Supporting Information

Ishii and Shimada 10.1073/pnas.1115133109

SI Text

Stage-structured Population Model. Our model is based on that of a previous study (1), which constructed a stage-structured difference equation to model the host–parasitoid system, including two of the same species used in our experiments, *Callosobruchus chinensis* and *Anisopteromalus calandrae*. The model includes a density-dependent host reproduction function, *rep*, and a Nicholson–Bailey-type function for escape from parasitoid attack, *fr*. The time step t is measured in units of 1 wk. As the generation time of both *C. chinensis* and *Callosobruchus maculatus* is approximately 4 wk, and the generation time of parasitoids is approximately 2 wk, four time steps for both hosts and two time steps for the parasitoids were selected. The population sizes of each developmental stage of *C. chinensis* and *C. maculatus* at time t were denoted as $X_{l1,t}$, $Y_{l1,t}$ (number of 1-wk-old host larvae); $X_{l2,t}$, $Y_{l2,t}$ (number of 2-wk-old host larvae); $X_{l3,t}$, $Y_{l3,t}$ (number of 3-wk-old host larvae and pupae); and $X_{a,t}$, $Y_{a,t}$ (number of adults), respectively. The population sizes of the parasitoid *A. calandrae* were denoted as $P_{l,t}$ (number of parasitoid larvae) and $P_{a,t}$ (number of parasitoid adults). Next, the stage structure of the host *C. chinensis* was defined as the following matrix.

$$\begin{pmatrix} X_{l1,t} \\ X_{l2,t} \\ X_{l3,t} \\ X_{a,t} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & rep(X_{a,t-1}, Y_{a,t-1}) \\ 1 & 0 & 0 & 0 \\ 0 & (1-U)fr(P_{a,t-1}) & 0 & 0 \\ 0 & Ufr(P_{a,t-1}) & 1 & 0 \end{pmatrix}$$
$$\times \begin{pmatrix} X_{l1,t-1} \\ X_{l2,t-1} \\ X_{l3,t-1} \\ X_{a,t-1} \end{pmatrix}$$

Host individuals varied in their maturation times; therefore, a proportion of pupae emerged as adults at wk 3. U is the proportion of the larvae that emerged as adults at wk 3 (from X_{l2} to X_a) compared with larvae that continued to develop to the next stage (from X_{l2} to X_{l3}).

The equations for each developmental stage are as follows:

$$X_{l1,t} = X_{a,t-1}rep(X_{a,t-1}, Y_{a,t-1})$$
$$= X_{a,t-1}\exp\{r_x - \log(1 + c_x(X_{a,t-1} + \alpha_{xy}Y_{a,t-1})^{b_x})\}$$
$$X_{l2,t} = X_{l1,t-1}$$
$$X_{l3,t} = (1-U)X_{l2,t-1}fr(P_{a,t-1})$$
$$= (1-U)X_{l2,t-1}\exp(-a_x P_{a,t-1}^{1-m})$$
$$X_{a,t} = UX_{l2,t-1}fr(P_{a,t-1}) + X_{l3,t-1}$$

where r_x is the maximum intrinsic rate of increase, and the parameters b_x and c_x are the empirical scale parameters. The interspecific competition coefficient, α_{xy}, represents the effect of the competitor *C. maculatus* on *C. chinensis* relative to intraspecific competition. The equations for *C. maculatus* were modeled as same stage structures with parameters r_y, b_y, c_y, and α_{yx}.

The equations for the parasitoids are as follows:

$$P_{l,t} = X_{l2,t-1}\{1 - \exp(-a_x P_{a,t-1}^{1-m})\}$$
$$+ Y_{l2,t-1}\{1 - \exp(-a_y P_{a,t-1}^{1-m})\}$$
$$P_{a,t} = P_{l,t-1}$$

where a_x, a_y are the attack rates of the parasitoid on *C. chinensis* and *C. maculatus*, respectively. We incorporated the mutual interference of *A. calandrae*, m (1–3).

Parameter Estimation. The model parameters for host recruitment (r_x, b_x, c_x, and α_{xy} for *C. chinensis* and r_y, b_y, c_y, and α_{yx} for *C. maculatus*) were estimated from the data of the single-generation interspecific competition experiments of our previous study (4) for both black-eye and azuki beans as a resource by maximum likelihood (ML) parameter estimation. The 95% confidence intervals were calculated from profile likelihoods. With these reproduction parameters held fixed at the ML estimates for either azuki or black-eye beans, we estimated the other parameters, a_x, a_y, m, and U, by fitting the three-species host–parasitoid time series data of the current experiments. We used the nine replicates time series data for each BR treatment, BR = 0.2, 0.5, and 0.8. (We did not use the time series data for BE = 0 and BR = 1, because the three-species population dynamics was not sufficiently long to estimate the parameters). The square root-transformed numbers of adults of each species were used to fit the model, omitting the first 10-wk points to remove any transient phase. The conditional least squares (CLS) method was used for the estimation of parameters (5). The 95% confidence intervals were obtained using 2,000 sets of bootstrapped CLS estimates (5). The noise variables of the demographic stochasticity were estimated from the residuals. All calculations were conducted using the software program R ver. 2.12.1 (6).

The estimated values for the stage-structured host–parasitoid model and their 95% confidence intervals for the parameters are summarized in Tables S1 and S2. The estimated values for the competition coefficient indicate a competitive superiority for *C. maculatus*, which have a tendency toward contest-type behavioral interference in resource competition (4). The parameters estimated from the host–parasitoid time series were very close to each other when the reproduction parameters were fixed to those for azuki beans and those for black-eye beans (Table S2). As expected, the estimated attack rates for both host species were higher for BR = 0.5 and BR = 0.8 than the attack rate for BR = 0.2.

Parasitoid Preference. To investigate the effect of parasitoid learning, we incorporated the host preference depending on the larvae frequency of the two host species. We assumed a linear trade-off between the attack rate for the two host species *C. chinensis*, a_z, and *C. maculatus*, a_y (7).

$$a_x + a_y = T$$

The attack rate at time t was determined by the degree of specialization on *C. chinensis*, z_t ($0 < z < 1$), which was calculated by the larvae density of the two host species:

$$a_{x,t} = Tz_t, a_{y,t} = T(1 - z_t).$$

$$z_t = \frac{\exp\{\gamma(X_{l2,t} - Y_{l2,t})/(X_{l2,t} + Y_{l2,t})\}}{1 + \exp\{\gamma(X_{l2,t} - Y_{l2,t})/(X_{l2,t} + Y_{l2,t})\}}$$

These equations simply represent the tendency of predators to have higher attack rates for more abundant prey species. The

parameter γ determines the degree of frequency dependence on choice behavior, with a larger γ indicating a stronger frequency dependence. We assumed instantaneous specialization for the current abundances of host types.

Numerical Simulations. We investigated the dynamics of the model with the estimated parameters. The interspecific competition outcome was calculated by deterministic numerical simulations that started from the arbitrary initial values for *C. chinensis* and *C. maculatus* (Fig. S1). The estimated model predicted different interspecific competition outcomes between resource beans, as reported in our previous study (4): an overall dominance of C. *maculatus* in azuki beans (Fig. S1*A*) and a frequency-dependent competition of the initial population size in black-eye beans (Fig. S1*B*). When the nonlearning parasitoid with the estimated parameters was included in the deterministic numerical simulation ($\gamma = 0$), the competition result did not change, whereas the coexistence time changed (as we will describe later). On the contrary, the introduction of the learning parasitoid yielded a range of parameter space in which two host species coexist in equilibrium in both resource beans (Fig. S1 *C* and *D*).

We calculated how the coexistence time was affected when the intensity of attack rate ($a_x = a_y$) and the degree of frequency dependence (γ) were altered. The coexistence time was calculated with normally distributed demographic noise. We initialized simulations using the same introduction densities as the experimental setup (the introduction of 10 adult individuals of the 2 host species at wk 1–3 and the introduction of 12 individual parasitoid adults at wk 9 and 10).The model predicted that parasitoid introduction promoted persistence time only for learning parasitoids at an intermediate attack rate. The demographic noise shortened the coexistence time compared with the deterministic model, because it caused the extinction of host species at low densities. In addition, we conducted a sensitivity analysis for the parameters m, U, and the parameters for re-

production in the range of the predicted 95% confidence intervals (Tables S1 and S2). The parameter for mutual interference m greatly affected the optimal attack rate, which prolonged coexistence and altered the degree of frequency dependence, γ, that is necessary to prolong the coexistence time because higher mutual interference reduces the attack rate at high parasitoid density (Fig. S2). The parameters of reproduction functions also affected the coexistence time; for example, higher frequency dependence is needed to prolong coexistence in azuki beans compared with black-eye beans (Fig. S2). The proportion of the larvae that emerge as adults at week 3 U did not have a significant effect on the coexistence time. This model consistently predicted the essential role of learning behavior in promoting the coexistence time with the range of estimated parameters. Although our model qualitatively showed the effect of frequency-dependent predation on the coexistence time, a more realistic quantitative model requires further study including behavioral experiments to investigate the more realistic link function of parasitoid preference and host frequency.

Bean Preference of Host Species. We investigated the oviposition preferences of the host species on the two types of resource beans. The individual adults of *C. chinensis* or *C. maculatus* were allowed to oviposit a mix of 5g of azuki beans and 5g of black-eye beans in a Petri dish until their death. We calculated the ratio of eggs oviposited on azuki beans to the sum of the entire oviposition (Fig. S3). *C. chinensis* showed a stronger preference for azuki beans over black-eye beans for oviposition. Although this may contribute to the lower attack rate of *A. calandrae* for *C. chinensis*, this preference may be cancelled out when many adults of the two host species oviposit simultaneously in the microcosm because of behavioral interference during oviposition. The effect of the use of the beans may be small, because we did not detect a difference in the estimated attack rate parameters for *C. chinensis* and *C. maculatus*.

1. Tuda M, Shimada M (2005) Complexity, evolution, and persistence in host-parasitoid experimental systems with *Callosobruchus* beetles as the host. *Adv Ecol Res* 37: 37–75.
2. Shimada M (1999) Population fluctuation and persistence of one-host–two-parasitoid systems depending on resource distribution: From parasitizing behavior to population dynamics. *Res Popul Ecol* 41:69–79.
3. Gokhman V, Fedina T, Timokhov A (1999) Life-history strategies in parasitic wasps of the *Anisopteromalus calandrae* complex (Hymenoptera: Pteromalidae). *Russian Entomological Journal* 8:201–211.

4. Ishii Y, Shimada M (2008) Competitive exclusion between contest and scramble strategists in *Callosobruchus* seed–beetle modeling. *Popul Ecol* 50:197–205.
5. Dennis B, Desharnais RA, Cushing JM, Henson SM, Costantino RF (2001) Estimating chaos and complex dynamics in an insect population. *Ecol Monogr* 71:277–303.
6. R Development Core Team (2010) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Austria). Available at http://www. R-project.org/. Accessed February 23, 2012.
7. Abrams PA, Kawecki TJ (1999) Adaptive host preference and the dynamics of host-parasitoid interactions. *Theor Popul Biol* 56:307–24.
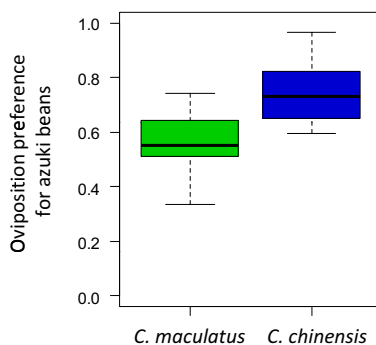
Azuki bean   **Black-eye bean**

Fig. S1. Predicted outcome of three-species population dynamics based on the model with estimated parameters in azuki (*Left*) and black-eye beans (*Right*). The green area indicates the survival of *C. maculatus*, the blue area indicates the survival of *C. chinensis*, and the white area indicates the coexistence of the two host species. (*Upper*) Results when the parasitoid is absent. (*Lower*) Results when the learning parasitoid was introduced with a_x, a_y, m, and U for BR = 0.8 (Table S2), with the strength of frequency dependence $\gamma = 0.6$ for azuki beans (*C*) and $\gamma = 0.4$ for black-eye beans (*D*). The time step was 500 wk.

Fig. S2. Predicted coexistence time against the attack rate a at varying degrees of specialization γ by the estimated model. The coexistence time was plotted when the parasitoid was absent (black line), when the nonlearning parasitoid was present (gray line; $\gamma = 0$), and when the learning parasitoid was present. *Upper* and *Lower* panels use the estimated parameters of the reproduction parameters for azuki and black-eye beans, respectively. The parameters for mutual interference were varied $m = 0.4$, 0.6, and 0.8, with $U = 0.3$ for all calculations. Persistence times are mean ± SEM of 100 replicate runs.

Fig. S3. Oviposition preference of *C. chinensis* and *C. maculatus* for azuki and black-eye beans.

Table S1. Estimated values for host reproduction parameters and their 95% confidence intervals

Parameter	Description	Azuki bean		Black-eye bean	
r_x	Growth rate of *C. chinensis*	3.21	(3.06, 3.38)	3.22	(3.06, 3.43)
r_y	Growth rate of *C. maculatus*	3.31	(3.01, 3.68)	3.58	(3.26, 3.92)
c_x	Scale parameters for the density dependence of *C. chinensis* recruitment	0.029	(0.024, 0.037)	0.029	(0.023, 0.039)
c_y	Scale parameters for the density dependence of *C. maculatus* recruitment	0.062	(0.040, 0.102)	0.096	(0.064 0.148)
b_x	Scale parameters for the density dependence of *C. chinensis* recruitment	1.40	(1.33, 1.47)	1.28	(1.20, 1.36)
b_y	Scale parameters for the density dependence of *C. maculatus* recruitment	1.16	(1.08, 1.25)	1.13	(1.07, 1.19)
α_{xy}	Competitive coefficient of *C. maculatus* on *C. chinensis*	3.72	(3.27, 4.26)	4.19	(3.59, 4.69)
α_{yx}	Competitive coefficient of *C. chinensis* on *C. maculatus*	0.76	(0.63, 0.91)	1.61	(1.35, 1.93)

Table S2. Estimated values using host–parasitoid time-series data and their 95% confidence intervals

Parameter	Description	Azuki bean		Black-eye bean	
BR = 0.2					
a_x	Attack rate for *C. chinensis*	0.097	(0.039, 0.130)	0.118	(0.058, 0.136)
a_y	Attack rate for *C. maculatus*	0.084	(0.039, 0.128)	0.083	(0.054, 0.131)
m	Mutual interference	0.509	(0.339, 0.571)	0.514	(0.380, 0.545)
U	Proportion of larvae that emerge as adults at week 3	0.284	(0.225, 0.342)	0.292	(0.258, 0.339)
BR = 0.5					
a_x	Attack rate for *C. chinensis*	0.767	(0.445, 0.968)	0.779	(0.441, 0.890)
a_y	Attack rate for *C. maculatus*	0.759	(0.453, 0.970)	0.678	(0.429, 0.869)
m	Mutual interference	0.911	(0.813, 0.962)	0.897	(0.791, 0.926)
U	Proportion of larvae that emerge as adults at week 3	0.290	(0.239, 0.365)	0.275	(0.229, 0.326)
BR = 0.8					
a_x	Attack rate for *C. chinensis*	0.738	(0.490, 0.889)	0.788	(0.572, 0.915)
a_y	Attack rate for *C. maculatus*	0.724	(0.527, 0.915)	0.700	(0.568, 0.889)
m	Mutual interference	0.850	(0.786, 0.892)	0.851	(0.790, 0.880)
U	Proportion of larvae that emerge as adults at week 3	0.391	(0.358, 0.442)	0.359	(0.329, 0.398)