incorporating the host population structure supported the observed persistence. Furthermore, the possible contribution of the timing of density-dependent competition of the host on the host-parasitoid persistence is predicted.

Key words: persistence, carrying capacity, vulnerable period, *Callosobruchus*, *Heterospilus prosopidis*.

Introduction

Although the world is a mosaic in space and time (Steele 1989), classical population models assume homogeneity within populations (Lotka 1925; Volterra 1926). Incorporating the intrinsic temporal/spatial structure of natural populations which had been noted earlier (Andrewartha and Birch 1954; Nicholson 1954), much work has been done to elaborate the classical models. However, empirical evaluation of spatially- and temporally-elaborated models and their predictions are still rare.

For spatially-structured models (see a summary by Kareiva 1990), many studies have been done focusing on the effect of dispersal between local patches with reference to well-designed laboratory studies (Huffaker 1958; Pimentel et al. 1963). By contrast, less attention has been paid to the effect of density dependence in local patches, such as the classical studies did. Many herbivorous insects in the immature stage stay relatively sessile at a

resource patch (Andrewartha and Birch 1954; Varley et al. 1973), and resource sharing within a patch and density dependent survival in a single-species population can affect the persistence both of itself and its interacting species (Tuda in preparation).

The extent of resource sharing is often correlated with other biological properties and collectively described as contest- and scramble-types (Nicholson 1954). One such property is the timing of density-dependent mortality; in a contest-type organism the population density is regulated in the early stages of development (Utida 1975). The effect of relative timing of parasitoid attack and density dependence in the host has been theoretically examined (Smith and Mead 1974; May et al. 1981). The formation of the population structure and its consequence may be better understood as interactive processes between space and time.

For temporally-structured models, simple discrete time steps were generally destabilizing because of time lags (Leslie 1945; Nicholson and Bailey 1935). However, age structure, by providing temporal heterogeneity, can be

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stabilizing depending on the form of age structure and parameter values (Smith and Mead 1974). For example, age structure promotes stability when immature (non-reproductive) stages of prey are vulnerable to predator attacks (Smith and Mead 1974; Murdoch et al. 1987). Further, stability increases as the proportion of prey vulnerable to attack decreases (Smith and Mead 1974). These quantitative predictions, however, have rarely been demonstrated by empirical results until recent laboratory studies (Tuda and Fujii 1992; Tuda and Shimada 1995). Yet, to my knowledge, no empirical studies have quantified the effect of population structure on multiple-species systems by integrating time (the vulnerable period) and space (local capacity or local density dependence).

By using different host species of *Callosobruchus* and different resources, the present study aimed to evaluate the combined effect of local capacity and the vulnerable period of the host on the persistence of host-parasitoid systems. Persistence, or time taken to extinction, is considered a more effective measure of stability than local stability as recent simulation studies suggest (Case 1995; Morton et al. 1996). A stage-structured model is developed based on short-term data to capture the combined effect of spatial and temporal structure of host immatures on system persistence. Furthermore, the effect of relative timing of density-dependent mortality is predicted.

Materials and methods

Callosobruchus maculatus (F.) and *C. phaseoli* (Coleoptera: Bruchidae) were used as host species and the experimental population dynamics of these two species have previously been studied (Ike 1984; Toquenaga and Fujii 1991). Stocks have been maintained under laboratory conditions, 70% R.H. and 16L : 8D, with azuki beans *Vigna angularis* var. *dainagon* as their resource.

Either the mung bean, *V. radiata*, or small grain varieties of the azuki bean *V. angularis* were used as resources in all experiments. The size of beans was uniformly maintained using a sieve (>No. 6 mesh).

Heterospilus prosopidis Vier. (Hymenoptera: Braconidae) was used as the parasitoid. The wasp parasitizes the final (fourth) instar larvae and pupae of several bruchid species of the genus *Callosobruchus* (Fujii 1983). It has been maintained under the above mentioned laboratory conditions, and supplied with *C. chinensis* larvae or pupae as its host.

Resource sharing in host

The number of host adults which emerged from each bean were examined. About 50 pairs of bruchid adults were allowed to deposit eggs on a layer of mung beans in a petri

dish (90 mm in diameter, 15 mm in depth) for up to 24 h. After the initial density of larvae was examined by counting hatched eggs, infested beans were put individually into wells of compartmentalized clear plastic cell-boxes (96 wells). Offspring which emerged from these beans were counted after about six weeks from the beginning of the experiment. The number of replicates for each density of larvae was between 12–24. Experiments were performed for all four bruchid-bean combinations.

Life history characteristics of host

Fecundity and longevity

For each of the two host species, pairs of adult beetles from either mung or azuki beans, which had emerged within a one hour period were introduced to petri dishes containing 10 g of beans. Death of the adults was checked and recorded every 24 h. Hatched and unhatched eggs on beans were counted a week after the female's death.

Larval survival rate and developmental period

For either host species, eggs which were deposited within two hours were put in a petri dish under laboratory conditions. Just before hatching, the egg density per bean was reduced to one. Emerging adults were counted and removed from the dish every 24 h.

Period of vulnerability and attack rate

The attack rates of *H. prosopidis* on hosts of various ages were examined to estimate the period during which the host is vulnerable to parasitoid attack. Density of hatched host eggs per bean was reduced to one as described above. On day 8, 10, 12, 14, 16, 17, 20, 22, 24, 26, 32, 34 and 36 respectively, I provided two female parasitoids, which had been allowed to mate for 24 h after emergence, with 25 infested beans in a petri dish. The parasitoids were removed after 24 h. Parasitoid emergence was counted after 16 days.

Dynamics and persistence of host-parasitoid systems

I used plastic containers (W120×D120×H30 mm) with four small dishes (57 mm in diameter) as arenas for the host and the parasitoid. Five grams of beans were placed every 10 days into one of the four dishes, each of which was replaced with the same amount of clean beans every 40 days. Ten pairs of hosts were introduced on days 0, 10 and 20 and five pairs of parasitoids on day 60. Live and dead adults of each species were counted every 10 days and dead ones removed. The number of adults which emerged were calculated as (no. of live adults)+(no. of dead adults)–(no. of live adults 10 days previously). For *C. phaseoli*, the adults which emerged from beans that had passed the 50 day mark from introduction were counted

and returned to the experimental arenas.

The system was judged to have collapsed by the absence of females for one generation (20 days for *H. prosopidis* and 30 days for *C. chinensis*) in either of the two species. Persistence time was defined as the time until the first census day on which absence of females was found. Five replicates were prepared for each system but one contaminated mung-*C. maculatus*-parasitoid system was excluded from analysis.

Besides the host-parasitoid systems, three replicates of single-species systems (beans and bruchids only) were built for each combination and censused until day 200.

Statistics

Local capacities were estimated by nonlinear regression (Wilkinson 1992) and to compare them among resource-beetle combinations, a Tukey-type multiple comparison test (Zar 1984) was applied after testing by two-way ANOVA. Two-way ANOVA was applied to test the effects of bruchid species and bean kinds on life history factors. A Tukey-type multiple comparison test was performed on larval survival rates among the 2 bruchids \times 2 beans combinations and also on the highest attack rates among different host ages. Two-way ANOVA and Tukey-type multiple comparison tests were applied to the carrying capacity for single-species systems. A two-way ANOVA was applied to test the effects of bruchid species and bean types on the log-transformed persistence times.

Results

Resource sharing in host

The 2 beans \times 2 bruchids combinations showed different local capacities, and hence a different extent of resource sharing (Fig. 1). Plots in Fig. 1 were fitted to eq. (3) and the local capacity K_l was calculated by

$$K_l = K_l' / [(b-1)\{b/(b-1)\}^b]. \quad (1)$$

The parameter values in Table 2 were referred to for K_l' and b . The local capacities were 1.5 for *C. maculatus*-mung, 2.7 for *C. maculatus*-azuki, 8.9 for *C. phaseoli*-mung and 7.1 for *C. phaseoli*-azuki. *C. maculatus* had a lower local capacity than *C. phaseoli*. More adults emerged from a single bean of the azuki than the mung.

Life history characteristics of host

Fecundity, or number of eggs deposited per female, was greater in *C. maculatus* and also greater when ovipositing on mung (Table 1). Hatchability was higher on mung beans. Larval survival rate was significantly lower in the

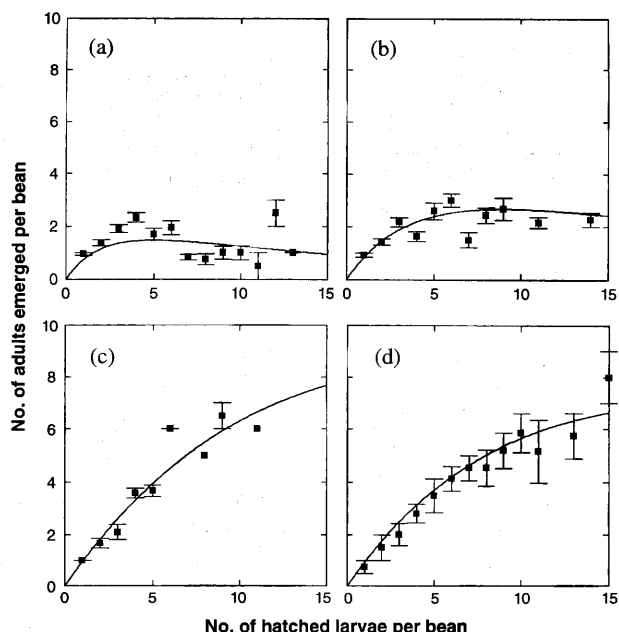


Fig. 1. Number of adults emerged per bean (mean \pm SE) for 2 \times 2 beetle-bean combinations. Eq. (3) was applied to estimate K_l' and b for each combination of resource and beetle. The fitted curves were superimposed on the data. (a) *C. maculatus*-mung; (b) *C. maculatus*-azuki; (c) *C. phaseoli*-mung; and (d) *C. phaseoli*-azuki. See Table 2 for the estimated parameters.

C. phaseoli-azuki combination. Developmental period was longer for *C. phaseoli* than for *C. maculatus* and also longer when grown on azuki than on mung. Longevity was longer in *C. phaseoli* for both sexes.

Period of vulnerability and attack rate

The highest attack rates did not differ among *C. maculatus*-mung, *C. maculatus*-azuki and *C. phaseoli*-mung (Fig. 2, Table 2). Only in *C. phaseoli*-azuki was the peak attack rate significantly lower (Fig. 2 d, for all comparisons with *C. phaseoli*-azuki, $df=16$, $k=4$, $P<0.001$). This may have resulted from lower survivorship of *C. phaseoli* on the azuki bean, and not from a lower attacking rate of the parasitoid. After correcting by the survival rate of host larvae, the difference was not significant (host species effect, $F=0.8$, $df=1$, $P=0.4$; bean effect, $F=2.8$, $df=1$, $P=0.1$). Therefore, there was no difference in *H. prosopidis* attack rate for all combinations of 2 bruchids \times 2 beans.

Dynamics and persistence of host-parasitoid systems

With all host-resource combinations, *H. prosopidis* showed large amplitude oscillations. The population,

Table 1. Life history characteristics of bruchids, *C. maculatus* and *C. phaseoli* with different resources. Mean \pm SE (n) is shown in each column.

	<i>C. maculatus</i>		<i>C. phaseoli</i>		<i>F</i>	
	Mung	Azuki	Mung	Azuki	bruchid	bean
Fecundity	92.0 \pm 3.1 (20)	85.3 \pm 4.0 (20)	51.5 \pm 3.0 (23)	30.9 \pm 3.6 (18)	171*	12*
Hatchability	0.95 \pm 0.01 (20)	0.91 \pm 0.02 (20)	0.98 \pm 0.01 (23)	0.89 \pm 0.03 (18)	0.1	13*
Larval survival rate	0.98 (100)	0.98 (100)	0.96 (50)	0.32* (50)		
Developmental period	21.8 \pm 0.1 (98)	23.7 \pm 0.2 (98)	24.7 \pm 0.1 (48)	33.0 \pm 0.7 (16)	578*	407*
Longevity						
Female	7.6 \pm 0.2 (20)	7.5 \pm 0.3 (20)	7.9 \pm 0.3 (23)	9.1 \pm 0.3 (18)	3.0	8.4*
Male	7.8 \pm 0.2 (20)	7.7 \pm 0.3 (20)	10.2 \pm 0.4 (23)	12.5 \pm 0.6 (18)	106*	11*

* $P < 0.01$.

however, crashed easily in the system using *C. phaseoli* as the host (Fig. 3 c and d). By contrast, in the *C. maculatus*-*H. prosopidis* system, the parasitoid was driven to low density but was likely to recover (Fig. 3 a and b). Further, when the resource was mung beans, the *C. maculatus*-*H. prosopidis* system lasted longer (Fig. 3 a). I frequently observed absence of host adult emergence for one census period, which was longer than parasitoid longevity (Fig. 3 b, c and d).

There was a significant difference in persistence, or time

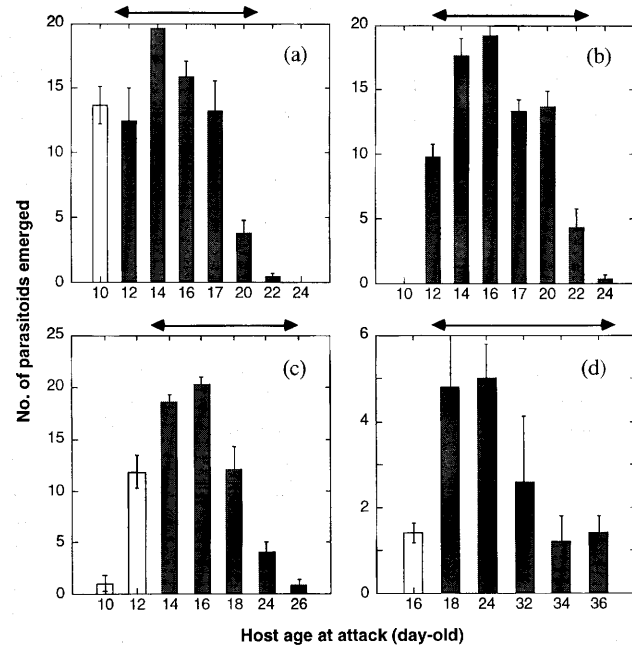


Fig. 2. Periods of host vulnerability to parasitoid attack indicated by arrows, estimated from the numbers of parasitoid emerging (mean \pm SE) > 1.0 . Open bars denote that all the parasitoids which emerged were small and suspected to have reproductive ability; and at these ages the host was defined as not vulnerable. (a) *C. maculatus*-mung; (b) *C. maculatus*-azuki; (c) *C. phaseoli*-mung; and (d) *C. phaseoli*-azuki, as in Fig. 1.

to extinction of a component species, between host species and bean kind (host species, $F=52$, $df=1$, $P < 0.001$; bean, $F=12$, $df=1$, $P=0.004$; interaction, $F=1.0$, $df=1$, $P=0.3$). Persistence was greater in *C. maculatus* and with mung beans.

In single-species systems, carrying capacity was higher for *C. phaseoli* (between bruchid species, $F=342$, $df=1$, $P < 0.001$; between beans, $F=2.1$, $df=1$, $P=0.2$; interaction, $F=12$, $df=1$, $P=0.01$) and also different between *C. phaseoli*-mung and *C. phaseoli*-azuki ($P=0.03$) combinations. There was no difference between *C. maculatus*-mung and *C. maculatus*-azuki ($P=0.6$) combinations. Mean population sizes (\pm SE) during days 100 to 200 of replicate systems were 94.4 \pm 1.4 in *C. maculatus*-mung, 110.6 \pm 10.6 in *C. maculatus*-azuki, 269.0 \pm 16.5 in *C. phaseoli*-mung and 230.2 \pm 15.5 in *C. phaseoli*-azuki.

Simulation

Stage-structured population model

To evaluate the relative importance of parameters, I applied a stage-structured model (Fig. 4), adding spatial structure for the immature hosts. Modeling on the bean scale

Table 2. Estimated parameters for the hosts.

Parameters	<i>C. maculatus</i>		<i>C. phaseoli</i>	
	Mung	Azuki	Mung	Azuki
r	92	85	52	31
c	0.017 ($r^2=0.95$)	0.023 ($r^2=0.98$)	0.024 ($r^2=0.96$)	0.009 ($r^2=0.88$)
K'_i	10	18	60	48
b	3 ($r^2=0.84$)	3 ($r^2=0.95$)	3 ($r^2=0.98$)	3 ($r^2=0.99$)
s	1.0	1.0	1.0	0.5
T_v	10	11	13	20
T_l	10	10	10	10

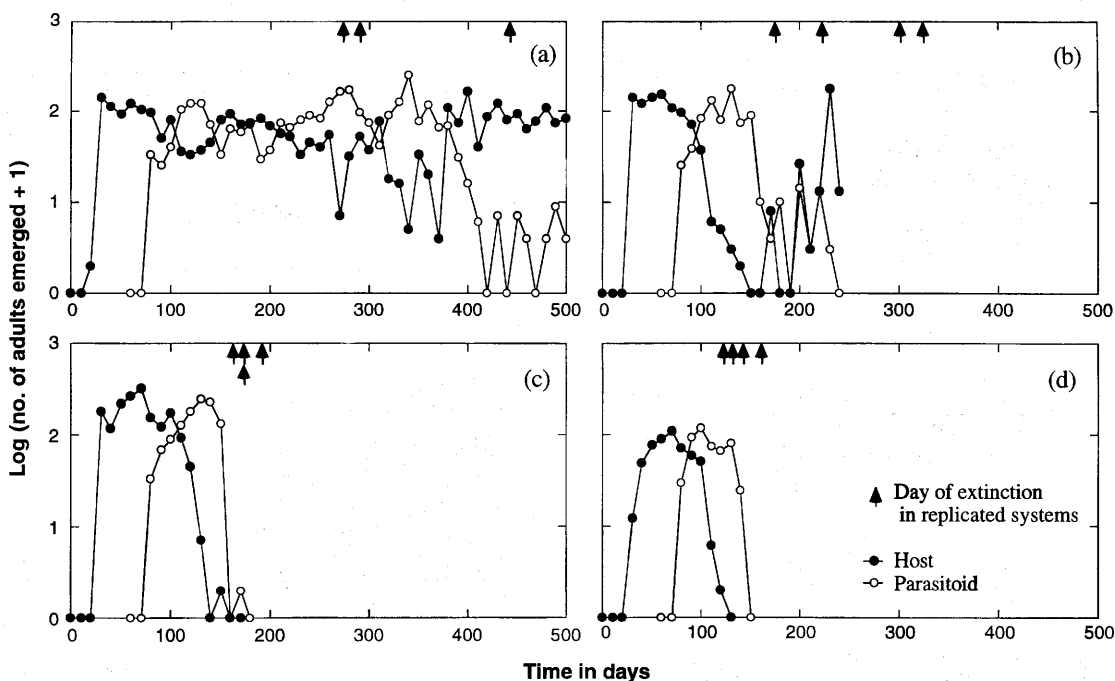


Fig. 3. Examples of the long-term dynamics of host-parasitoid systems and the persistence time (days) of the replicated systems as indicated by arrows. (a) *C. maculatus*-mung; (b) *C. maculatus*-azuki; (c) *C. phaseoli*-mung; and (d) *C. phaseoli*-azuki, as in Fig. 1.

was necessary to capture density-dependent growth in the bruchid beetle (Tuda 1993). Estimated parameter values are listed in Table 2. Using these parameters, the model generated dynamics that fits well to the observed dynamics (Fig. 5).

I assumed that the vulnerable period was $T_v = T_{hdp}/2$ based on Fig. 2, and that eggs are normally distributed among beans. Then, larvae survive competition in a density-dependent manner in each bean, with the local capacity calculated by eq. (1). At this stage, the vulnerable period to parasitoid attack starts and ends by the time the host completes development and emerges as an adult.

Briefly, the reproduction and growth of the hosts was phrased by logistic equations (Hassell 1975): assuming all oviposited eggs will hatch, the number of invulnerable larvae hatched on a bean is distributed normally with a mean:

$$H_{0,t+1} = 0.5r' H_{a,t} / (1 + cH_{a,t}), \quad (2)$$

where $H_{a,t}$ is the number of adults at t . The fecundity r (Tables 1 and 2) was divided by the number of beans, 100, to be applied to r' . The number of stage T_v larvae after competition at t is,

$$H_{Tv,t+1} = H_{Tv,t} / (1 + H_{v,t}/K)^b \quad (3)$$

where H_v is the number of larvae older than T_{dd} , the stage host larvae suffer density-dependent mortality. Setting $T_{dd} = T_v$, H_v is the number of vulnerable larvae. From the experimental results, b was held constant for all resource-

host combinations, then K 's were estimated by nonlinear regression (Wilkinson 1992).

The parasitoid attack and reproduction is described as

$$P_{t+1} = f(H_{v,t}, P_t) H_{v,t}, \quad (4)$$

where the attack rate f of parasitoids was phrased by the Holling type II (saturating) functional response, with

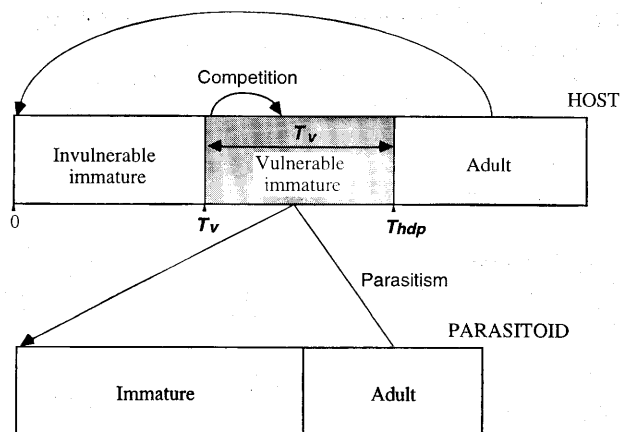


Fig. 4. Stage-structured population model with resource compartments for the host during the immature stages. Vulnerable immature refers to the final-instar larva and the pupa. The vulnerable period T_v and the developmental period T_{hdp} of host were manipulated and $T_v = T_{hdp}/2$. For details, see text.

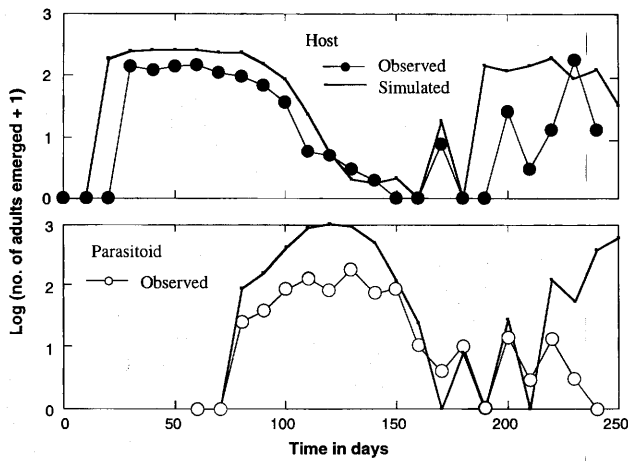


Fig. 5. Simulated dynamics with parameter values of *C. maculatus* feeding on azuki in Table 2, superimposed on the observed dynamics shown in Fig. 3b. Parameters for the parasitoid are $a'=0.092$, $m=0.4$ and $t_h=0.066$.

mutual interference m (Hassell and May 1973):

$$f(H_v, P_t) = aP_t / (1 + at_h H_v), \quad (5)$$

$$a = a' P_t^{-m}.$$

The parameters for the parasitoid were estimated from experimental data on *C. chinensis* (Tuda, unpublished data), following the method used by Tuda and Shimada (1995).

The model system was judged to have collapsed when the population size was below 2.0 in the parasitoid. Allee effects on finding a mate are incorporated; the number of adults are considered to be 0 when adults were below (2 individuals/adult longevity). The time step of the simulation

Table 3. Simulated persistence times (days) when each of the baseline parameters was changed by $\times 2$ or $\times 1/2$. The baseline parameter set was that of *C. maculatus*-mung (see Table 2). All the other systems were less persistent than the *C. maculatus*-mung system. An underlined simulated persistence time shows that when the parameter was manipulated to resemble those observed in the other three systems, it reduced the system persistence.

Changed parameter	Change given to baseline parameter	
	$\times 2$	$\times 1/2$
None (Baseline)	1000	
r	155	1000
c	1000	160
b	1000	160
K_i'	<u>160</u>	1000
T_v	<u>160</u>	1000
T_l	1000	1000
s	—	1000
T_{dd}	160	1000

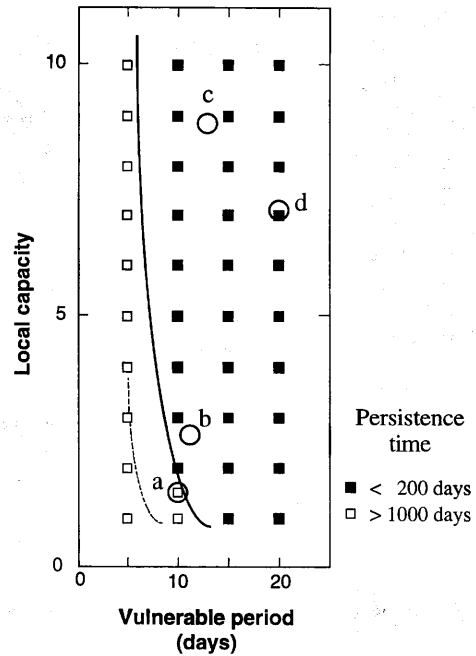


Fig. 6. Effects of the local capacity and the vulnerable period of the host on system persistence as predicted by the model. Black squares show persistence times of < 200 days and white squares persistence times of > 1000 days. The observed values of T_v and K_i are shown by circles for *C. maculatus*-mung (a), *C. maculatus*-azuki (b), *C. phaseoli*-mung (c) and *C. phaseoli*-azuki (d). The curved line shows the boundary between persistent and non-persistent parameter space, and the area left of the broken line refers to point stability.

was 5 days.

Simulation result

The simulation predicted 1000, 680, 165 and 170 days of persistence for mung-*C. maculatus*-parasitoid, azuki-*C. maculatus*-parasitoid, mung-*C. phaseoli*-parasitoid and azuki-*C. phaseoli*-parasitoid systems, respectively (Fig. 5). These were qualitatively consistent with the observed persistence in Fig. 3.

Changes in system persistence with the observed deviation in each parameter was examined to determine which parameter change(s) affected the time to extinction most. With increase ($\times 2$) or decrease ($\times 1/2$) in a single parameter value from that of the most persistent system, mung-*C. maculatus*-*H. prosopidis*, a simulation was run with other parameter values unchanged. The change in the persistence time was qualitatively equivalent among the changes in K_i and T_v ($= T_{hdp}/2$); greater K_i and T_v reduced persistence (Table 3).

Effects of K_i and T_v were further examined with other parameters fixed on the mung-*C. maculatus*-*H. prosopidis* system. It was clear that the effects of the lowest K_i and of

the shortest T_v contribute to the longest persistence time of this system (Fig. 6). Especially with $T_v \leq 5$, the model system was very likely to persist until day 1000, irrespective of T_v (Fig. 6). K_l affected persistence interactively with T_v .

Discussion

The persistence of the system with *C. maculatus* as host was greater than that with *C. phaseoli* as host (Fig. 3). The two host species were different in local capacity, or the extent of resource sharing (Fig. 1), and in their vulnerable period (Fig. 2) as well as in several life history characters (Table 1). The persistence of host-parasitoid systems was also affected by the host resource; the system lasted longer with mung bean as resource (Fig. 3). Vulnerable period and many life history parameters were affected by resource (Fig. 2 and Table 1).

Analyzed further by simulation, the greatest persistence of the mung-*C. maculatus*-*H. prosopidis* system was ascribed to the combined effect of the least resource sharing (the lowest K_l) and the shortest vulnerable period (the shortest T_v) (Tables 2 and 3, Fig. 6).

Effect of resource sharing of host

The more the host individuals shared a resource patch (i.e., a bean), the less persistent the host-parasitoid system (Figs. 1, 3 and 6, Table 3). More sharing, hence higher local capacity, in *C. phaseoli* resulted in a higher carrying capacity with the same amount of resource, reducing the persistence of host-parasitoid system.

Studies on structurally similar systems support the present study's conclusion; in comparison with mung-*C. maculatus*-*H. prosopidis*, mung-*C. chinensis*-*H. prosopidis*, in which the host exhibits higher local capacity, was less stable and took a shorter time to extinction (Tuda, manuscript in preparation). Another example is the more stable dynamics in the contest-type *C. analis* than in the scramble-type *C. phaseoli*, each parasitized by *H. prosopidis* (Ohdate 1980).

In addition, scramble-type populations, sharing with many conspecifics, suffers from density-dependent mortality at later stages of development (Utida 1975). The effect of the relative timing of parasitism and density-dependent host survival has been studied theoretically (Smith and Mead 1974; May et al. 1981). The present simulation showed that the timing of density-dependent host mortality at a later stage reduced the persistence of the host-parasitoid system, which probably corresponds to the difference between Models 2 and 3 at $k > 1$ and $q < 1$ in May et al. (1981) (see $T_{dd} \times 2$ in Table 3). Therefore, both of the two correlated properties, high local capacity and

later density dependence, can contribute to the observed reduction in system persistence. There has been no clear evidence of early population regulation in the contest-type life cycle because of the difficulty in defining the timing of density dependence in mortality in bruchid beetles and therefore future study is required on this aspect.

Effect of vulnerable period of host

The experimental results showed that a longer vulnerable period reduced persistence time (Figs. 2, 3 and 6, Table 3). Especially, lower persistence of azuki-*C. phaseoli*-*H. prosopidis* than that of mung-*C. phaseoli*-*H. prosopidis* was due to the longer vulnerable period of *C. phaseoli* feeding on the azuki bean (Figs. 2 and 3, Tables 2 and 3), and which agrees with the conclusion of Tuda and Shimada (1995).

Reduction in the proportion of the vulnerable period to the developmental period of the host is predicted to stabilize host-parasitoid systems (Smith and Mead 1974). This study, by contrast, shows that the absolute length of the host vulnerable period, with its proportion to the developmental period fixed, still greatly affected the dynamics and persistence of host-parasitoid systems (Tables 2 and 3, Figs. 3, 4 and 6). This empirical result is the first quantitative evaluation on the effect of the vulnerable period on the persistence (stability) of host-parasitoid systems (see also Tuda and Shimada 1995).

Biotic interactions form intrinsic temporal/spatial structures within a population and each additional interaction with other species makes such structures more complex. This study demonstrated that quantitative differences in the structure, in terms of local capacity and vulnerable period, affected the dynamical property of host-parasitoid systems on an ecological time scale. Evolutionary change in the population structure will be reported elsewhere (Tuda and Iwasa, unpublished).

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