I. SUMMARY

Experimental laboratory systems of bruchid beetles, *Callosobruchus* in particular, and their parasitoids have been used as models to study population dynamics of single species and host-parasitoid interactions since the early 1940s. First, this paper reviews the recent advances in ecological studies on laboratory systems of bruchid hosts and their parasitoids as represented by bottom-up and top-down controls. Factors controlling the persistence of simple host-parasitoid systems that can be modified by an evolutionary change in a host beetle are demonstrated with reference to local carrying capacity, vulnerable time window of hosts to parasitism, and functional
response of parasitoids. Second, we present experimental results on persistence of larger species assemblies analyzed in the light of the simple two-species host-parasitoid control factors. The most persistent association of species showed that both host and parasitoid control factors in the simple host-parasitoid system were consistently effective in the larger species complexes. There was also a general loss of persistence of host-parasitoid associations as species richness increased. Finally, at the interface between simple and complex assemblies, we asked how an addition of a third species to a simple host-parasitoid system affects resilience and duration of transients, with the Callosobruchus beetles as the host and two parasitoids (the pteromalid Anisopteromalus calandrae and braconid Heterospilus prosopidis). Semi-mechanistic models parameterized by fitting to the population data were constructed to help understand the driving forces that govern the behavior of interacting populations. The population dynamics of the three-species system was ascribed to cyclic/chaotic transient dynamics towards an attractor that has potential of not only a stable equilibrium but also a chaotic one. By comparing the three-species dynamics to the stable two-species (one host-one parasitoid) dynamics before H. prosopidis was introduced, the instability that leads to chaos was revealed to be induced by density-dependent host-feeding by A. calandrae. Although the destabilizing host-feeding was under the control of a stabilizing effect of mutual interference, the effect was estimated to be weakened by the introduction of the second parasitoid, H. prosopidis.

II. GENERAL INTRODUCTION

Following Pearl's (1927) seminal work, laboratory experiments under controlled environmental conditions have played a key role in testing ecological hypotheses. In the late 1930s, Syunro Utida was the first to initiate studies on laboratory experimental systems, using Callosobruchus beetles and their parasitoids; a series of publications followed in the 1940s (e.g., Utida 1943a,b, 1944a,b). Since then, the biology of intraspecific and interspecific density dependence and the consequences on dynamic behavior in the bruchid and parasitoid populations have provided a useful model for testing theories in ecology and for the development of new theoretical perspectives. Thus, these host-parasitoid model systems play a similar role to that of model organisms such as Drosophila (Pimentel and Stone, 1968) and Plodia Begon et al., 1995) as the host.

Beetles of the genus Callosobruchus (Coleoptera: Chrysomeloidae: Bruchidae) and their parasitoids, A. calandrae (Hymenoptera: Pteromalidae) and H. prosopidis (Hymenoptera: Braconidae), are the model organisms we used in the series of experiments on population dynamics of host-parasitoid systems. Their basic ecology is well studied and described in Appendix 1. In this paper, we review recent advances in ecological studies of bruchid hosts and their parasitoids in laboratory systems. Bottom-up (competition over resource) and top-down (parasitism) controls on the persistence of simple host-parasitoid systems, which can be modified by the evolutionary change in resource competition in a host beetle, are reviewed. Particular reference is made to local carrying capacity, vulnerable time window of hosts and functional response of parasitoids as the control factors. We also present findings from experimental tests on persistence of larger species assemblies analyzed in the light of these control factors as well as number of species. Finally, at the interface between simple and complex assemblies, we asked how addition of a second parasitoid species to a simple host-parasitoid system affects stability. As a measure of stability, we used both persistence time and resilience.

III. PERSISTENCE OF A SIMPLE HOST-PARASITOID SYSTEM

To examine life history and behavioral characters that promote persistence of host-parasitoid associations, the simplest possible host-parasitoid systems were studied with different combinations of resource and host species, each assembled with the same species of parasitoid (Tuda, 1996b). The resources used were the mung bean, Vigna radiata, and azuki, V. angularis; the hosts were the cowpea beetle, Callosobruchus maculatus and C. phaseoli, and the parasitoid was H. prosopidis. V. radiata is more suitable for the development of the two bruchids, and the bruchids differ in the degree of scramble competition; C. phaseoli exhibits a higher degree of scramble competition (many individuals share a bean) than C. maculatus. It should be noted that C. maculatus, exhibits an extreme variation in larval competition between geographical populations; the population used here as well as the one in the following section was of the scramble type in that multiple individuals survive in a single bean but closer to the contest type (a single individual dominates a bean) in that survivors are close to one.

A. Bottom-Up Control Factors

1. Local Carrying Capacity or Larval Competition Type

Two life history characters have proven to be the causes of persistence of host-parasitoid systems: local/global carrying capacity and duration of vulnerability to parasitoid attacks (Tuda, 1996b). Local carrying capacity in
bruchids on the bean scale is a direct result of density-dependent competition of larvae in a confined (bean) resource (Appendix 1); a population of contest type competitors, because of its higher resource requirement, has a lower local carrying capacity, and consequently a lower global carrying capacity at the population level.

Lower local/global carrying capacity of the host C. maculatus than that of C. phaseoli significantly promoted persistence of the host-parasitoid system (Fig. 1) (Tuda, 1996b). Simulation of a Nicholson-Bailey type model with age structure also supported the effect of local carrying capacity, with parameter values estimated independently of the long-term experiments. This result is consistent with the prediction of the paradox of enrichment, in which the increase in (global) carrying capacity reduces stability (Rosenzweig, 1971). On the contrary, when the global carrying capacity is increased by the addition of a greater resource for the host, longer coexistence was achieved (Tuda, 1999, unpublished data). Therefore, parallel increases in local and global carrying capacities or increases in global carrying capacity by changing the degree of density dependence (or nonlinearity) rather than by increasing resource patches, is the key to the paradox of enrichment, which may often be implicitly violated in the field (Tuda, 1999, unpublished data).

In a competition system, the intraspecific contest-type of C. maculatus is also a superior interspecific competitor (Toquenaga and Fujii, 1991) that can competitively exclude other bruchid species in assemblies of bean resource and herbivores.

Bruchid beetles that utilize small beans of wild legumes are the contest type, that is, only a single individual that dominates (bean) resource can survive in each grain of beans, whereas pest species such as the azuki bean beetle, Callosobruchus chinensis and Zabrotes subfasciatus, are (or evolved to be) the scramble type, with multiple individuals sharing single grains of beans. This would predict that population dynamics of pest species, that are likely to have high carrying capacities because of resource sharing, can be destabilized by introduction of a parasitoid for control, which allows both outbreaks and extinction of the pests. Selection for either the scramble or contest competition types will be discussed further in the subsection on evolutionary change.

2. Vulnerable Time Window

It has been shown that the duration of the vulnerable developmental stages in the host to parasitism is one of the factors that have the greatest effect on the persistence of host-parasitoid dynamics (Tuda and Shimada, 1995; Tuda, 1996b). The longer the vulnerable period, the less persistent the host-parasitoid system, which was observed in host-parasitoid systems with azuki as the resource that elongates developmental time in both C. maculatus and C. phaseoli (Fig. 1). Feeding on poor-quality plants hinders development of herbivorous insects, increasing the time window of susceptibility to natural enemies and leads to higher mortality of the herbivores (Johnson and Gould, 1992; Benrey and Denno, 1997). However, this slow-growth-high-mortality relation is not always observed in nature because of confounding interactions (Clancy and Price, 1987; Benrey and Denno, 1997). Slow development can also be associated with low fecundity. Model simulations to test this possibility, however, showed that the effect of such low fecundity is minor compared to that of a vulnerable time window for a parasitoid with high searching efficiency as in H. prosopidis (Tuda, 1996b). Resource is not the only factor that affects the vulnerable time window of the host. Increase in temperature elongated the vulnerable time window of C. chinensis to H. prosopidis, which reduced persistence, or time to extinction, of the host-parasitoid system (Tuda and Shimada, 1995).
3. Evolutionary Change

We often assume characters that play an important role in determining persistence of host-parasitoid systems are constant over time. This assumption, however, can be violated as observed in the host *C. maculatus* during a long-term experiment of a host-parasitoid system. Larval competition of *C. maculatus* was initially the scramble type, and two to three individuals survived from a small *V. radiata* seed (Fig. 2a). When the experiment was terminated on day 800, only single adults emerged indicating the larval competition was of the contest type (Fig. 2a) (Tuda, 1998). This population of *C. maculatus* was brought into the laboratory relatively recently (two years prior to experimentation), unlike the other populations of bruchids and parasitoids in our laboratory. There was no difference in the attack rates between pre- and post-experiment of the parasitoid *H. prosopidis*, which has been maintained in the laboratory for about 20 years. The change in the population dynamics occurred approximately at 20 generations of the host (Fig. 2b), and the post-experimental host and parasitoid after 800 days of coexistence showed stable population dynamics unlike the initial oscillations when they were returned to initial densities (Fig. 2c). This confirms the change was not temporal.

With a parameterized game-theoretical model, Tuda and Iwasa (1998) showed that the evolutionary change in larval competition towards the contest type can induce a large shift in the population dynamics of host and parasitoid as observed in the experimental system. For such rapid evolutionary change to occur, 20 generations was shown to be sufficient by the model with the following assumptions: 1) a small fraction of initial population was a contest-type competitor, in which the phenotype is genetically determined; and 2) the contest competitor consumes a certain volume of bean and kills other individuals in that volume, enabling a scramble competitor to survive only when beans are large enough. It is worth noting that random parasitoid attacks did not alter the evolution towards contest type but can slow the evolution.

This explains the results of experiments on a single-species *C. maculatus* population by Toquenaga et al. (1994), in which competition type was estimated based on the resemblance of dynamical trajectories. Their study also indicated that the transition from scramble to contest type occurred on a time scale consistent with the prediction of the present model (i.e., 20 generations). The time scale required for such a change also corresponds to the one observed in Nicholson’s laboratory blowfly population (Nicholson, 1957; Stokes et al., 1988). This similarity may arise not only from the stable laboratory conditions but also from a common biological mechanism, e.g., density-dependent processes in the insects.

**Figure 2** (a) Evolutionary change in the number of emerged adults that survived from larval competition of the host *C. maculatus* in the replicate shown in Figure 1a. Redrawn from Tuda (1998). (b) Temporal change observed in population dynamics of the *C. maculatus-H. prosopidis* host-parasitoid system (the replicate shown in Figure 1a). Redrawn from Tuda and Iwasa (1998). (c) A representative replicate of population dynamics of post-experimental host and parasitoid populations collected after 800 days from the replicate shown in Figure 2b. The open and closed circles as in Figure 1.
Because the contest type in the host is stabilizing in host-parasitoid dynamics, this bottom-up herbivore evolution enhanced the persistence of the host-parasitoid (C. maculatus-H. prosopidis) system. Genetic variability retained in the host probably facilitated the evolutionary change. Recently, the effect of genetic variability was directly tested on the persistence of the C. chinensis-H. prosopidis host-parasitoid system (Imura et al., 2003). The system with an F1 generation derived from a cross of two different strains of host as a founder persisted longer than those with single strains as founders. What is not known is how general this is and whether genetic variability in the parasitoid population has the same effect. The model prediction is that genetic variability that exhibits a trade-off in the parasitoid population does not have a critical effect, whereas that in the host population enables coexistence when the parasitoid attack rate is moderate which allows host-parasitoid coexistence in the early phase (Tuda and Bonsall, 1999).

Such evolutionary change in host-parasitoid dynamics may not be rare, especially when the insect populations are brought recently into the laboratory or a new environment. The population dynamics of C. chinensis-H. prosopidis system studied by Utida (1957a,b) appears to change over time (Utida, 1957a,b; Royama, 992). Parameterization of a subset of the three-species model, by fitting to the time-series, indicated that there was indeed a decrease in the attack rate of the parasitoid as time windows for fitting are shifted gradually from the onset of the experiment to the end of the time series (Tuda, 2003, unpublished data). Evolutionary flexibility and phenotypic plasticity as a modification force on the food-web has been discussed theoretically and empirically (Pimentel, 1968; Pimentel and Stone, 1968; Thompson, 1998; Abrams, 2000; Agrawal, 2001; Kondoh, 2003). What we observed in the bruchid-parasitoid system illustrates how evolution can promote persistence of species coexistence that, in the first place, is attained ecologically. Although evolution can also reduce persistence of a host-parasitoid system, it is more difficult to capture once coexistence is terminated by extinction. For this reason, biological assemblies we see in nature may be biased examples of selection 'towards coexistence'. Experimental tests on the possibility of evolution 'against coexistence' are intriguing future challenges.

4. Spatial and Temporal Heterogeneity

Distribution of resources or plants for herbivores, which is often determined by environmental factors, is also crucial for host-parasitoid interactions to persist. Shimada (1999) showed that the degree of patchiness of resource for C. chinensis affected variability of population dynamics of one of the two parasitoids, A. calandrae and H. prosopidis. The differential effect of patchiness between the two parasitoids is ascribed to their different searching behavior (Shimada, 1999). By comparing spatial to temporal heterogeneity of resources using two species of legumes, Mitsunaga and Fujii (1997) concluded that temporal heterogeneity or altering two resources in sequence contributed to the persistence of a two hosts-one parasitoid system. The conclusions of the two studies cannot be compared as they are because of the different structures of the assemblies. The host-parasitoid systems with different architectures have potential to be subjected to further testing for generality of the conclusions on the effect of heterogeneity, with a different combination of species.

B. Top-Down Control Factors

Functional response, or the number of attacked hosts as a function of host density, of parasitoid can be an important top-down control on host (Hassell, 1978). The attack rate of A. calandrae is characterized by the following: first, the number of attacked hosts increases gradually with increasing host density, specifically per-bean density, which itself is destabilizing (Utida, 1943b; Utida, 1957a; Kistler, 1985, unpublished data; Shimada and Fujii, 1985; Mitsunaga and Fujii, 1999); second, at a high density of A. calandrae, strong mutual interference stabilizes its population dynamics with the host. The C. chinensis-A. calandrae system with azuki beans (Vigna angularis), for example, exhibits mild oscillations with a small amplitude (Utida, 1946b, 1957a; Fujii, 1983). On the contrary, with blackeye bean, V. unguiculata as the resource, A. calandrae is able to attack more efficiently even when the density of host beetles is low, because the thin seed coat of the bean allows easier penetration of the ovipositor of the parasitoid. Eventually, host-parasitoid interaction ended with extinction probably because the destabilizing effect of host-feeding was greater than the stabilizing effect of mutual interference.

H. prosopidis has a high attack rate independent of host density but is limited by the number of eggs, which results in saturation in the number of attacked hosts as host density increases (Utida, 1957a). A C. chinensis-H. prosopidis system with azuki beans fluctuates with large amplitudes, sometimes showing population cycles of 100 days or longer (Utida, 1957a,b; Fujii, 1983; Tuda and Shimada, 1995). During the low-density phase, the system is likely to become extinct (Fujii, 1983; Tuda and Shimada, 1995), although it does persist for a fairly long time in some experimental replicates (Utida, 1957a,b).
IV. PERSISTENCE OF COMPLEX HOST-PARASITOID ASSEMBLIES

There is controversy over the relation between complexity and stability in a biological community. Random assembly models predict that complexity (in terms of species richness) reduces local stability and connectance (May, 1972), whereas Elton (1927) suggested that complexity enhances stability. In terms of global stability and permanence, which guarantee persistent coexistence of species, stability decreases with increasing complexity, which is consistent with May’s prediction (Chen and Cohen, 2001b). Recent studies indicate that adaptive evolutionary changes in component species can either increase or decrease diversity (Abrams, 2000; Kondoh, 2003). Studies using micro-organisms supported May’s prediction (Hasten et al., 1968; Lawler, 1993; Lawler and Morin, 1993). Accumulation of sound empirical evidence is required for assemblies of higher organisms. Here, we review recent advances in empirical tests on the complexity-stability hypothesis in the experimental assembly of bruchid hosts and their parasitoids.

Tuda (1996a) and Tuda and Kondoh (2003, unpublished data) analyzed experimental results that tested the complexity-stability hypothesis by using bruchid beetles and their parasitoid (Ohdate, 1980; Fuji, 1981, 1994). The experimental design was as follows: each of the four compartments of a petri dish was filled with 5 g of azuki beans, then bruchids, followed by parasitoids. The maximum number of the initial component species was 5, i.e., three bruchid species (C. maculatus, C. chinensis and Z. subfuscatus) and two parasitoid species (A. calandrae and H. prosopidis), and the minimum was 2, i.e., two bruchid species (Fujii, 1994). Initial assemblies were replicated up to three times. As each species becomes extinct, different initial assemblies can end up with the same assembly, and replicated assemblies can lose different species. Each such transient assembly is treated as an additional replicate. Bean supply was continued until the assembly reached stable states, or stable species compositions. Persistence, or time to extinction of a species, of each assembly type was recorded. The original records were transformed to mean probability of extinction per generation of a component species (Tuda and Kondoh, 2003, unpublished data). The results indicate that extinction probability increased as the number of species increased (Tuda and Kondoh, 2003, unpublished data), and persistence decreased with the increasing number of species (Tuda, 1996a). While this supports May’s complexity-instability relationship found from random combination of species, there was something beyond the prediction: a clear pattern in the composition of species in the final experimental assemblies (Ohdate, 1980; Fuji, 1983, 1994). The final assemblies were composed of either single bruchid, C. maculatus, or single host-single parasitoid, C. maculatus-A. calandrae. This shows that the bottom-up (contest competition or resultant low local carrying capacity of C. maculatus) and self-regulating top-down (mutual interference of A. calandrae) control factors proved critical in the previous section, stay effective in the larger species assemblies (Tuda, 1996a).

The experiment on the large species assembly in this section illustrated that it is not only the number of species itself but also the characteristics of species interactions that determine the persistence or stability of a host-parasitoid assembly.

V. POPULATION DYNAMICS IN A THREE-SPECIES SYSTEM: AT THE INTERFACE BETWEEN SIMPLICITY AND COMPLEXITY

Recent studies of insect and animal populations demonstrated complex nonlinear dynamics (including chaos) are ubiquitous in single – as well as paired – species populations (Nicholson, 1954; Hanski et al., 1993; Costantino et al., 1995, 1997; Ellner and Turchin, 1995; Falck et al., 1995; Turchin, 1996; Turchin and Ellner, 2000). In nature, almost all populations are concurrently interacting with multiple species, as predator and prey or as host and parasite/parasitoid. Three-species systems are one of the simplest and most intriguing candidates to allow an understanding of irregular, complex population dynamics of multi-species assemblies, with emerging effects of indirect interactions (Holt, 1977; Sih et al., 1985; Briggs, 1993). An example is a laboratory experimental system with a seed beetle host and two parasitoid wasps that persisted for a fairly long time with irregular population fluctuations of the three component species (Utida, 1957a).

Detection of mechanisms by parameterized models from population time-series has become a promising approach in ecology in recent years with the application of extensive statistical tools (e.g., Dennis et al., 1995, 1997, 2001; Kendall et al., 1999; Jost and Arditi, 2001; Kristoffersen et al., 2001; Turchin and Hanski, 2001).

With parameterized semi-mechanistic models, this paper aims to: 1) characterize persistent population dynamics of the same three species as Utida (1957a); 2) detect any change in the dynamic property and effect induced by the addition of the third species, by comparing the three-species dynamics with the two-species dynamics; and 3) clarify which characteristic(s) of the three species induced alteration of dynamic behavior.

A. Experiment

All of the experiments were conducted at 30°C, 65% relative humidity and 16: 8-hour light: dark cycles. Our system was first designed with only the host, C. chinensis, in a square plastic case (15 cm x 15 cm x 4 cm) in which
four round dishes (diameter 6 cm), each with 10 g of azuki beans (Vigna angularis) were set as resource patches. Live and dead adult insects were censused in each of three replicate systems at each 10-day interval, the oldest resource patch being replaced with uninfested azuki beans. The two parasitoid species were introduced sequentially into the system after the host population had converged to the equilibrium density: A. calandrae on days 130 and 140, then H. prosopidis on days 440 and 450. Population censuses were continued until the extinction of the host on day 1550. The number of adults that emerged during the preceding 10 days was calculated as: (number of the live adults at \(t\)) + (number of the dead adults at \(t\)) - (number of the live adults at \(t-1\)) in each species.

In the host-only phase, C. chinensis reached the equilibrium population size of about 350 between day 50 and day 100 (Fig. 3). After adding the first parasitoid, A. calandrae, on day 130 the host-A. calandrae system showed stable population dynamics with small oscillations around the equilibrium population sizes of the host (70 to 90) and A. calandrae (150 to 180) in all three replicate systems. However, after introduction of the second parasitoid, H. prosopidis, on day 440, the stable dynamics of the host and A. calandrae were disrupted and changed to irregular fluctuations with a large amplitude (Fig. 3).

Persistence of the three-species system ranged from 100 days (replicate C, not shown) to longer than 800 days (replicate B, Fig. 3b). Replicate C collapsed after one peak of H. prosopidis population outbreak because the wasp parasitized all the hosts. In replicates A and B, however, the three-species assembly persisted for 450 and 860 days (Fig. 3). Since H. prosopidis went essentially extinct in replicate A on day 890 (all emergents were males), 4 males and 8 females of newly emerged H. prosopidis were introduced, the effect of which was small on the time-series of the host and A. calandrae in comparison with usual demographic stochasticity. Replicate A continued thereafter until day 1,230, when finally H. prosopidis went extinct again, which was followed by rapid convergence to the original host-A. calandrae equilibrium states (Fig. 3a). The coexistence of the host and A. calandrae persisted thereafter until day 1,550 when we ended the long-term experiment.

In replicate B, on the other hand, the three-species assembly persisted for longer than 800 days from day 440 to day 1,300, during which population fluctuations were much larger in the host and A. calandrae after introduction of H. prosopidis than before (Fig. 3b). Both parasitoids went extinct simultaneously on day 1,300 after very low population densities of the host. When the host population had recovered, we re-introduced H. prosopidis only into the system to observe population dynamics of the host-H. prosopidis assembly. After an outbreak of host and H. prosopidis populations, all of the hosts were parasitized and the system collapsed on day 1,450 (not shown).

Population fluctuation of the host became abruptly larger after a low-density phase of A. calandrae between day 1,180 and 1,210, so we omitted the time-series after day 1,200 of replicate B from later analyses in the host and A. calandrae.
B. Detection of Chaos by a Non-Mechanistic Model

The computer programs LENNS (Lyapunov Exponent of Noisy Nonlinear Systems) and RSM (Response Surface Methodology) were applied to estimate the dominant Lyapunov exponent (LE), used as a measure of chaotic dynamics (Ellner et al., 1992; Turchin and Taylor, 1992). The 10 best fits by LENNS and the single best-fit estimates by RSM were selected to compute the LEs. Using LENNS, they were either positive (host in replicate B), zero (host in replicate A), or slightly negative (A. calandrae in both replicates) (Fig. 4a). Using RSM, the LEs in the three-species system were either positive (host population in both replicates and A. calandrae in replicate B) or slightly negative (A. calandrae in replicate A) (Fig. 4b). These estimates indicate that the one host-two parasitoid system can be chaotic but the result is not consistent among component species and replicates.

For comparison, the programs were also applied to the population dynamics of the two-species, or host-A. calandrae system (Fig. 4c, d). Both methods estimated large negative LEs for all four time-series except a positive exponent for the host in replicate A by LENNS.

By comparing the estimates between the two-species and three-species time series, the following characteristic differences were found: 1) the three-species system is less stable than the two-species system (Fig. 4); 2) the lag tends to be shorter in the three-species system (LENNS result in Table 1); and 3) the dimension is higher in the three-species system (Table 1).

C. Parameter Estimation and Reconstruction of Population Dynamics by a Semi-Mechanistic Model

1. Deterministic Model

The deterministic model is formulated with a Moran-Ricker equation for host density-dependent growth (Moran, 1950; Ricker, 1954) and a Nicholson-Bailey type equation for escape from parasitoid attack (Nicholson, 1933; Nicholson and Bailey, 1935). The selected model, based on the likelihood ratio test (Appendix 2), includes host reproduction followed by density-dependent survival of eggs according to adult density, density-dependent larval survival, and recruitment of adults from the previous time step in the host (Tuda, 2003, unpublished).

For generation time, two time units for the host and A. calandrae and one time unit for H. prosopidis were selected based on the time required for development from the egg to the reproducing female adult that is elongated by synergistic host feeding in A. calandrae (Appendix 1).
Table 1  Best fit parameters and the coefficient of determination ($r^2$) in LENNS and RSM. LENNS-estimated Lyapunov exponents, $A'$s, are the means of the 10 best fits and $l$ (the lag), $d$ (the number of lags or embedding dimensions), and $k$ (the number of nodes in the hidden layer), based on GCV (generalized cross validation) criterion (Ellner and Turchin, 1995). Numbers in parentheses indicate the second frequent $l$, $d$, or $k$ in the 10 best fits. The RSM-estimated $A'$s are, on the other hand, the best fit at the best $l$ (the time lag = 1), $d$ (number of lags or dimensions), and $q$ (the order of a polynomial), based on cross-validation criterion (Turchin and Taylor, 1992). The number at the head of each time series corresponds to the number in Figure 4. The range of days shows the time series that was used for calculation.

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Host-A. calandrae

Replicate A (day 140–440)

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<td>parasitoid H. prosopisidis</td>
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</tbody>
</table>

Multiparasitized (i.e., co-parasitized) hosts were assumed to produce each parasitoid with an equal chance (Appendix 1), thus the probability of producing A. calandrae is the sum of the probability of being attacked at least once by A. calandrae but not by H. prosopisidis, which is $\exp(-a'Z_{l-1})\{1-\exp(-a'Y_{l-1})\}$ and the probability of being attacked by both parasitoids and only A. calandrae surviving, that is $\{1-\exp(-a'Z_{l-1})\}\{1-\exp(-a'Y_{l-1})\}/2$. The sum is reduced to the form: $\{1+\exp(-a'Z_{l-1})\}\{1-\exp(-a'Y_{l-1})\}/2$. The same can be done for H. prosopisidis. Population sizes of each developmental stage of the host (X, Y) and parasitoids, A. calandrae (Y, Y) and H. prosopisidis (Z), at time t are thus described as:

$$X_{lt} = \lambda X_{l,t-1}\exp(-b_0X_{a,l,t-1} - b_1\lambda X_{a,t-1}\exp(-b_0X_{a,t-1}))$$

$$X_{a,t} = X_{l,t-1} + X_{a,l-1}\exp(-a'Y_{l-1}-a'Y_{l-1}) + s X_{a,t-1}$$

$$Y_{l,t} = Y_{l,t-1} + Y_{l,t-1}\exp(-a'Z_{l-1})\{1-\exp(-a'Y_{l-1})\}/2$$

$$Z_{l,t} = Z_{l,t-1} + Z_{l,t-1}\exp(-a'Z_{l-1})\{1-\exp(-a'Z_{l-1})\}/2.$$
reduces the attack rate as adult densities of A. calandrae increase (Shimada, 1999). H. prosopidis searches and parasitizes hosts efficiently but soon depletes its eggs by doing so, as in a typical type II functional response (Holling, 1959; Royama, 1971; Rogers, 1972). And it does not host-feed. Thus, the attack rates of the parasitoids are formulated as:

\[ a'_y = a_y \exp(fX_{t-1}) Y_{t-1}^{-m} \]

(6)

\[ a'_z = a_z / (1 + a_z c z X_{t-1}) \]

(7)

Not all of the developmental stages in equations 1 to 5, however, can be observed. Larval stages of the host and parasitoid are invisible from outside the beans. The equations for the larval stages (equations 1 and 3) are embedded into equations 2 and 4, respectively. Thus, the deterministic model is represented by three state variables:

\[ X_{a,t} = H_{t-2} \exp(-d'_y Y_{t-1} - d'_z Z_{t-1}) + s X_{a,t-1} \]

(8)

\[ Y_{a,t} = H_{t-3} \{1 + \exp(-d'_z Z_{t-2})\} \{1 - \exp(-d'_y Y_{t-2})\}/2 \]

(9)

\[ Z_{t} = H_{t-2} \{1 + \exp(-d'_y Y_{t-1})\} \{1 - \exp(-d'_z Z_{t-1})\}/2, \]

(10)

where

\[ d'_{y,t-1} = a_y \exp(fH_{t-1}) Y_{t-1}^{-m} \]

(11)

\[ a_{z,t-1} = a_z / (1 + a_z c z H_{t-1}) \]

(12)

\[ H_{t-1} = \lambda X_{a,t-1} \exp\{-b_0 X_{a,t-1} - b_1 \lambda X_{a,t-1} \exp(-b_0 X_{a,t-1})\}. \]

(13)

2. Stochastic Model and Fitting to Time-Series Data

In the observed time series, noise is added to the deterministic dynamics. Demographic noise presumably dominates, relative to environmental noise in our controlled growth-chamber environment. Host reproduction is assumed to follow a Poisson distribution with mean \( \lambda X_{a,t-1} \). Survival through density-dependent competition and parasitism can be described as a binomial distribution. A binomially distributed variable with Poisson-distributed mean \( n \) and probability \( p \) is known to follow Poisson distribution with mean \( \mu p \), where \( \mu \) is the mean of the Poisson distribution of \( n \) (Boswell et al., 1979). Therefore, all the variables on the left hand of equations 1 to 5 can be approximated by a Poisson distribution. The numbers in the present data set are square-root transformed to normalize the Poisson distribution (Dennis et al., 2001). Stochastic realization of the model with demographic noise is as follows:

\[ x_{a,t}^{1/2} = \{h_{t-2} \exp(-d'_y Y_{t-1} - d'_z Z_{t-1}) + s X_{a,t-1}\}^{1/2} + E_{x,t} \]

(14)

\[ y_{a,t}^{1/2} = [h_{t-3} \{1 + \exp(-d'_z Z_{t-2})\} \{1 - \exp(-d'_y Y_{t-2})\}/2]^{1/2} + E_{y,t} \]

(15)

\[ z_{t}^{1/2} = [h_{t-2} \{1 + \exp(-d'_y Y_{t-1})\} \{1 - \exp(-d'_z Z_{t-1})\}/2]^{1/2} + E_{z,t}. \]

(16)

For the assumptions on the noise and parameter estimation, see Appendix 3.

Numbers of adults of each species from day 430 to 870 in replicate A and day 430 to 1270 in replicate B were used as time series to fit the model.

3. Two-Species Dynamics

The host-A. calandrae dynamics before the introduction of H. prosopidis were fit by a subset of the three-species model to see if any factor was modified by the presence of H. prosopidis. The deterministic model for the host \( (X_a) \) and A. calandrae \( (Y_a) \) was a modified version of equations 8 and 9:

\[ X_{a,t} = H_{t-2} \exp(-d'_y Y_{t-1}^r) + s X_{a,t-1} \]

(17)

\[ Y_{a,t} = H_{t-3} \{1 - \exp(-d'_y Y_{t-2})\}. \]

(18)

A stochastic model for the two species with normally-distributed demographic noise was modified from equations 14 and 15:

\[ x_{a,t}^{1/2} = \{h_{t-2} \exp(-d'_y Y_{t-1}^r) + s X_{a,t-1}\}^{1/2} + E_{x,t} \]

(19)

\[ y_{a,t}^{1/2} = [h_{t-3} \{1 - \exp(-d'_y Y_{t-2})\}]^{1/2} + E_{y,t}. \]

(20)

Observed population sizes of each replicate were used for the initial values in the simulations: replicate A; \( X_1 = 80, X_2 = 61, X_3 = 57, Y_2 = 169, Y_3 = 142, Z_2 = 12, \) and \( Z_3 = 13 \); and replicate B; \( X_1 = 85, X_2 = 55, X_3 = 42, Y_2 = 218, Y_3 = 96, Z_2 = 12, \) and \( Z_3 = 17 \) for the three-species system (day 430 to 450). Replicate A; \( X_1 = 410, X_2 = 274, X_3 = 212, Y_2 = 8, \) and \( Y_3 = 158 \) and replicate B; \( X_1 = 351, X_2 = 343, X_3 = 140, Y_2 = 8, \) and \( Y_3 = 132 \) were used for the two-species system (day 130 to 150).

4. Estimation of Dominant LE

The dominant LE was estimated from a time-series of time unit (\( t \)) 1,001–2,000 (1 time unit = 10 days), omitting the first 1,000 points to remove any transient phase. The Jacobian matrix of partial derivatives of equations...
1 to 5 was used to estimate LE by applying the chain rule and then averaging the exponential divergence rates of initial perturbation over time. Bootstrapped datasets were constructed to estimate the confidence intervals of LEs, following Dennis et al. (2001). The error terms of the three populations as a set were resampled 1,000 times with replacement after standardization. Except for the first three data points, the bootstrapped errors were added to (square-rooted) population densities generated by deterministic simulation of the models with maximum likelihood (ML) estimates, and squared. When the population densities with added noise were <0, they were set to 0.5 before squared. The resultant data with the first three observed data in each replicate were fitted by the model to estimate LE. The 2.5th and 97.5th percentiles of the LE distribution were considered as 95% confidence limits of the LE.

D. Results and Discussion

1. Three-Species Population Dynamics

The results of the fit by the model and stochastic simulation are shown in Fig. 5. The ML estimates and 95% confidence intervals (CI) were as shown in Table 3.

The dominant LE estimated from a deterministic simulation of the model with the ML estimates was slightly negative, -0.0510 (bootstrap 95% CI, -0.684, 0.0014 for lower and upper confidence limits (CL) Fig. 6a). Simulated population dynamics with ML estimates had transients to stable equilibrium (Table 3) reached at time unit 472 (bootstrap 95% CI for duration of transient dynamics, 46, 2000 <). The equilibrium may not be reached in the experiments that persisted for 10, 45, and 86 time units. Among estimates for all the bootstrapped data, 9.3% exhibited complex dynamics (Fig. 6b) (about 8% were either chaotic or quasi-periodic and about 1% were long chaotic transient dynamics). The LEs were also estimated with the 95% CL of the parameters and were either positive or 0 at the lower limits of parameters \( a_Y \) and \( m \) for A. calandrae (equation 11), whereas at the other limits the LEs were all negative but with small absolute values (Table 3; Fig. 7 for one-dimensional bifurcation diagrams). The LE can be used as an index of resilience (i.e., ability to recover from a small perturbation; Gunderson, 2000) because the larger absolute values of negative LE, the more rapid convergence to an equilibrium (a strong positive correlation between inverse of the duration of transients and absolute values of negative LE, \( r = 0.992, n = 128, p < 0.0001 \)). In multi-dimensional bifurcation, where all parameters were estimated for each value of a parameter changed within its confidence interval, LEs monotonically increased with decreasing \( a_Y \) and \( m \) that can induce complex population dynamics (i.e., chaos and quasi-periodicity).

Within the confidence interval of LE, these chaotic, quasi-periodic, or chaotic transient behaviors resembled cycles of periods that varied from 3–4 to 18–19 time steps (typically 4 and 11 time steps, that is, 2 and 5.5 host generations). When the attractor is a point equilibrium, long transients of quasi-period of 10–25 (about 5–12.5 host generations) were seen before reaching the equilibrium state. During low-density phases of such periods, a population is vulnerable to extinction especially with demographic noise. Extinctions that occurred at time units 10 (replicate C), 45 (replicate A), and 86 (replicate B) in the three experimental replicates may correspond to such low densities in quasi-cycles. Incorporation of demographic stochasticity
Table 3  Estimated values and their 95% confidence intervals of parameters, and property of attractors at the confidence limits of the three-species system, C. chinensis (host) and two parasitoids, A. calandrae and H. prosopidis. An asterisk indicates a significant difference from the parameter value estimated from the two-species system. The Lyapunov exponent for ML estimate was -0.0510 (bootstrap 95% CI, -0.684, 0.0014) and simulated dynamics showed chaotic transients to stable equilibrium \((X, Y, Z) = (30.33, 42.83, 87.92)\). The absolute of eigen values at the equilibrium were all <1. Estimated elements in variance-covariance matrix were \(\sigma_{11} = 10.38, \sigma_{22} = 12.40, \sigma_{33} = 6.899, \sigma_{12} = \sigma_{21} = 0.1411, \sigma_{13} = \sigma_{31} = 1.292, \sigma_{23} = \sigma_{32} = -1.719\).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>ML Estimate (95% CI)</th>
<th>Lyapunov Exponent With 95% CL</th>
<th>Attractor With 95% CL</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\lambda)</td>
<td>7.580 (5.726, 11.52)</td>
<td>(-0.0219, -0.143)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(b_0)</td>
<td>0.004658 (0.002584, 0.006560)</td>
<td>(-0.0325, -0.124)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(b_1)</td>
<td>0.001168 (0.0006660, 0.001529)</td>
<td>(-0.0192, -0.141)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(s)</td>
<td>0.09774 (0.03996, 0.1723)</td>
<td>(-0.0502, -0.0655)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(a_y)</td>
<td>0.07168 (0.02517, 0.1796)</td>
<td>(0.0003, 0.0780)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(f)</td>
<td>0.002082 (0.0005473)</td>
<td>(-0.0704, -0.0370)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(m)</td>
<td>0.4480 * (0.2684, 0.6024)</td>
<td>(-0.0003, -0.0903)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(c_x)</td>
<td>0.1580 (0.04885, 1.0)</td>
<td>(-0.0546, -0.0223)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>(c_z)</td>
<td>0.1891 (0.1156, 0.2545)</td>
<td>(-0.0257, -0.152)</td>
<td>(equilibrium, equilibrium)</td>
</tr>
</tbody>
</table>

was likely to terminate the system. The dynamics of the three-species assembly is concluded to be long cyclic/chaotic transients towards an attractor that is either point equilibrium, cycles, quasi-cycles, or chaos, judging on a realistic time scale. In summary, complex population dynamics in the three-species assembly are likely either when the searching efficiency of \(H.\) prosopidis is high (Fig. 7a), when the searching efficiency of \(A.\) calandrae is low (Fig. 7b) that it associates with the high rate of synergistic host feeding, or when the mutual interference of \(A.\) calandrae is low (Fig. 7c). Both synergistic host feeding and low mutual interference are generally destabilizing (May and Hassell, 1973, 1981; Briggs et al., 1995).

The model that assumes different host developmental stages are vulnerable to the two parasitoids (with \(H.\) prosopidis attacking the host first), had a lower ML (-948.972) and, therefore, was declined despite its simplicity. The model with a generation time of \(A.\) calandrae of 1 time unit instead of 2 had a lower ML (-992.770), which was also declined. Our semi-mechanistic model is different from the non-parametric (or non-mechanistic) model proposed by Kristoffersen et al. (2001), in that multiparasitism (i.e., co-parasitism) is incorporated and mutual interference is present in \(A.\) calandrae. In their study, multiparasitism was assumed negligible based on experimental results by Shimada (1985). Our explicit statistical comparison of models
with and without multiparasitism showed that multiparasitism by the two parasitoids is not negligible. We interpret the experimental result on the niche modification by the two coexisting parasitoid species (Shimada and Fujii, 1985) as follows: The separation of the host stages that the two parasitoids utilize was only partial, which probably enabled the coexistence of the parasitoids for more than 100 days (7-9 generations) even when the single stage of hosts was provided (Shimada, 1985). Previous experiments showed that mutual interference is present in A. calandrae (Shimada, 1999) which is consistent with our result. In H. prosopidis, on the other hand, the effect of mutual interference becomes manifest only when its density is extremely high (Shimada, 1999), which may be the cause of exclusion of mutual interference by the present analysis. The time series used for analysis in Kristoffersen et al. (2001) was different from the one used here (i.e., the former excluded the initial part of both replicates and the last part of replicate B and included the last part of replicate A), which might explain the different density-dependence structures. Furthermore, mutual interference that remains constant along its density (i.e., a constant negative slope along logged densities), as in A. calandrae (Shimada, 1999), is more likely to be detected in functional response, embedded in Nicholson-Bailey type model (our model), than in total density (Kristoffersen et al. [2001] model).

The estimated parameter set at the confidence intervals indicated some correlations between parameters; positive correlations among $\lambda$, $b_0$, and $b_1$ (between $\lambda$ and $b_0$, $r = 0.823$, $n = 19$, $p < 0.001$; between $\lambda$ and $b_1$, $r = 0.863$, $p < 0.001$) and between $a_2$ and $c_2$ ($r = 0.690$, $p < 0.05$), and a negative correlation between $a_\gamma$ and $f$ ($r = -0.743$, $p < 0.01$).

2. Two-Species Population Dynamics

The host-A. calandrae dynamics before introduction of H. prosopidis were fit by a subset of the three-species model (Equations 19 and 20) to determine if any factor was modified by the presence of H. prosopidis (Fig. 8). The ML estimates and 95% confidence intervals are given in Table 4. The LE with ML estimates was negative, -0.889 (bootstrap 95% CI, -1.692, -0.585). The bootstrapped LE for the two-species system was significantly smaller than that for the three-species (Fig. 6a) (Bartlett's test for homogeneity of variance, $F = 141.5$, d.f. = 1, $p < 0.0001$; Welch's ANOVA, $F = 4,533.2$, numerator d.f. = 1, denominator d.f. = 1,764.8, $p < 0.0001$) and the simulated dynamics for all the bootstrapped data quickly converged to a stable equilibrium at the time unit, 35 (bootstrap 95% CI, 19, 49 time units) (Fig. 6c, Table 4). Among the estimated parameters, $m$ for mutual

Figure 7 (continued)
Table 4 Estimated parameter values and their 95% confidence intervals for the two-species system, *C. chinensis* (host) and *A. calandrae*. An asterisk indicates a significant difference from the parameter value estimated from the three-species system. The Lyapunov exponent with ML estimate was $-0.889$ (bootstrap 95% CI, $-1.692, -0.585$) and simulated dynamics showed quick convergence to stable equilibrium ($X_0 = 81.56, Y_0 = 147.32$). Estimated elements in variance-covariance matrix were $\sigma_{11} = 0.8513, \sigma_{22} = 2.965, \sigma_{12} = \sigma_{21} = -0.2112$

<table>
<thead>
<tr>
<th>Parameters</th>
<th>ML Estimate (95% CI)</th>
<th>Lyapunov Exponent With 95% CI</th>
<th>Attractor With 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda$</td>
<td>$6.776 \ (5.157, 9.529)$</td>
<td>$(-1.06, -0.843)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$b_0$</td>
<td>$0.003654 \ (0.001540, 0.005352)$</td>
<td>$(-0.986, -0.817)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$b_1$</td>
<td>$0.001398 \ (0.001013, 0.001585)$</td>
<td>$(-1.15, -0.708)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$s$</td>
<td>$0 \ (0, 0.1506)$</td>
<td>$(-0.888, -0.698)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$a_Y$</td>
<td>$0.2473 \ (0.08347, 0.6547)$</td>
<td>$(-0.670, -0.741)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$f$</td>
<td>$0.006286 \ (0.003209, 0.01107)$</td>
<td>$(-1.01, -0.546)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
<tr>
<td>$m$</td>
<td>$1.005 \ * (0.8636, 1.154)$</td>
<td>$(-0.638, -0.470)$</td>
<td>(equilibrium, equilibrium)</td>
</tr>
</tbody>
</table>

Figure 7  Bifurcation diagrams and corresponding dominant Lyapunov exponents for (a) $a_Z$, (b) $a_Y$, and (c) $m$ in three-species system within 95% confidence interval of respective parameter and (d) $m$ in two-species system with extended lower limit of its 95% confidence interval to compare to that of three species.

interference that can stabilize the system was significantly larger in the two-species system than in the three-species system with *H. prosopidis* (Welch's $t = -4.93, p < 0.001$) (Tables 3 and 4). A bifurcation diagram showed that a reduction in $m$ results in chaotic dynamics (Fig. 7d).

The larger values of $m$ in the two-species system can be explained by the higher density of *A. calandrae* relative to the host density, in the absence of *H. prosopidis*. With the addition of the third species (or the second parasitoid), hosts, on average, became less available and consequently *A. calandrae* did not increase to the population level that triggers mutual interference behavior because of limited host-feeding on a less abundant host. However, during chaotic transients the host can become temporarily super-abundant following low density of parasitoids, which may be the cause of the reduced self-regulation effect of mutual interference among *A. calandrae*.

On the other hand, the *C. chinensis*-H. *prosopidis* system was diagnosed as a long chaotic transient, and there were no significant changes in the parameter values from those in the three-species system, indicating asymmetric interspecific interactions between the two parasitoids (Tuda, 2004, unpublished).
The dynamics of interacting populations that we observe may often display transient behavior because it is likely that they have been driven away from intrinsic attractors by recent natural as well as human-induced changes. The characteristics of attractors themselves may be altered by evolution of component species in the assemblies (e.g., Tuda and Iwasa, 1998). Understanding non-equilibrium (i.e., transient and/or evolutionary) dynamics is crucial for the prediction on dynamics of biological assembly under changing environments. Laboratory experimental host-parasitoid systems will provide us with tools for further testing of ecological and evolutionary topics.

VI. HOST-PARASITOID INTERACTION AND BEYOND

In brief, ecological rules on population dynamics of interacting species discovered from host-parasitoid experimental systems with bruchid beetles as the host are as follows:

**Transient dynamics**: The attractor of the three-species system has both stable and chaotic features. In the chaotic region of the attractor, quasi-cycles of a period of multiple (and, in some cases, partial) generations of host and parasitoids appeared in the simulation. Even when the attractor is a point equilibrium, a long transient phase of quasi-cycles of multiple generations preceded, and the time required to reach equilibrium states is beyond the time of observed coexistence. The population dynamics of three-species host-parasitoid dynamics, therefore, is ascribed to a chaotic transient to a stable/chaotic attractor. Such intrinsically long transients can easily be elongated by demographic and environmental noise that constantly excites the population dynamics away from an equilibrium state (Bauch and Earn, 2003).
Bottom-up cascade control: Species of bean resources (plant) can control persistence of interactions of herbivores and parasitoids. In the simple Callosobruchus-parasitoid systems, the window of vulnerability was elongated by host-plant shift, which resulted in termination of the Callosobruchus-parasitoid interaction because of increased vulnerability of the host Callosobruchus to parasitism.

Evolutionary cascade effect: Evolutionary change occurred in the Callosobruchus beetle within a relatively short time span, as it shifted to a new bean resource that differs in size from its original bean. This change not only affected its own population dynamics but also modified host-parasitoid dynamics. An implication of the result for agricultural selection of larger and nutrient-rich crops is that pests can become more scramble-type competitors that allow more serious outbreaks of a pest population even under a control of parasitoid. It should be noted that the biology of evolution of contest/scramble competition can be more profound than shown in the present paper; the selection background of different geographical populations constrains artificial selection in the laboratory (Takano et al., 2001; Kawecki and Mery, 2003; Tuda, 2005, unpublished).

In the future, how evolutionary changes modify behavior of interacting species and eventually stability/persistence of overall assembly of hosts and parasitoids will be a next theme to pursue. As described in the section on bottom-up control, experimental tests on the possibility of evolution 'against coexistence' are intriguing future challenges. Does evolutionary capacity of species tend to vary between trophic levels? Does it depend on the number of interacting species (generalist vs. specialist, herbivore vs. carnivore, intraguild predator vs. non-intraguild predator, and so on)? These are some of the questions that do not yet have concrete empirical answers, however, they are crucial for the prediction of possible outcomes on the whole assembly when a species either is introduced or goes extinct. Evolutionary scheme of ecological stability/persistence of biological interactions may also be extended to include a lower trophic level (i.e., producer or plant) which could be much more complex. What is known from the investigation on insect fauna associated with leguminous plants, however, suggests that it may not complicate our understandings but rather simplify them: ecological characteristics of legume species such as their distributional range (similar to island-size effect), morphology (tree or herb), and historical background (introduced, native or endemic) are found to be excellent predictors of species richness of their seed predators, including bruchid beetles, and consequently their parasitoids (Tuda et al., 1998, unpublished). The process of accumulation of insect herbivores, followed by parasitoids on introduced plants or that of parasitoid on invading insect herbivores is not well understood (Tuda et al., 2001); this should include learning and evolutionary processes in insects. Patterns of species richness in nature such as this will be readily tested for their ecological and evolutionary processes, using laboratory experimental systems of bruchid beetles and their parasitoid (for a list of new candidates of Callosobruchus species for future laboratory experiments on species richness, see Tuda et al., 2005, and Tuda, 2003).

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APPENDICES

Appendix 1. Basic Ecology of the Experimental Organisms

Beetles of the genus Callosobruchus (Chrysomeloidea: Bruchidae) utilize beans or seeds of leguminous plants as the resource for their larvae. Adults deposit eggs and hatching larvae bore into not only immature, soft seeds but also mature, dried ones. Consequently, the beetles are stored bean pests. Since Callosobruchus larvae, except those at the late fourth (last) stage, cannot survive once they are removed from beans, the beans they bore into are the only resource they consume. During development, therefore, the larvae can suffer from competition with other individuals in the beans when the density of the beetles is high relative to the resource requirement. There are two parasitoids of Callosobruchus that are well studied for host-parasitoid population dynamics. They are Anisopteromalus calandrae (Hymenoptera: Pteromalidae) and Heterospilus prosopidis (Hymenoptera: Braconidae), which are solitary ectoparasitoids of late stages of larvae and prepupae of Bruchidae. The former widely utilizes coleopterous pests of stored products such as grain weevils (Curculionoidea: Rhynchophoridae) and biscuit beetles (Bostrychoidea: Anobiidae) as its hosts (Ghani and Sweetman, 1955). These parasitoids deposit a single egg on the host by inserting their ovipositor into beans. When they superparasitize (i.e., deposit multiple eggs) a host, only a single wasp individual can survive and emerge as an adult.
I: d, w , a r}~_ I ) } {
q
is the transpose of the vector e, and prosopid is
Li f e
aZ; _I )
is the joint transition probability density function for W[ in maximum likelihood function to be estimated (Dennis et al., 1995).

For A. calandrae, we incorporated mutual interference but not handling time, based on the result of the likelihood ratio test. A host-feeding parameter of the parasitoid was incorporated despite its insignificance in the three-species model but because of its statistical significance in the two-species model (Tuda, 2003, unpublished).

For H. prosopidis, a simple type II functional response was applied since the likelihood ratio test indicated the model with mutual interference that is either constant or increasing with its density was not significantly different from that without it (Tuda, 2003, unpublished).

Appendix 3. Assumption of Noise and Parameter Estimation

The noise is assumed to follow a multivariate normal distribution with multiple parameters in the model and elements in variance-covariance matrix Σ in maximum likelihood function to be estimated (Dennis et al., 1995, 2001):

\[ L(\theta, \Sigma) = \prod_{t=1}^{q} p(w_t | w_{t-1}), \]  

where \( p(w_t | w_{t-1}) \) is the joint transition probability density function for \( W_t \) conditional on \( W_{t-1} = w_{t-1}, q \) is the length of time series and \( \theta \) is the vector of unknown parameters of functions:

\[ g(w_{t-1}) = \begin{bmatrix}
[h_t \exp(-a_y y'_{t-1} - a_z z'_{t-1}) + s_x x_{a, t-1}]^{1/2} \\
[h_t \{1 + \exp(-a_z z'_{t-1})\}\{1 - \exp(-a_y y'_{t-1})\}]^{1/2}
end{bmatrix}^{1/2}
\]

and

\[ p(w_t | w_{t-1}) = (2\pi)^{d/2} |\Sigma|^{1/2} \exp(-e_t \Sigma^{-1} e_t/2), \]

where \( e_t = w_t - hw_{t-1} \), \( e_t \) is the transpose of the vector \( e_t \), and \( d \) is the number of dimensions or state variables. The distribution of the noise is assumed uncorrelated through time but correlated with each other between species.
at time $t$. The latter assumption requires estimation of three covariance elements in addition to three variance elements in the variance-covariance matrix. Log-likelihood was maximized by Nelder-Mead's simplex method, implemented in MATLAB 6.5.1 for Windows. The 95% confidence intervals of parameters were calculated based on profile likelihood that uses a likelihood ratio test (Venzon and Moolgavkar, 1988; McCullagh and Nelder, 1989; Lebreton et al., 1992; Dennis et al., 1995).

REFERENCES


population on the growth of host population and also of the parasite population. 


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