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Evolution of contest competition and its effect on host–parasitoid dynamics

MIDORI TUDA[1]* and YOH IWASA[2]

[1]Department of Systems Science, University of Tokyo, Komaba, Meguro 153 and [2]Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812-8581, Japan

Summary

In experimental populations of the cowpea bean weevil *Callosobruchus maculatus* (Coleoptera: Bruchidae) and a parasitic wasp *Heterospilus prosopidis* (Hymenoptera: Braconidae), large changes in the abundances and the fluctuations of both species occurred after approximately 20 generations. In this paper, we examine the hypothesis that this observed change in the dynamics may have been caused by an evolutionary shift in the mode of competition among the bean weevils. A Nicholson-Bailey type model is developed using parameters measured from the experiments. The host larvae can differ in the type of competitive behaviour that they exhibit, which can be either of a contest type or of a scramble type. If a bean contains one or more larvae of the contest type, only one of these will survive and any scramble-type larvae in the bean will be killed. If no contest-type larvae are present within a bean, multiple individuals of the scramble type can emerge from a single bean. The model assumes many genotypes, differing in the fraction of offspring of the two types. If a high per capita resource availability is maintained, then the scramble type is selected for, but if resources are limited, then the contest type is selected for. The host population at the start of the experiment, taken from a stock culture, was composed mostly of the scramble type. The model is successful in explaining the initial quick increase in the host's abundance, followed by the evolutionary increase in the fraction of the contest type among hosts, resulting in the more stable population dynamics of the host–parasitoid system, as observed in the experiments. However, it predicts a parasitoid abundance much higher than that observed. We discuss alternative hypotheses to explain the observed evolutionary shift in the population dynamics. We also examine the effect of the difference in size of the beans in the stock culture and those used in the experiments.

Keywords: *Callosobruchus maculatus*; evolutionarily stable strategy; evolutionary speed; *Heterospilus prosopidis*; laboratory system

Introduction

Populations of animals and plants in experimentally controlled environments sometimes show long-term changes in dynamics that occur over many generations (Nicholson, 1957; Utida, 1957; Pimentel and Stone, 1968). Some of these changes may simply be a result of long transients in the dynamics while returning to an equilibrium state(s), but there are clear examples of outcomes of evolutionary (or co-evolutionary) modification in the component species of the system. Although some pioneering models have analysed evolutionary processes in single-species populations (Stokes *et al*., 1988; Toquenaga *et al*., 1994), few two-species systems have been subjected to experimental tests of the mechanism leading to long-term changes in population dynamics (but see Pimentel *et al*., 1963; C.J. Briggs *et al*., unpublished).

In a laboratory host–parasitoid system consisting of the mung bean, the cowpea bean weevil and a parasitic wasp, Tuda (1996) demonstrated that the host and parasitoid populations showed three

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*Address all correspondence to Midori Tuda, Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan.

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large oscillations, and then they suddenly stabilized at about the twentieth host generation and simultaneously the mean population size of the parasitoid was lowered (Fig. 1). By examining the pre- and post-experimental insects, Tuda (in press) found that the host had changed its larval competition habit from the scramble type to the contest type, and the post-experimental hosts had several properties distinguishable from the hosts in the stock culture. There was no change in the parasitoid in terms of the maximum attack rate and the duration of attacking host stages (or the period of host vulnerability).

In this paper, we examine the hypothesis that the change in the host–parasitoid dynamics was primarily due to the evolution of the competition type in the host larvae, rather than a change in the nature of the host–parasitoid interaction. After examining the evolutionary model describing the shift in the larval competition mode of the host during experiments, we incorporate random removal of host adults to assess its impact on the rate of evolutionary change. The model is then extended to study the effect of attack by the parasitoids, in a Nicholson-Bailey framework, host–parasitoid dynamics and the rate of host evolution. We also examine the effect of alternative timing of parasitization and the two modes of competition, and the effect of sizes of beans, to explain the observed population dynamics.

The model

We first consider the evolution of the host in the absence of the parasitoid. Consider two phenotypes of individuals – contest type and scramble type – differing in the behaviour of larval stages. Contest-type larvae fight within a bean and at most one individual can emerge from a bean. Scramble-type larvae do not attempt to kill others in the same bean but adults emerging from a bean with many larvae are small, having lower fecundity than an individual which has grown singly during the larval period.

We assume that females lay only a single egg onto each bean, but many larvae may exist in a single bean if laid by multiple females. Based on this assumption, the larvae in a single bean are not related.

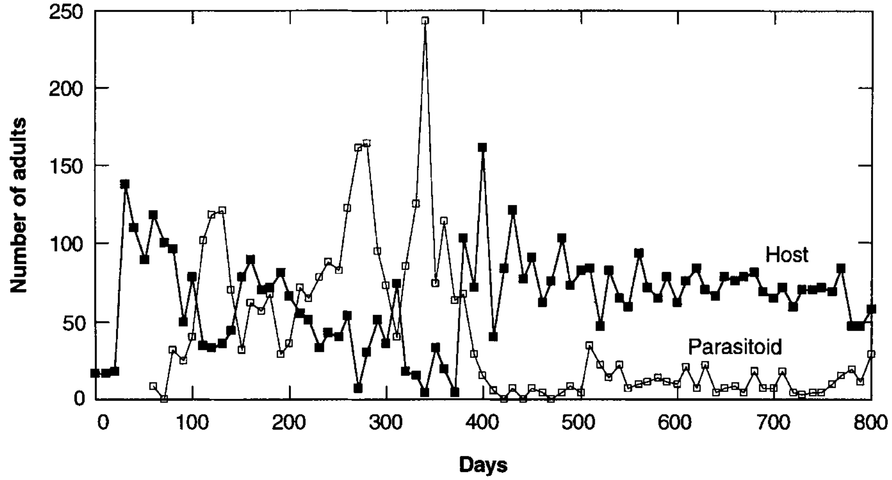


Figure 1. Population dynamics of a laboratory host–parasitoid system. The solid squares are the abundances of the host, the cowpea bean weevil *Callosobruchus maculatus*, and the open squares are those of the parasitoid, a braconid wasp *Heterospilus prosopidis*. The method is described in Tuda (1996).

Since novel mutations occurring during the experiment are unlikely to be frequent enough to explain the large change in the competitive behaviour, the initial population must have genetic variability in terms of the propensity to produce contest-type larvae. We here assume that there is a series of genotypes, each having a different probability of becoming larvae of the two types (i.e. the larval competition type is controlled probabilistically by the genotype). We assume the simplest possible genetic model to explain the observed evolutionary changes in bean weevil population: a haploid population with multiple alleles at one locus controlling the probability q of being a contest-type larva, as is often assumed in evolutionary game theory (Maynard Smith, 1982). We can easily extend it to the additive polygenic system controlling the fraction of contest-type larvae (Iwasa *et al*., 1991). We neglect new mutations, as we discuss events occurring in less than 100 generations.

Suppose that there are n genotypes indicated by $i\,(i = 1, 2, \dots, n)$, with the i-th type having a probability of being a contest-type larva q_i. In the numerical examples below, we use $q_i = (i - 1)/(n - 1)$, where the first genotype is a pure scramble-type larva ($q_1 = 0$) and the n-th genotype is a pure contest-type larva ($q_n = 1$), and all other $n - 2$ types give mixed strategies of different probabilities of being a contest-type larva.

Let x_i be the number of adults of the i-th genotype. From $x_1, x_2, \dots, x_n$, we can compute the total number of adults H, and the average fraction of the contest type $\bar{q}$, as follows:

$$H = \sum_{i=1}^{n} x_i \tag{1a}$$

$$\bar{q} = \sum_{i=1}^{n} q_i x_i \,/H \tag{1b}$$

The average number of eggs per adult is denoted λ, which is half of the number of eggs produced per female, assuming a 1:1 sex ratio. The number of eggs becoming contest-type larvae and the number of eggs becoming scramble-type larvae are denoted by C and N, respectively. They are simply:

$$C = \lambda \sum_{i=1}^{n} q_i x_i \qquad N = \lambda \sum_{i=1}^{n} (1 - q_i) x_i \tag{2}$$

Let m be the number of beans. The numbers of eggs of the contest type and scramble type laid on a bean follow independent Poisson distributions with means C/m and N/m, respectively. The hatchability of eggs and density-independent survivorship may differ between two types: their product is h_C for the contest type and h_N for the scramble type. Then, among contest competitors, only one larva per bean can survive to become an adult. The fitness of a contest-type individual is the product of fecundity λ and the survivorship until maturity:

$$w_C(C) = \lambda m (1 - \mathrm{e}^{-h_C C/m})/C \tag{3}$$

The term $(1 - \mathrm{e}^{-h_C C/m})$ is the probability of a bean having at least one contest-type larva, where $\mathrm{e}^{-h_C C/m}$ is the zero-th term of the Poisson distribution with mean $h_C C/m$. The product of $m(1 - \mathrm{e}^{-h_C C/m})$ is the number of adults from contest-type larvae. It is divided by the number of contest-type eggs C to give the survivorship from eggs to adults. Then it is multiplied by λ to give the fitness w_C in Equation (3). Note that the fitness of contest-type individuals is independent of the presence of scramble-type individuals.

The scramble-type larvae, on the other hand, can survive only in beans that lack contest-type larvae. We use $\mathrm{e}^{-\beta(y-1)}$ to denote the density-dependent survival among y scramble larvae per bean, where β is the strength of competition among scramble-type larvae. This function fits closely the observed survival curve for larvae on mung beans (Tuda, in press). We assume that a scramble-type individual has the same fecundity (λ) as a contest-type individual. The probability of a bean having y scramble-type larvae follows the Poisson distribution:

$$\frac{(h_N N/m)^y}{y!} \mathrm{e}^{-h_N N/m}$$

The product of these factors, if summed over y up to infinity, yields:

$$\mathrm{e}^{-h_C C/m} \sum_{y=1}^{\infty} \frac{(h_N N/m)^y}{y!} \mathrm{e}^{-h_N N/m} y\lambda \mathrm{e}^{-\beta(y-1)}$$

the number of the scramble type in the next generation. Finally, divided by N and multiplied by m, it becomes the fitness (or per capita reproductive rate) of a scramble-type individual:

$$w_N(C, N) = \lambda h_N \exp[-h_C C/m - h_N(1 - \mathrm{e}^{-\beta})N/m] \tag{4}$$

We estimated values for the host parameters from short-term experiments performed separately from the long-term census of the population dynamics (Tuda, in press). These values are listed in Table 1.

The evolutionarily stable fraction of contest-type larvae

In the next generation, x_i, the abundance of the i-th genotype producing fraction q_i of the contest type, becomes:

$$x_{i,t+1} = \{q_i w_C(C_t) + (1 - q_i) w_N(C_t, N_t)\} x_{i,t} \tag{5}$$

The fitness of the i-th genotype is an arithmetic average of the fitness for contest-type larvae and the fitness for scramble-type larvae, as each egg of genotype i becomes contest and scramble type with probability q_i and $(1 - q_i)$, respectively. Once x_i $(i = 1, 2, \ldots, n)$ is known, we can calculate the average fraction of the contest type in the host population using Equation (1a) and the total adult hosts using Equation (1b).

Starting with an initial distribution with a sharp peak near $q_1 (= 0)$, and hence a small average fraction of the contest type, and using the estimated parameter values in Table 1, the number of contest-type adults rapidly increases at first and then gradually saturates (Fig. 2). The number of individuals at saturation is about 90, the number of beans maintained in the experiment. This is quite close to the observed level of 94.4 ± 1.4 (mean ± S.E.) (Tuda, 1995). Changes in λ do not affect the final level much, but decreasing λ slows the spread of the contest type.

In generating the initial distribution of x_i we chose:

$$H_0 \mathrm{e}^{-\mu i} \Bigg/ \sum_{j=1}^{n} \mathrm{e}^{-\mu j}$$

where H_0 is the initial population density of the host ($H_0 = 60$). The variance of this distribution, controlled by μ, also influences the speed of evolution (Figs 2a,b).

Equation (5) gives the full dynamics of genotypes, describing both the population dynamic change in the total population size and the evolutionary change in the fraction of contest-type larvae $\bar{q}$. However, the following intuitive argument and the simple formulae are useful in calculating the evolutionarily equilibrium (see Appendix 1 for further argument): If an evolutionarily stable population includes a mixture of larvae of both contest and scramble types, then the expected fitnesses of the contest and scramble types must be the same; otherwise, producing a larger

Table 1. Definition of variables and parameters[a]

Variable and parameter	Definition	Unit	Parameter value
Host			
H	total number of adult hosts	individuals	
C	number of eggs for contest-type larvae	individuals	
N	number of eggs for scramble-type larvae	individuals	
q_i	proportion of *i*-th genotype becoming contest-type		
x_i	number of adults of the *i*-th genotype	individuals	
λ	fecundity (per capita adult), half of fecundity per female	eggs per individual	17.6
h_C	hatchability of eggs multiplied by the density-independent larval survivorship of contest type		0.86
h_N	hatchability of eggs multiplied by the density-independent larval survivorship of scramble type		1.0
β	strength of density dependence in larval survival of the scramble type		0.234
Parasitoid			
P	number of parasitoid adults	individuals	
a	attack rate	1/(generation individual)	0.0125–0.03
s_P	larval survival rate	1/generation	0.9
Bean			
m	number of beans		90

[a] Parameter values for the host are estimated from independent short-term experiments (Tuda, in press).

(or a smaller) fraction of contest types would become more advantageous, which is in conflict with the assumption of evolutionary stability. In addition, since the fitness is the same as the population multiplicative rate (as indicated in Equation 5), the fitness of the type remaining in the population must be equal to 1. From these two considerations, we have:

$$w_C(C^*) = w_N(C^*, N^*) = 1 \qquad \text{if } \bar{q} \text{ is an intermediate value} \tag{6a}$$

$$w_C(C^*) < w_N(C^*, N^*) = 1 \qquad \text{if } \bar{q} = 0 \tag{6b}$$

$$w_N(C^*, N^*) < w_C(C^*) = 1 \qquad \text{if } \bar{q} = 1 \tag{6c}$$

from which we can calculate the evolutionarily stable fraction of the contest-type larvae.

Consider the case in which the evolutionarily stable population (or ESS) includes both contest and scramble types. Let C^* and N^* be the values in the putative ESS solution. Then, from Equations (3) and (6a), C^* is a single positive solution of:

$$\lambda m(1 - \mathrm{e}^{-h_C C^*/m}) - C^* = 0 \tag{7a}$$

From Equations (4) and (6a), we have:

$$N^* = (m \ln \lambda h_N - h_C C^*)/\{h_N(1 - e^{-\beta})\} \tag{7b}$$

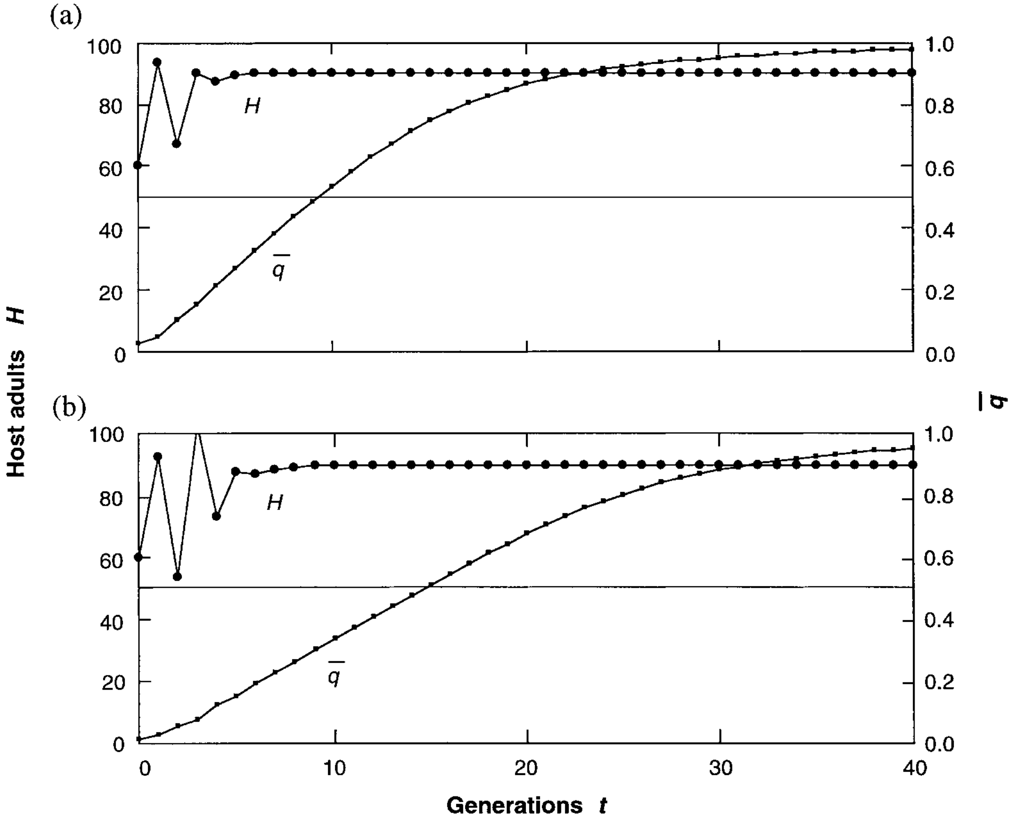


Figure 2. Population dynamics (H) and average fraction of the contest type ($\bar{q}$) in the bean weevil with parameter values estimated from short-term experiments: $\lambda = 17.6$, $h_C = 0.86$, $h_N = 1.0$ and $\beta = 0.234$ (Equations 3, 4 and 5). We chose $H_0 e^{-\mu i} / \sum_{j=1}^{n} e^{-\mu j}$ to generate the initial distribution of x_i, whose variance is controlled by μ. The initial $\bar{q}$ values are (a) 0.03 and (b) 0.014.

The conditions for the two types to co-exist (i.e. $C^* > 0$ and $N^* > 0$) are:

$$\lambda h_C > 1 \qquad \lambda h_N > 1 \qquad m \ln \lambda h_N > h_C C^* \tag{8}$$

For the parameter values listed in Table 1, the third inequality is not satisfied, and thus the co-existence of the two competition types is impossible in the host-only population.

Random removal of the host

In the stock culture, a large fraction of adults was removed every generation, to keep the availability of beans per individual sufficiently high. One of the potential reasons why the initial population of bean weevils was composed mostly of individuals engaging in scramble-type competition (rather than contest-type competition) is that removal during stock-keeping procedures might have favoured scramble-type competition by maintaining a low weevil density per bean.

If adults of the host are removed randomly with rate R $(0 < R < 1)$, the number of the i-th genotype in the next generation is:

$$x_{i,t+1} = x_{i,t}\{q_i w_C(C_t) + (1-q_i) w_N(C_t,N_t)\}(1-R) \tag{9}$$

With this additional factor $(1-R)$, we have modified the equations for the ESS population as explained in Appendix 2, from which we can calculate the evolutionarily stable population for different values of R.

As shown in Fig. 3a, for a wide range of R, the contest type is always selected for and the scramble type is predicted to be eliminated. However, for a sufficiently large R ($R > 0.921$ in Fig. 3a), the contest type and scramble type co-exist in the evolutionarily stable population. As R increases further, the fraction of the contest type drops rapidly and is replaced by the scramble type, the latter coming to dominate only at very large R ($R > 0.934$ in Fig. 3a). At even higher R, neither of the two types can persist in the stock ($R > 0.943$ in Fig. 3a). The range of the parameter R for the evolutionarily stable population to include both types is quite narrow ($0.921 < R < 0.934$), but the range of removal rate R for the ESS to be pure scramble type is even narrower ($0.934 < R < 0.943$) (see Appendix 2 for the analysis).

Figure 3a shows that the final value of $\bar{q}$ is 1 for most values of R, and Fig. 3b shows that, except for very large R, the rate of increase in $\bar{q}$ is also insensitive to the removal rate. Figure 4 illustrates several trajectories of $\bar{q}$, which shows that large removal rates, especially $R > 0.9$, tend to slow down the evolution of contest types.

This makes it difficult to explain why the initial host population derived from the stock culture is composed predominantly of scramble types, because the range of removal rate R for this to hold is very restrictive. Later, we will consider an alternative mechanism to explain this, based on the possibility for a large-sized bean used in the stock to support both scramble types and contest types in the same bean.

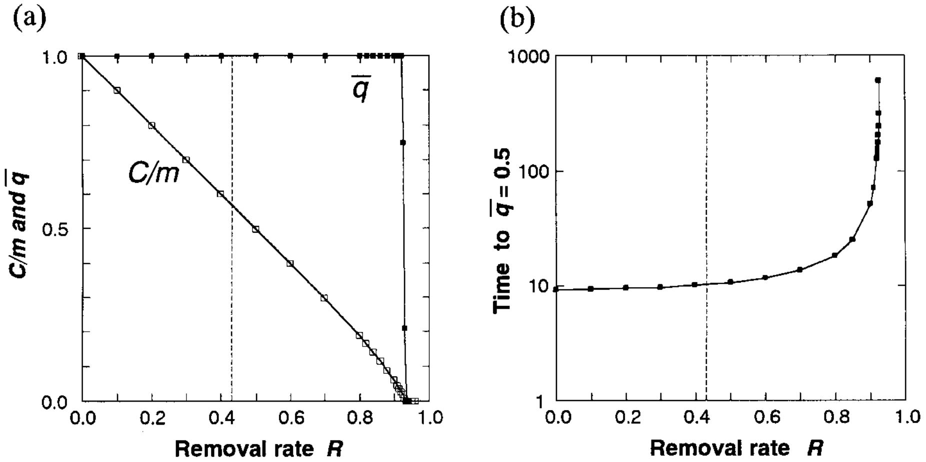


Figure 3. Effect of random removal of bean weevil adults on (a) the evolutionarily stable fraction of the contest type and (b) the time (the number of generations, in log scale) required for $\bar{q}$ to reach 0.5 (Equation 9). The broken lines show the estimated removal rate caused by parasitoid attack in the experimental host–parasitoid system for days 60–390.

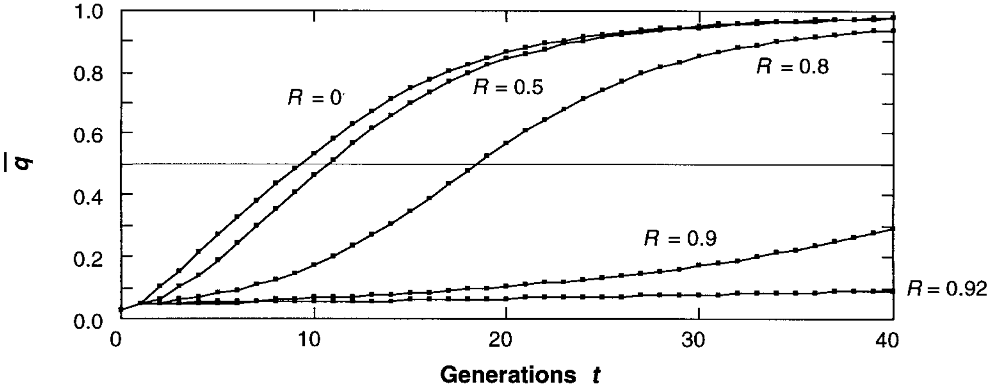


Figure 4. Simulated dynamics of $\bar{q}$ for different values of R. A high random removal rate R slows the rate of increase in $\bar{q}$, especially during the early phase of the increase (Equation 9; see also Fig. 3b).

Parasitoid–host interaction

Now we consider host evolution in the presence of parasitoids that attack hosts. The parasitoid causes an additional mortality to the host population and thus works in a way similar to random removal. We would expect the presence of parasitoids to cause a slower evolution of contest-type competition in hosts. In addition, parasitoid population dynamics are coupled with those of host population dynamics to cause limit cycle oscillations or chaotic fluctuations, rather than just a stable equilibrium, and these dynamical behaviours can also be modified by host evolution.

We assume that parasitoids attack hosts randomly, and irrespective of the competition types. Hence, the number of the i-th genotype hosts in the next generation is expressed in a simple Nicholson-Bailey form:

$$x_{i,t+1} = x_{i,t}\{q_i w_C(C_t) + (1 - q_i) w_N(C_t, N_t)\} e^{-f(P_t)} \tag{10}$$

where $e^{-f(P_t)}$ is the escape rate of the host from parasitism and

$$f(P_t) = aP_t \tag{11}$$

Note that we can derive Equation (10) from Equation (9) simply by replacing $(1 - R)$ with $e^{-f(P_t)}$.

We assume that parasitoids attack hosts only after the completion of larval competition. Thus the number of parasitoids in the next generation is:

$$P_{t+1} = s_P(1 - e^{-f(P_t)})H_{t+1} \tag{12}$$

where s_P is the survivorship of the parasitoid larvae and H_{t+1} is the total number of vulnerable hosts that survive competition. H_{t+1} is equal to the total number of adults at time $t + 1$ prior to the stage vulnerable to parasitoids.

Although parasitoid attack slows down evolution towards the contest type, the contest type reaches a high fraction after 40 generations (in contrast to 20 generations without parasitoids) if all the other parameters are the same (Fig. 5b). In the absence of the contest type, the host and parasitoid populations show unstable dynamics (Fig. 5a), while the contest-type-only population stabilizes after short transients (Fig. 5c). The increase in the average fraction of the contest type is accompanied by the stabilization of population dynamics of both host and parasitoid.

Alternative timing of parasitization and the two modes of competition

The above analysis assumes that scramble-type and contest-type competition occur simultaneously. However, scramble-type competition is likely to occur at a later developmental stage than contest-type competition, rather than vice versa, because larval contest competition occurs in the early stages before resources are depleted (Utida, 1975; Tuda, in press). In addition, in experimental systems, parasitism is likely to occur just before scramble-type competition. We next assume that the parasitoid attacks host larvae at the stage after contest competition but before scramble competition. This modification leads to the following equations, instead of Equation (12):

$$P_{t+1} = s_P(1 - \mathrm{e}^{-f(P_t)})\tilde{H}_{t+1} \tag{13a}$$

where $\tilde{H}$ is the number of vulnerable larvae. However, the definition of vulnerable larvae is now contest-type larvae surviving competition and scramble-type larvae after suffering contest competition but before scramble competition takes place:

$$\tilde{H} = \sum_{i=1}^{n} x_{i,t}\{q_i w_C(C_t) + (1 - q_i)\lambda h_N \mathrm{e}^{-h_C C_t/m}\} \tag{13b}$$

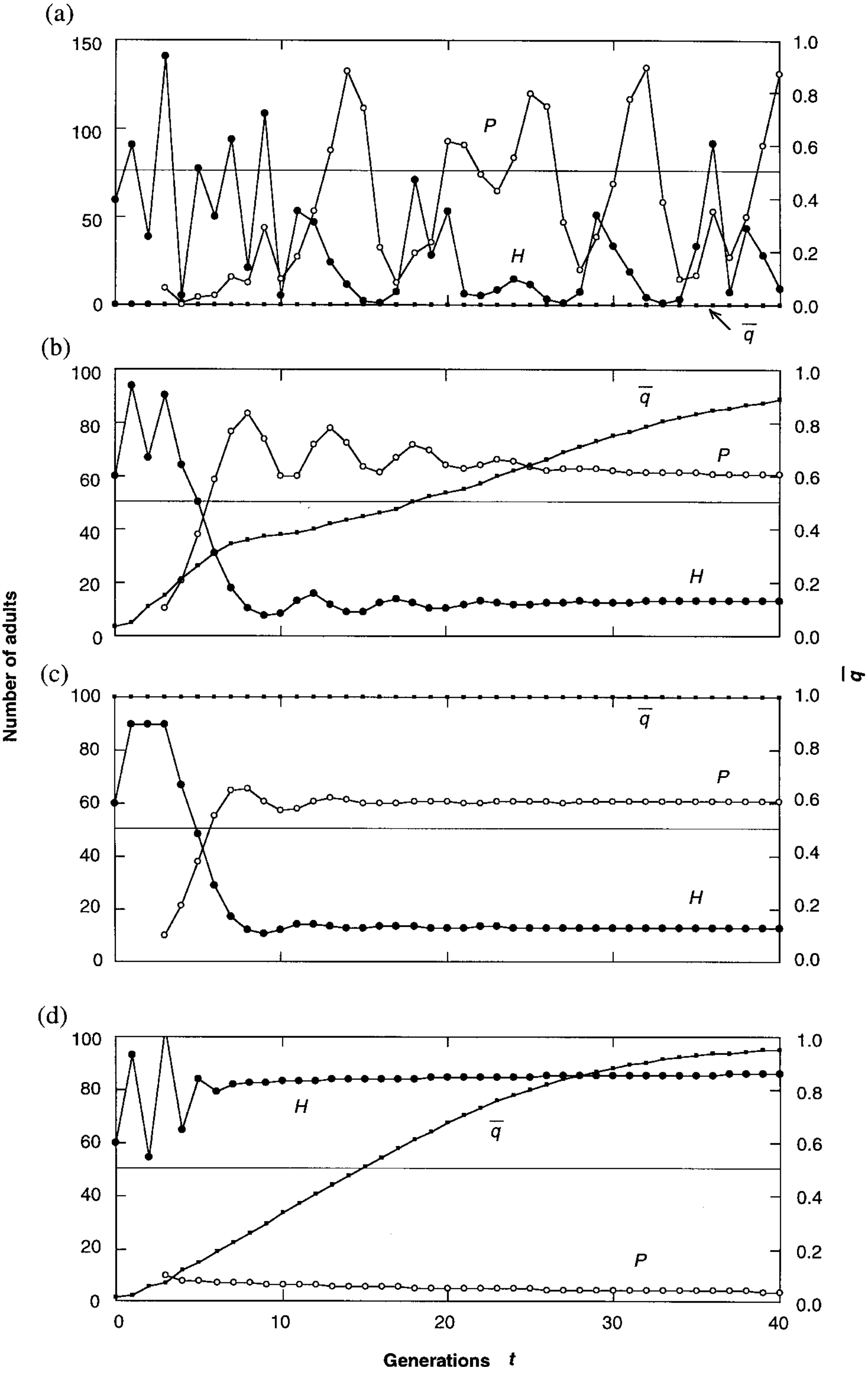
Parasitoid abundance increases by attacking abundant scramble-type larvae just before, rather than after, the scramble competition that reduces their number (Fig. 6). High parasitoid densities slow down the evolution of the contest type, given that the parameter values are the same as those applied in the previous section. This enables even smaller values of a or initial $\bar{q}$ to generate a few large oscillations before the evolution of the contest type stabilizes the dynamics. The smaller a lowers the parasitoid equilibrium density, while raising that of the host (Figs 5d and 6).

Size of beans

As shown earlier, a large random removal of hosts in the procedures maintaining the stock culture population may in principle explain why the initial host population was composed predominantly of scramble types. However, for this to hold in the basic model analysed, the removal rate must be within a very limited range. The removal rate during culture storage was approximately 0.8, which is not consistent with the pure random removal explaining the initial scramble population. In this section, we focus on the possible role of the difference in size of the beans in the stock culture and those used in the experiment.

Contest and scramble types differ with respect to their spatial feeding site within a bean: contest-type larvae feed at the centre of beans but scramble-type larvae feed at the periphery of beans (Umeya *et al.*, 1975). Let k be the relative size of beans used in the stock culture to those used in the experiment, which is larger than 1 ($k > 1$). Since contest-type larvae attempt to occupy the central part of the bean, they compete among themselves; the remaining peripheral part, with volume $(k - 1)$, will be available for the scramble-type larvae. Thus, in a large bean, some scramble-type larvae can survive when a contest-type larva is present. In beans without contest-type larvae, the whole of the bean will be used by scramble-type larvae.

The fitness of the contest type is the same as before and given by Equation (3). The density of scramble-type larvae per bean is y/k; hence the density-dependent survival and size-dependent fecundity becomes $\mathrm{e}^{-\beta(y/k-1)}$, where k is the relative size of beans, y is the number of scramble-type larvae per bean, and β is the strength of scramble competition as before. The fitness of the scramble-type larvae feeding on beans of size k is:


(a)
(b)
(c)
(d)
P
H
q̄
Number of adults
q̄
Generations t
150
100
50
0
80
60
40
20
1.0
0.8
0.6
0.4
0.2
0.0
10
30
40

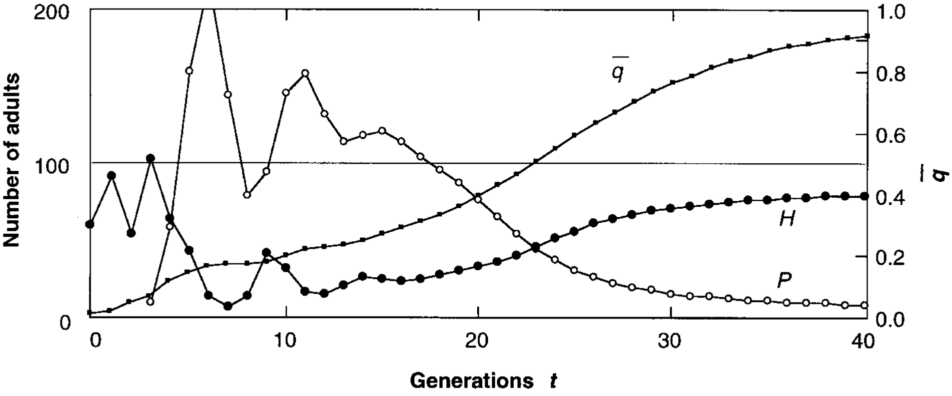


Figure 6. Effect of different relative timings of competition to parasitism between the contest and scramble types on the population dynamics (*H* and *P*) and the average fraction of the contest type ($\bar{q}$) (Equations 10 and 13). The parameter values are those in Fig. 2 for the host and $a = 0.0125$ and $s_P = 0.9$ for the parasitoid. Initial $\bar{q} = 0.014$.

$$\begin{aligned}\tilde{w}_N(C,N) &= \lambda h_N[\mathrm{e}^{-h_C C/m}\exp\{-h_N(1-\mathrm{e}^{-\beta/k})N/m+\beta(k-1)/k\} \\ &\quad + (1-\mathrm{e}^{-h_C C/m})\exp\{-h_N(1-\mathrm{e}^{-\beta/(k-1)})N/m+\beta(k-2)/(k-1)\}]\end{aligned} \qquad (14)$$

The first term shows competition among the scramble-type individuals only and can be derived in the same way as Equation (4) with a modified density of scramble-type larvae. It is equivalent to Equation (4) when $k = 1$. The second term describes scramble competition over the remaining bean content, with volume $(k - 1)$, in beans with a contest-type larva occupying the central volume. The expected fraction of the scramble type is simply the same as the first term with k replaced by $k - 1$. Based on the competition curve measured for the scramble-type *C. maculatus* feeding on either small or large mung beans (Toquenaga and Fujii, 1991), the parameter β was estimated, which did not change with k.

Figure 7 shows the results of the analysis using Equations (4), (9) and (14) with different random removal rates R. The average fraction of the contest type is reduced as k increases because it increases the size of the refuge for scramble-type larvae. Compared to the cases with $k = 1$, it is much easier for both types to co-exist in the population and also there is a relatively broad range of removal rate R that allows the scramble type to dominate in the evolutionarily stable population. This effect outweighs that of adult removal unless the removal rate is extremely high.

Discussion

Our model shows that, in the absence of the parasitoid, the bean weevil population with an initial high fraction of the scramble type becomes rapidly dominated by the contest type (Fig. 2). This

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Figure 5. Effect of random attack by parasitoids on the evolutionary changes in the population dynamics (*H* and *P*) and the average fraction of the contest type ($\bar{q}$) (Equations 10 and 12). (a) A scramble-type-only population; (b) a mixed population of the two competition types, with the initial $\bar{q} = 0.03$; and (c) a contest-type-only population. The parameter values are those in Fig. 2 for the host and $a = 0.03$ and $s_P = 0.9$ for the parasitoid. (d) A mixed population of the two competition types, with initial $\bar{q} = 0.014$ and $a = 0.0125$.

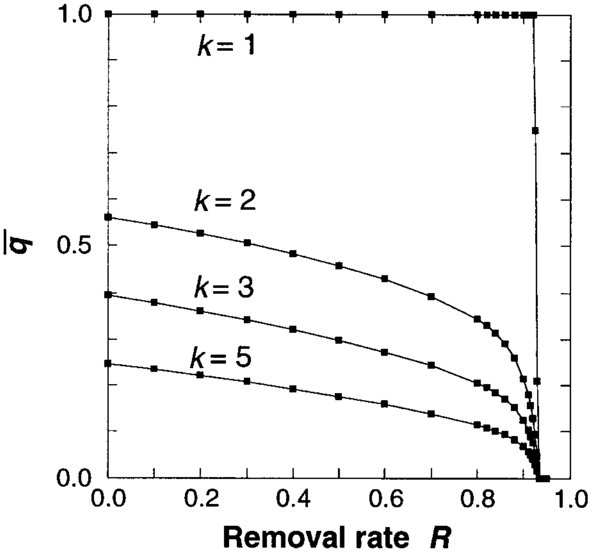

Figure 7. Effects of bean size and random removal rate on the evolutionarily stable fraction of the contest type (Equation 14).

explains the results of experiments on a single-species *C. maculatus* population by Toquenaga *et al.* (1994), in which, however, competition type was distinguished based on the resemblance of dynamical trajectories and not on the observation of competition outcome in a single bean. 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. Toquenaga *et al.* (1994) developed a genetic algorithm model, assuming additive genetics, which exhibited a gradual increase in the average fraction of the contest type; this parallels the result shown in Fig. 2 of our simple one-locus haploid genetic model.

If the parasitoid has a mildly high attack rate, the introduction of a parasitoid does not affect the direction of the selection pressure working on the larval competition type (Fig. 3). However, both the parasitoid and random removal of host adults slow down evolution towards contest-type larvae (Figs 4 and 5b, in contrast to Fig. 2).

In our basic model (up to Equation 12), evolution of the host towards contest competition stabilizes – otherwise, there will be unstable oscillations of the host and parasitoid – and this is consistent with the reduced oscillations in the experimental system (Fig. 1). However, the basic model did not explain the following two characteristics of the observed dynamics: (1) the dominance of the scramble type in the founder population derived from the stock culture, and (2) the drastic reduction in the initially high density of the parasitoid (Fig. 1).

The first point stems from Fig. 3, which suggests that the fixation of the contest type is the likely outcome at all but high removal rates. This is because one individual of the contest type is enough to exclude the scramble type at each bean of small size (i.e. $k = 1$). With larger beans, however, scramble-type individuals survive competition with contest-type individuals because of refuge from the contest type at the periphery of beans (Fig. 7). Using this modification, we can overcome the first problem. In fact, the stock population was maintained in beans about three times larger in volume than those used in the experiment. Smith and Lessells (1985) incorporated the bean size difference into a model for competition among bean weevils in terms of differential encounter rate of larvae within a bean. We, however, chose not to use this formalism because, at present, the encounter rates of individual larvae of the two competition types inside beans are extremely difficult to measure, not only because they are morphologically indistinguishable but also because opening beans inevitably kills the developing larvae (Tuda, 1995).

For the second point, we considered an alternative temporal order of competition and parasitism. Indeed, if scramble competition occurs later than parasitism, the initial densities of the parasitoid become much higher and evolution towards contest types brings the population to an equilibrium which can be much lower than the initial densities depending on the values of a (Fig. 6, in contrast to Fig. 5d). Theoretical studies have suggested that density-dependent mortality that occurs before random parasitism is more stabilizing than when it occurs later (Smith and Mead, 1974; May *et al.*, 1981). Therefore, if evolution from the scramble type to the contest type is accompanied by a shift of the temporal order of competition and random parasitism, the stabilization effect of contest competition is two-fold, compared to scramble competition. The present study also shows that, during the course of evolution and transients, the change in the temporal order of interactions can produce even greater variety of dynamics than suggested theoretically (Fig. 6).

Although our model assumed a density-independent fecundity (λ), a scramble-type individual from a crowded bean normally has a smaller body size and a smaller fecundity than λ, the fecundity of an adult grown singly. A parasitoid emerging from a smaller host also has a smaller fecundity than a parasitoid from a host grown singly. When density-dependent fecundity is important, we can still use the same model if the combined effect of density-dependent larval survivorship and density-dependent fecundity are expressed as $\lambda e^{-\beta(y-1)}$, and if the fecundity of a parasitoid from the host is proportional to the same factor. We simply need to regard $x_{i,t}$ as the effective number of adults of genotype i, defined as the number of eggs of genotype i divided by maximum fecundity λ, and H as the total effective number of adults. In fact, β in Table 1 was estimated from experiments considering the combined effect of density-dependent fecundity and density-dependent larval survivorship.

The possibility of parasitoid evolution, which was not examined in the present paper, is a process that might, in principle, explain the change in the dynamics. However, we believe that it is less likely to be important than host evolution, because the genetic variability in the laboratory parasitoid population is likely to have decreased to a minimal level, as the population has been cultured over 50 years since Professor Syunro Utida's time. The host, on the other hand, had been kept for 2 years only in the laboratory. This reminds us of the gradual reduction in the parasitoid density in Utida's host–parasitoid system. As stated above, however, laboratory populations kept for generations also have less tendency to evolve (Sait *et al.*, 1994; M. Boots, personal communication). In this sense, the population of *H. prosopidis*, in its early laboratory history, may still have retained a potential to evolve as Utida suggested (Utida, 1957).

We conclude that the evolution of the contest-type host explains both the stabilization of the population dynamics and the reduction in the parasitoid population size, which subsequently changed the host–parasitoid interaction. Analyses of other long-term laboratory time-series data, such as those of Utida, will improve our understanding of the evolution of interacting species.

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References

Iwasa, Y., Pomiankowski, A. and Nee, S. (1991) The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution* **45**, 1431–1442.

May, R.M., Hassell, M.P., Anderson, R.M. and Tonkyn, D.W. (1981) Density dependence in host–parasitoid models. *J. Anim. Ecol.* **50**, 855–865.

Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Nicholson, A.J. (1957) The self-adjustment of populations to change. *Cold Spring Harbor Symp. Quant. Biol.* **22**, 153–173.

Pimentel, D. and Stone, F.A. (1968) Evolution and population ecology of parasite–host systems. *Can. Ent.* **100**, 655–662.

Pimentel, D., Nagel, W.P. and Madden, J.L. (1963) Space–time structure of the environment and the survival of parasite–host systems. *Am. Nat.* **97**, 141–167.

Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan, New York.

Sait, S.M., Begon, M. and Thompson, D.J. (1994) Long-term population dynamics of the Indian meal moth *Plodia interpunctella* and its granulosis virus. *J. Anim. Ecol.* **63**, 861–870.

Smith, R.H. and Lessells, C.M. (1985) Oviposition, ovicide and larval competition in granivorous insects. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (R.M. Sibly and R.H. Smith, eds), pp. 423–484. Blackwell, Oxford.

Smith, R.H. and Mead, R. (1974) Age structure and stability in models of prey–predator systems. *Theor. Popul. Biol.* **6**, 308–322.

Stokes, T.K., Gurney, W.S.C., Nisbet, R.M. and Blythe, S.P. (1988) Parameter evolution in a laboratory insect population. *Theor. Popul. Biol.* **34**, 248–265.

Toquenaga, Y. (1993) Contest and scramble competitions in *Callosobruchus maculatus* (Coleoptera: Bruchidae). II. Larval competition and interference mechanisms. *Res. Popul. Ecol.* **35**, 57–68.

Toquenaga, Y. and Fujii, K. (1991) Contest and scramble competitions in *Callosobruchus maculatus* (Coleoptera: Bruchidae). I. Larval competition curves and resource sharing patterns. *Res. Popul. Ecol.* **33**, 199–211.

Toquenaga, Y., Ichinose, M., Hoshino, T. and Fujii, K. (1994) Contest and scramble competitions in an artificial world: Genetic analysis with GA. In *Artificial Life III* (C.G. Langton, ed.), pp. 177–199. Addison-Wesley, Reading, MA.

Tuda, M. (1995) Spatio-temporal population structures and host–parasitoid system dynamics. PhD thesis, University of Tokyo.

Tuda, M. (1996) Temporal/spatial structure and the dynamical property of laboratory host–parasitoid systems. *Res. Popul. Ecol.* **38**, 133–140.

Tuda, M. (in press) Evolutionary character changes and population responses in an insect host–parasitoid experimental system. *Res. Popul. Ecol.*

Umeya, K., Kato, T. and Kocha, T. (1975) Studies on the comparative ecology of bean weevils. VI. Intraspecific larval competition in *Callosobruchus analis* (F.). *Jap. J. Appl. Ent. Zool.* **19**, 47–53.

Utida, S. (1957) Cyclic fluctuations of population density intrinsic to the host–parasite system. *Ecology* **38**, 442–449.

Utida, S. (1975) *Animal Population Ecology* (in Japanese). Kyoritsu, Tokyo.

Appendix 1

The dynamics of genotypes given by Equation (5) include both the dynamics of total population size $\sum_{i=1}^{n} x_{i,t}$ and the evolutionary dynamics of average trait $\overline{q}$, as is common to other density-dependent natural selection models (e.g. Roughgarden, 1979).

First, we note that the sum of Equation (5) over different i is:

$$\sum_{i=1}^{n} x_{i,t+1} = \sum_{i=1}^{n} (q_i w_C + (1 - q_i) w_N) x_{i,t}$$

$$= \sum_{i=1}^{n} x_{i,t} (\overline{q} w_C + (1 - \overline{q}) w_N) \tag{A1}$$

At the population dynamic equilibria, $\sum_{i=1}^{n} x_{i,t+1} = \sum_{i=1}^{n} x_{i,t}$ holds and Equation (A1) becomes:

$$1 = \overline{q} w_C + (1 - \overline{q}) w_N \tag{A2}$$

which indicates that the average fitness must be equal to 1 at the population dynamic equilibrium.

Second, straightforward calculation from Equation (5) shows that the one-generation change in the average fraction of contest type $\overline{q}$, defined as Equation (1b), is:

$$\Delta \overline{q} = \frac{\mathrm{var}(q)}{\overline{w}} (w_C(C_t) - w_N(C_t, N_t)) \tag{A3a}$$

where $\mathrm{var}(q)$ is the additive genetic variance of contest type fraction q and $\overline{w}$ is the average fitness:

$$\mathrm{var}(q) = \sum q_i^2 x_i \Big/ \sum x_i - \overline{q}^2 \tag{A3b}$$

$$\overline{w} = \sum_{i=1}^{n} (q_i w_C + (1 - q_i) w_N) x_i \Big/ \sum_{i=1}^{n} x_i \tag{A3c}$$

Equation (A3a) suggests to us that, as long as some additive genetic variance remains in the population ($\mathrm{var}(q) > 0$), the average fraction of the contest type tends to evolve to realize:

$$w_C(C_t) = w_N(C_t, N_t) \tag{A4}$$

if the evolutionarily stable $\bar{q}$ is an intermediate value ($0 < \bar{q} < 1$). Then, Equations (A2) and (A4) give Equation (6a) in the text.

On the other hand, if the final $\overline{q}$ is the lowest possible value ($\overline{q} = 0$), the evolutionary stability requires natural selection not to favour the increase in $\overline{q}$. From Equation (A3a), this becomes Equation (6b) in the text. A similar consideration suggests the condition in Equation (6c) when $\bar{q} = 1$ is evolutionarily stable.

Appendix 2

Random removal of the host

If the host is randomly removed at rate R, Equation (6a) becomes:

$$w_C(C^*) = w_N(C^*, N^*) = 1/(1 - R) \tag{B1}$$

From Equation (3), a numerical solution for C^* is obtained by solving:

$$\lambda m (1 - \mathrm{e}^{-h_C C^*/m})(1 - R) - C^* = 0 \tag{B2a}$$

Replacing Equation (4) we obtain:

$$N^* = (m \ln \lambda h_N (1 - R) - h_C C^*) / \{h_N (1 - \mathrm{e}^{-\beta})\} \tag{B2b}$$

The conditions for two competition types to co-exist are:

$$\lambda h_C(1-R) > 1 \qquad \lambda h_N(1-R) > 1 \qquad m \ln \lambda h_N(1-R) > h_C C^* \tag{B3}$$

Parasitoid–host interaction

The equilibrium population size of the parasitoid is obtained from Equations (9) and (10) under the condition of Equation (A1) with $1 - R = \exp(-aP_{t+1})$ and

$$P_{t+1} = P_t \tag{B4}$$

where P_{t+1} is given by Equation (12).

With the estimated parameter values, simulations of the model show that 40 generations may not be long enough for the host and parasitoid populations to reach equilibrium.