The Effect of Evolution on Host–Parasitoid Systems

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It is well known that a simple first-order difference equation can exhibit complex population dynamics, such as sustained oscillations and chaos. An interesting problem is whether such oscillatory dynamics are expected to occur in real populations. This paper assumes that the resident system is composed of 1-host and 1-parasitoid and that only the host is allowed to evolve, but not the parasitoid. Based on the invasibility of a host to host–parasitoid systems, we investigate the dynamics of the host–parasitoid system favored by natural selection. We consider two cases. In the first case, the host's evolution involving both the intrinsic growth rate and the sensitivity to density is considered. In the second case, the host's evolution involving both the intrinsic growth rate and the vulnerability to the parasitoid is considered. In both cases, we see that the dynamics with a stable equilibrium will not be favored by natural selection without the trade-off between the host's traits which are allowed to evolve. The host–parasitoid system with a stable equilibrium will be eventually invaded by a host type that develops an unstable equilibrium with the parasitoid. If there is a trade-off between the host's traits which are allowed to evolve, a host–parasitoid system with a stable equilibrium can be favored by natural selection.

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1. Introduction

Many previous works show that some population models can have very complex dynamics, namely sustained oscillations and chaos. In particular, such complex dynamics are easily found in discrete-time density-dependent models even if their dimension is low. For example, May & Oster (1976) investigated such a population model and showed that it has three regimes of dynamic solution specified in its parameter space, namely a stable equilibrium, a stable cycle and chaos. An interesting problem is whether the combinations of parameters that exhibit these oscillatory dynamics are expected to occur in real populations.

A natural ecosystem is by no means arbitrary, because it is the result of a long evolutionary process. Therefore, the distribution of demographic parameters corresponding to real populations can be expected by a theory of evolution. This means that investigations into the dynamics favored by natural selection are important to consider the possibility that oscillatory dynamics occur in real populations.

In this paper, we investigate the dynamics favored by natural selection in host–parasitoid systems. The effect of evolution on a single-species model, which is the simplest population model, has been investigated in some literature (see Godfray *et al.*, 1991; Metz *et al.*, 1992; Gatto, 1993). From these studies, it is proved that we cannot simply conclude that either a stable or an oscillatory dynamics is favored by natural

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selection if no constraint of model parameters is assumed [but see Doebeli (1995), which considered the evolution leading the chaotic system to the stable one]. To extend these studies, we investigate the effect of evolution of a host on a host–parasitoid system because it is one of the simplest multi-species systems. The host–parasitoid model used in this paper is an extension of Gatto's (1993) model for host dynamics.

Evolution in a two-species system has also been examined. For instance, Hochberg & Holt (1995) examined the evolution of refuges for hosts in host–parasitoid systems. They used the discrete-time model as we use, but the model is different from the one developed in this paper. Abrams & Matsuda (1997) examined the evolution of the prey's intrinsic growth rate and vulnerability to the predator in a prey–predator system, whose dynamics obey differential equations. These studies show that evolution has an important influence on the stability of a population dynamics.

This paper is organized as follows. In Section 2, we introduce a simple host–parasitoid system without mutant hosts and investigate the stability of the system. This stability analysis gives a parameter space demarcated with dynamical properties of the host–parasitoid model, which is necessary to discuss the evolution of host's demographic parameters. In Section 3, we introduce a model describing the interaction between two hosts and one parasitoid (2-host 1-parasitoid model). This model gives a population-dynamics in the case where a mutant host appears in a resident host–parasitoid system. By analyzing this three-species model, we obtain the invasibility of the mutant to the resident system. In Section 4, we investigate the dynamics of the host–parasitoid system favored by natural selection by using the results obtained in the previous sections. The final section includes discussions. Some proofs of mathematical properties are given in the appendices.

2. Host–Parasitoid Model

In this section, we introduce a simple host–parasitoid model without mutant hosts and investigate its stability. The generalized host–parasitoid model is given as follows (see Hassell, 1978):

$$u(n + 1) = ru(n)g[u(n)]f[u(n), v(n)],$$
$$v(n + 1) = bu(n)(1 - f[u(n), v(n)]),$$

where $u(n)$ and $v(n)$ are the population densities of the host and the parasitoid, respectively, in generation n, the parameters r and b are the intrinsic growth rate of the host and the number of parasitoids emerging from each parasitized host, respectively, and the functions g and f define the density dependence in the host population growth and the fraction of hosts escaping parasitism, respectively. Note that in this model the density dependence in the host population is assumed to act on the hosts regardless of whether they were parasitized, after the parasitism. That is, g is a function of $u(n)$ not of $u(n)f[u(n), v(n)]$. Other orderings of the density dependence in the host's life cycle are possible (see e.g. Hochberg & Holt, 1995).

Although there are a number of forms for expressing the density dependence (see May & Oster, 1976), we use the following function, which is used in a Ricker model, in order to compare the results obtained by Gatto (1993) and the one obtained in this paper:

$$g[u] = \exp[-\mu u],$$

where μ represents sensitivity of hosts to their density. Similarly, various functions f have been used in ecology (see e.g. May, 1978; Kaitala et al., 1999). In this paper, according to a Nicholson–Bailey model we use the following function:

$$f[u, v] = \exp[-av],$$

where a is the per capita parasitoid attack rate. This fraction is given on the assumption that the parasitoids are distributed randomly among the available host and have a linear functional response.

Substituting the above f and g into the generalized host–parasitoid model, we obtain the following specific host–parasitoid model:

$$u(n + 1) = ru(n)\exp[-\mu u(n)]\exp[-av(n)],$$
$$v(n + 1) = bu(n)(1 - \exp[-av(n)]),$$

(1)

where the parameters r, μ, a and b are positive constants. This model in the absence of the parasitoid ($v(n) = 0$) is reduced to the Ricker model,

whose dynamics was investigated by May & Oster (1976). Beddington *et al.* (1975) carried out a local stability analysis of a positive equilibrium of model (1), and showed that its dynamics indicates a periodic or chaotic oscillation according to the values of the parameters. Hereafter, we show that model (1) exhibits a complicated dynamics and present the stability conditions of its equilibria in the parameter space.

Model (1) can have three nonnegative equilibrium points,

$$E_{00} = (0, 0), \quad E_{+0} = \left(\frac{\ln r}{\mu}, 0\right)$$

$$\text{and} \quad E_{++} = (u^*, v^*),$$

where (u^*, v^*) is a positive root of the following equations:

$$u^* = \begin{cases} \dfrac{v^*}{b(1 - \exp[-av^*])}, \\ \dfrac{\ln r - av^*}{\mu}, \end{cases} \tag{2}$$

which is given by setting $u(n + 1) = u(n) = u^*$, $v(n + 1) = v(n) = v^*$ in eqn (1) and assuming $u^* > 0, v^* > 0$. The value of this positive equilibrium cannot be obtained explicitly.

The point E_{00} always exists. The point E_{+0} exists if and only if $\ln r > 0$. The point E_{++} exists if and only if $\ln r/\mu > 1/(ab)$ because of the following properties of the function $(x/\{b(1 - \exp[-ax])\}) - (\ln r - ax)/\mu$:

$$\frac{\mathrm{d}}{\mathrm{d}x}\left(\frac{x}{b(1 - \exp[-ax])} - \frac{\ln r - ax}{\mu}\right)$$

$$= \frac{1 - (1 + ax)\exp[-ax]}{b(1 - \exp[-ax])^2} + \frac{a}{\mu} > 0 \quad \text{for} \quad x > 0,$$

$$\lim_{x \to 0}\left[\frac{x}{b(1 - \exp[-ax])} - \frac{\ln r - ax}{\mu}\right] = \frac{1}{ab} - \frac{\ln r}{\mu},$$

$$\lim_{x \to \infty}\left[\frac{x}{b(1 - \exp[-ax])} - \frac{\ln r - ax}{\mu}\right] = \infty.$$

This shows that two curves given by eqn (2) intersect in the first quadrant of (u, v) plane if and only if $\ln r/\mu > 1/(ab)$ (see Fig. 1).

We now consider the local stability of the equilibria. The local stability properties are elucidated by linearizing equation (1) about the equilibrium. The point E_{00} is locally stable if $\ln r < 0$. The point E_{+0} is locally stable if $0 < \ln r < 2$ and $0 < \ln r < \mu/(ab)$. The point E_{++} is locally stable if $|\lambda_1| < 1$ and $|\lambda_2| < 1$, where λ_1 and λ_2 are the roots of the following characteristic equation:

$$\lambda^2 - (1 - \ln r + abu^*)\lambda$$

$$+ u^*\{ab - (\mu + ab)\mu u^* + \mu \ln r\} = 0.$$

Summarizing the above results leads to the following table.

	$\ln r < 0$	$0 < \ln r < \mu/(ab)$	$\mu/(ab) < \ln r$
E_{00}	Stable	Unstable	Unstable
E_{+0}	Does not exist	Stable if $\ln r < 2$	Unstable
E_{++}	Does not exist	Does not exist	Stable if $|\lambda_1| < 1$ and $|\lambda_2| < 1$

As described in Beddington *et al.* (1975), we can investigate the stability of the point E_{++} by using the Schur–Cohn criterion (see Kocic & Ladas, 1993) and the Routh–Hurwitz criterion. From these analyses we can obtain the region in which the positive equilibrium of this model is stable (see Fig. 2). This region [(S2)i in Fig. 2] is enclosed by two curves, which can be obtained numerically, and the line that corresponds to the boundary of the condition for the existence of the positive equilibrium ($\ln r/\mu > 1/(ab)$) (see Appendix A).

Model (1) exhibits a complicated dynamics when the positive equilibrium is unstable (see Beddington *et al.*, 1975). A bifurcation diagram of model (1) is shown in Fig. 3. From Fig. 3 we see
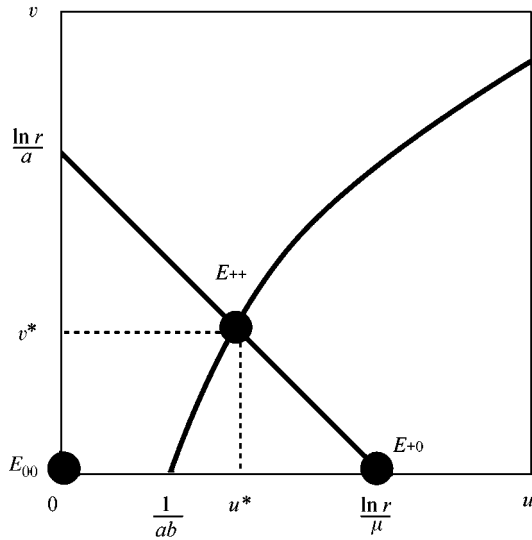
FIG. 1. The null clines for system (1). Each dot represents the equilibrium point of system (1). The curve and the straight line represent the first and the second equations of eqn (2), respectively.
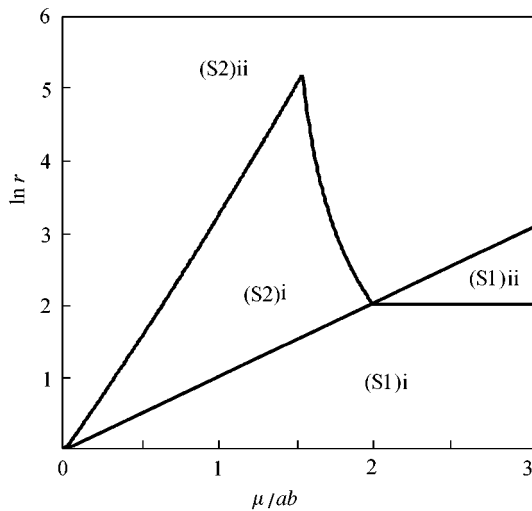

FIG. 2. The $\mu/(ab)$-$\ln r$ parameter space demarcated with the stability properties of model (1). The solid lines demarcate regions of the parameter space with different stability properties. Since $\ln r > 0$, the point E_{00} is always unstable. (S1)i: Model (1) does not have a positive equilibrium and the boundary equilibrium E_{+0} is stable, (S1)ii: Model (1) does not have a positive equilibrium and the point E_{+0} is unstable, (S2)i: Model (1) has a stable positive equilibrium, (S2)ii: Model (1) has an unstable positive equilibrium. The parasitoid can go to extinction with the large r (see Fig. 3).

that when the positive equilibrium of model (1) is unstable [the parameters belong to (S2)ii in Fig. 2], it usually exhibits sustained oscillations and chaos. Note that if the positive equilibrium is
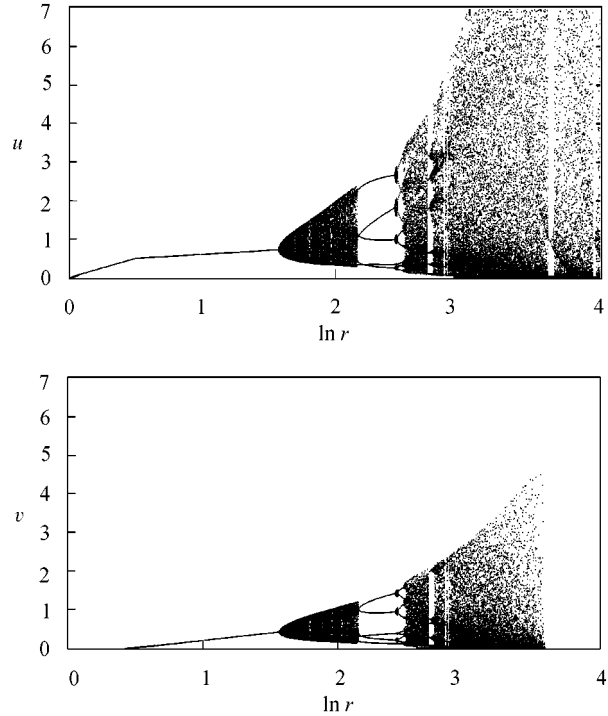

FIG. 3. The bifurcation diagram of system (1) (with respect to the parameter r) when $\mu = 1$, $a = 2$ and $b = 1$. The dynamics of model (1) for increasing values of $\ln r$ ($\ln r = 0 \sim 4$) shifts from a stable equilibrium to sustained oscillations and to chaos. At the higher r, note that the parasitoid goes to extinction.

unstable, the host and the parasitoid do not always coexist with sustained oscillations or chaos but it is possible that the parasitoid becomes extinct (see the lower picture of Fig. 3). In fact, the periodic orbits on the u-axis can be stable even if model (1) has a positive equilibrium. This means that model (1) is not always permanent, which ensures the coexistence of the host and the parasitoid for a long time, even if it has a positive equilibrium [see Kon & Takeuchi, preprint-a].

3. Competition Model (2-Host 1-Parasitoid)

In this section, we introduce a 2-host 1-parasitoid model which describes an interaction between the resident host–parasitoid system and the mutant host.

We use the following 2-host 1-parasitoid model:

$$u_1(n + 1) = r_1 u_1(n) \exp[-\mu_1(u_1(n)$$

$$+ u_2(n))] \exp[-a_1 v(n)],$$

$$v(n + 1) = \sum_{i=1}^{2} b_i u_i(n)(1 - \exp[-a_i v(n)]), \quad (3)$$

$$u_2(n + 1) = r_2 u_2(n) \exp[-\mu_2(u_1(n)$$

$$+ u_2(n))] \exp[-a_2 v(n)],$$

where u_1 is a resident, u_2 is an invader and the subscripts 1 and 2 to the symbols (μ, r, a, b) indicate the type of the hosts. The competitive ability of each type of the hosts is identified by the pair (μ, r, a, b). Note that the dynamics of model (3) in the absence of the parasitoid ($v(n) = 0$) was investigated by Gatto (1993) and the one in the absence of one host ($u_2(n) = 0$) was investigated by Beddington *et al.* (1975) [model (1)]. Model (3), which is an exploitative competition model, is the special case of the model which was investigated by Comins & Hassell (1976). They considered the effect of a top predator on the stability of a system of competing prey species and showed that predators enhance prey species diversity.

When the resident system (u_1, v) [described by (1) with $u = u_1$, $\mu = \mu_1$, $r = r_1$, $a = a_1$ and $b = b_1$] has a stable cycle (equilibrium or sustained oscillation) of period m, the criterion for invasibility of u_2 to this resident system is given as follows:

$$\ln r_2 > \frac{\sum_{i=1}^{m} u_1(i)}{m} \mu_2 + \frac{\sum_{i=1}^{m} v(i)}{m} a_2, \quad (4)$$

where $\{(u_1(i), v(i))\}_{i=1,\ldots,m}$ is the periodic orbit of period m of the resident system and satisfies the following equation:

$$\ln r_1 = \frac{\sum_{i=1}^{m} u_1(i)}{m} \mu_1 + \frac{\sum_{i=1}^{m} v(i)}{m} a_1, \quad (5)$$

(see Appendix B and Kon & Takeuchi, preprint-b). This criterion for invasibility is given by the instability to the u_2-direction of the periodic orbit $\{(u_1(i), v(i), 0)\}_{i=1,\ldots,m}$ in the phase space (u_1, v, u_2). When the parameter (μ_2, r_2, a_2, b_2) satisfies eqn (4), the host u_2 can invade the resident system (u_1, v). The boundary of the invasibility to the system (u_1, v) is given by

$$\ln r_2 = \frac{\sum_{i=1}^{m} u_1(i)}{m} \mu_2 + \frac{\sum_{i=1}^{m} v(i)}{m} a_2. \quad (6)$$

Criterion (4) is identical with the following equation when $v(i) = 0$, ($i = 1, 2, \ldots, m$) (which means the absence of the parasitoid):

$$\frac{\ln r_2}{\mu_2} > \frac{\ln r_1}{\mu_1}, \quad (7)$$

which is given by Gatto (1993).

4. Evolution of Host

By using the results obtained in Sections 2 and 3, we investigate the host–parasitoid system favored by natural selection.

First, we consider the case where the resident system (u_1, v) does not have a positive equilibrium. From the discussion in Section 2, the parameters of this resident system belong to the region (S1)i or (S1)ii in Fig. 2, that is, they satisfy the condition $\ln r_1/\mu_1 < 1/(a_1 b_1)$. From numerical investigations (see e.g. the population density of the parasitoid with the parameter $\ln r = 0 \sim 0.5$ in Fig. 3), it is expected that the parasitoid in this resident system always goes to extinction, so that we assume that in this case the parasitoid goes to extinction. From this assumption, the criterion for invasibility of the host to the resident system (u_1, v) is given by eqn (7). Note that it does not depend on the parameters a_i and b_i ($i = 1, 2$). Criterion (7) means that the host with a higher carrying capacity ($\ln r_i/\mu_i$) can invade the resident system and replace the resident host. If there is no constraint on the parameters, the carrying capacity of the resident host will exceed the value $1/(a_1 b_1)$ after several invasions of the host. This means that the host with no parasitoid will evolve to have a positive (stable or unstable) equilibrium of system (1) (see Fig. 4).

Next, we consider the case where the resident system (u_1, v) has a positive equilibrium. The parameters of this resident system belong to the region (S2)i or (S2)ii in Fig. 2 and satisfy $\ln r_1/\mu_1 > 1/(a_1 b_1)$. If the parameters are in (S2)i, the resident system has a stable positive equilibrium (u_1^*, v^*), so that the boundary for invasibility to this resident system is

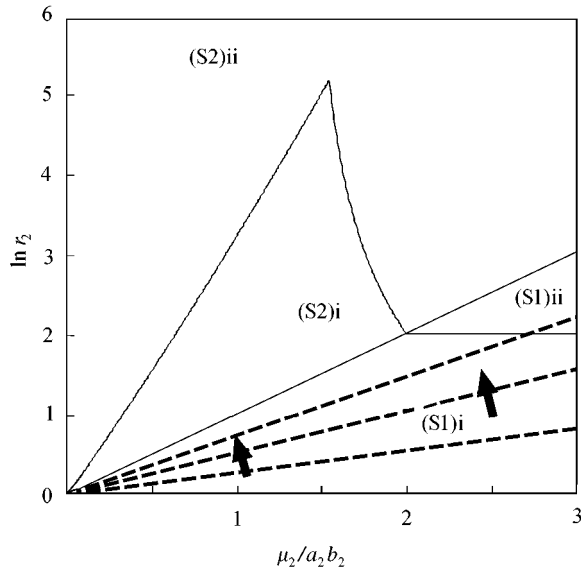$$\ln r_2 = \mu_2 u_1^* + a_2 v^*, \quad (8)$$

FIG. 4. The $\mu_2/(a_c b_c)$-$\ln r_2$ parameter space. The dashed lines represent the boundary of the invasibility in the absence of the parasitoid [eqn (7)]. The solid arrows represent the direction of evolution in the absence of the parasitoid [i.e. in (S1)i and (S1)ii in Fig. 2]. The host without parasitoid will evolve to have a positive [stable (in (S2)i) or unstable (in (S2)ii)] equilibrium of eqn (1).

where the point (u_1^*, v^*) depends only on the parameter set (r_1, μ_1, a_1, b_1). To discuss the evolution of the host's traits on the two-dimensional parameter space, we consider the following two cases. In the first case, we assume that only the host's intrinsic growth rate (r) and sensitivity to the density (μ) are allowed to evolve (i.e. fix $a_1 = a_2 \equiv a_c$ and $b_1 = b_2 \equiv b_c$). In the second case, the host's intrinsic growth rate (r) and vulnerability to the parasitoid (a) are allowed to evolve (i.e. fix $\mu_1 = \mu_2 \equiv \mu_c$ and $b_1 = b_2 \equiv b_c$).

4.1. EVOLUTION OF r AND μ

Consider the first case of evolution, where the boundary of the invasibility is given by eqn (8) with $a_1 = a_2 = a_c$ and $b_1 = b_2 = b_c$, so that it becomes a line through the point $(\mu_1/(a_c b_c), \ln r_1)$ on the $\mu_2/(a_c b_c)$-$\ln r_2$ parameter space. If the parameters of the invader host satisfy $\ln r_2/\mu_2 < 1/(a_c b_c)$ (that is the parameters in (S1)i or (S1)ii), then this host cannot invade the resident system whose parameters belong to the region (S2)i. In fact, from $1/(a_c b_c) < u_1^*$ (see Fig.1),

we have

$$\ln r_2 - \mu_2 u_1^* - a_c v^*$$

$$< \ln r_2 - \frac{\mu_2}{a_c b_c} - a_c v^*$$

$$= \mu_2 \left(\frac{\ln r_2}{\mu_2} - \frac{1}{a_c b_c} \right) - a_c v^* < 0,$$

which does not satisfy the invasibility criterion given by eqn (4). This means that if the resident system has a stable positive equilibrium, the host which can invade this resident system must have the parameters belonging to (S2)i or (S2)ii. Some boundaries of the invasibility to the resident system with parameters in (S2)i are shown in Fig. 5(a). Each of these boundaries does not intersect on the $\mu_2/(a_c b_c)$-$\ln r_2$ parameter space (see Appendix C). These boundaries can be treated as contour lines which represent fitness values. The higher the parameters above the contour line the resident system has, the harder it is to be invaded, that is, the resident with parameters at the tip of the solid arrows in Fig. 5(a) is more resistant to invasion than the one with parameters at the tail of the arrows. Note that the solid arrows do not represent the trajectories of evolution. From Fig. 5(a), we see that the host–parasitoid system whose parameters belong to the region (S2)i will be eventually invaded by the host with parameters belonging to the region (S2)ii. Furthermore, there is the host–parasitoid system which has the parameters belonging to the region (S2)ii and is not invadable by the host with parameters belonging to the region (S2)i. The example is shown in Fig. 5(b). From numerical investigations, we see that system (1) has a stable periodic solution of period 7 at A in Fig. 5(a) and the region above the boundary of the invasibility [the dot–dashed line in Fig. 5(a)], which is given by eqn (4), does not contain any points of the region (S2)i [see Fig. 5(a)]. This means that there is the host–parasitoid system with an unstable positive equilibrium which is not invadable by any host which develops a stable positive equilibrium with the parasitoid. Note that system (1) in the absence of the parasitoid, which is a single-species system, can always be invaded by the host which makes the dynamics stable (see
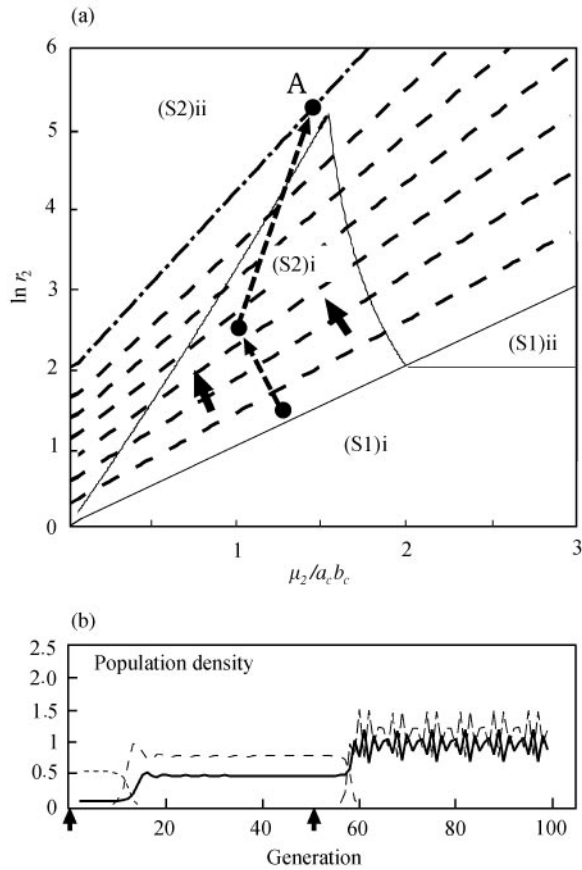
(a)

(b)

FIG. 5. (a) The $\mu_2/(a_c b_c)$-$\ln r_2$ parameter space. The dashed lines represent the boundary of the invasibility to the system composed of 1-host and 1-parasitoid which coexist at a stable positive equilibrium. The solid arrows represent the direction of evolution of the system. The dot–dashed line ($\ln r_2 = 2.29932\mu_2/(a_c b_c) + 1.91598$), which passes through the point A $(\mu_2/(a_c b_c), \ln r_2) = (1.45, 5.25)$, is the boundary of the invasibility to the system with the parameter $(\mu_2/(a_c b_c), \ln r_2) = (1.45, 5.25)$. The parameters a and b are fixed ($a_c = 2$, $b_c = 1$). The dots $((\mu_2/(a_c b_c), \ln r_2) = (1.25, 1.5), (1.0, 2.5), (1.45, 5.25))$ represent the example of the sequence of invasions and a population dynamics shown in (b). (b) The temporal fluctuation of the population densities when the hosts with the parameter values given by the dots in (a) invade. The dashed and the solid lines represent the host and the parasitoid population densities, respectively. The initial host–parasitoid system is at the stable equilibrium. Each invader, of which the initial population densities are 0.00001, invades after 50 generations. The first and the second invaders appear at the 0th and 50th generations, respectively, which are represented by arrows. The final system has a stable periodic solution of period 7 (periodic points are $\{(u(i), v(i))\}_{i=1,\ldots,7} = \{(1.175805, 0.883273), (1.265633, 0.974834), (0.874213, 1.085507), (1.50582, 0.774498), (0.773725, 1.185893), (1.459179, 0.701526), (0.993227, 1.100446)\}$).

Gatto, 1993 and Fig. 6). This is not the case for system (1) with the parasitoid. Therefore the system composed of 1-host and 1-parasitoid which
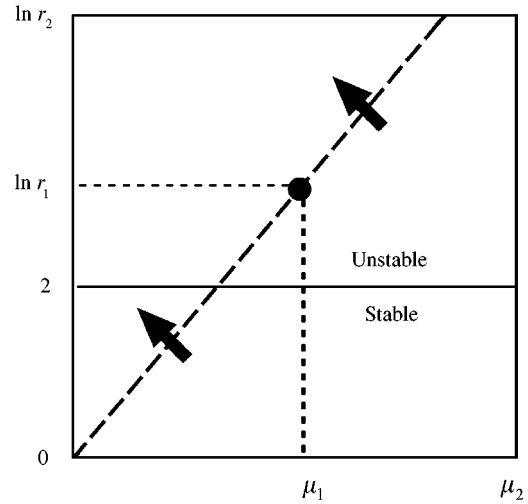

FIG. 6. The μ_2-$\ln r_2$ parameter space. The parameter space is demarcated with the dynamical property of system (1) with $v(n) = 0$. If $0 < \ln r < 2$, then this single-species system is stable. If $\ln r > 2$, then it is unstable. The interaction between the resident host and the invader host in the absence of the parasitoid is given by eqn (3) with $v(n) = 0$, so that the invasibility criterion of the host u_2 to the resident system composed only of the host u_1 is given by eqn (7). Its boundary is represented by the dashed line [eqn (7) with equality]. It is a straight line which passes through the origin and the point $(\mu_1, \ln r_1)$ irrespective of the resident dynamics. Hence, we see that there always exists a host which makes the resident system stable whenever it is unstable ($\ln r_1 > 2$).

coexist at a stable positive equilibrium will not be favored by natural selection without the constraint on the parameters.

Now, we assume that there is a trade-off between parameters (r and μ). Gatto (1993) assumed that along the boundary of the feasibility set of parameters any invader that entails an increase in the intrinsic growth rate r also entails an increase in the self-regulation parameter μ. According to this assumption, we consider the feasibility set shown in Fig. 7. Considering the trade-off, we see that the parameters favored by natural selection (i.e. the parameters for an optimal invader) are given by the point of tangency between the boundary of the feasibility set and the boundary of the invasibility. Hence, we see that both the stable [Fig. 8(a) and (b)] and the unstable [Fig. 8(c) and (d)] host–parasitoid systems can be favored by natural selection. Some parameter sets favored by natural selection are calculated for the specific feasibility sets in Fig. 8.
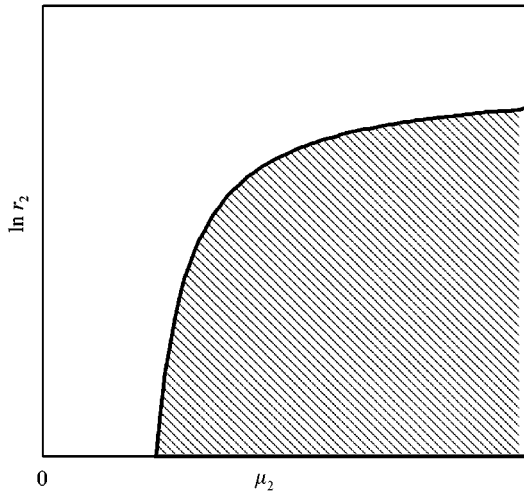
FIG. 7. The feasibility set of the parameters μ and $\ln r$. The host can have the parameters in the hatched region. Along the boundary of the feasibility set of the parameters any invader that entails an increase in the intrinsic growth rate (r) also entails an increase in the sensitivity to the density (μ).

Hereafter, let us compare the stability of host's population dynamics selected in the system without the parasitoid and in the one with the parasitoid when the feasibility set of the parameters is imposed. In the absence of the parasitoid the boundary of the invasibility is given by the following equation on the $\mu_2 - \ln r_2$ parameter space:

$$\ln r_2 = \frac{\ln r_1}{\mu_1}\mu_2. \qquad (9)$$

Then the point $(\mu_{op}, \ln r_{op})$ which is favored by natural selection is a tangent point between eqn (9) and the boundary of the feasibility set (see Fig. 9). The slope of the boundary of the feasibility set at the point $(\mu_{op}, \ln r_{op})$ is

$$\frac{\ln r_{op}}{\mu_{op}}. \qquad (10)$$

Next assume that the resident host which has the parameter $(\mu_{op}, r_{op}, a_c, b_c)$ coexists with the parasitoid with a stable m-cycle $\{(u_{op}(i), v_{op}(i))\}_{i=1,\dots,m}$. The boundary of the invasibility of the host to this resident system is given by the following equation [see eqn (6)]:

$$\ln r_2 = \frac{\sum_{i=1}^{m} u_{op}(i)}{m}\mu_2 + \frac{\sum_{i=1}^{m} v_{op}(i)}{m}a_c, \qquad (11)$$

where $\{(u_{op}(i), v_{op}(i))\}_{i=1,\dots,m}$ satisfies the following equation [see eqn (5)]:

$$\ln r_{op} = \frac{\sum_{i=1}^{m} u_{op}(i)}{m}\mu_{op} + \frac{\sum_{i=1}^{m} v_{op}(i)}{m}a_c. \qquad (12)$$

The slope of the boundary of the above invasibility at the point (μ_{op}, r_{op}) is given as follows and satisfies

$$\frac{\sum_{i=1}^{m} u_{op}(i)}{m} < \frac{\ln r_{op}}{\mu_{op}},$$

where the last inequality is obtained by eqn (12). Hence, we see that the boundary of the invasibility of a host in the host–parasitoid system is not a tangent to the boundary of the feasibility set and intersects at $(\mu_{op}, \ln r_{op})$. This result shows that there is a host with $(\mu'_{op}, r'_{op}, a_c, b_c)$ satisfying the inequalities $\mu'_{op} > \mu_{op}$ and $r'_{op} > r_{op}$ which can invade the resident host–parasitoid system with $(\mu_{op}, r_{op}, a_c, b_c)$. Therefore, the parameter favored by natural selection with the parasitoid, $(\mu'_{op}, r'_{op}, a_c, b_c)$, is given by the point of tangency between the boundary of the invasibility (11) and the feasibility set (see Fig. 9). The stability of the system with the parameter $(\mu'_{op}, r'_{op}, a_c, b_c)$ depends on the specific shape of the feasibility set. We cannot generally decide with what kind of dynamics the host and parasitoid coexist, but we see that the host with the parasitoid will evolve to have a higher r than the one without the parasitoid and the higher r represents an unstable dynamics in the system without the parasitoid.

4.2. EVOLUTION OF r AND a

Consider the second case of evolution. In this case, the boundary of the invasibility is given by eqn (8) with $\mu_1 = \mu_2 = \mu_c$ and $b_1 = b_2 = b_c$ so that it becomes a curve through the point $(\mu_c/(a_1 b_c), \ln r_1)$ on the $\mu_c/(a_2 b_c)$-$\ln r_2$ parameter space. Some boundaries of the invasibility to the resident system with parameters in (S2)i are shown in Fig. 10(a). These boundaries can intersect each other, so that depending on the way of their intersection the coexistence of the three species in system (3) with the parameters in (S2)i is possible even if the parameters satisfy $\mu_1 = \mu_2$ and $b_1 = b_2$ (see Fig. 11). Although this case of
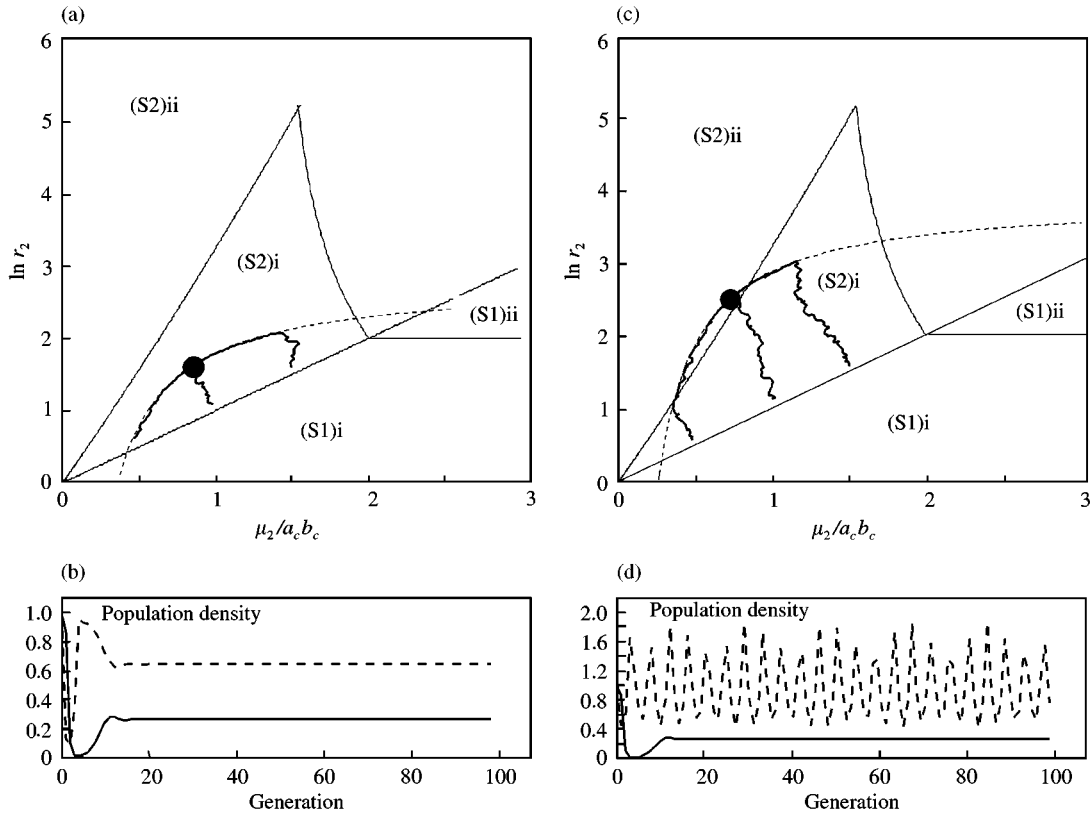
FIG. 8. The examples of the calculations of the optimal parameters for the specific feasibility set of the parameters. We chose $a_c = 2$ and $b_c = 1$. The optimal parameters $(\mu_{op}, \ln r_{op})$ (●), which are approximately (1.74, 1.66) in (a) and (1.4, 2.6) in (c), are calculated by numerical investigations. The dashed lines, which are $\ln r_2 = -a_c b_c / \mu_2 + 2.8$ in (a) and $\ln r_2 = -a_c b_c / \mu_2 + 3.9$ in (c), represent the boundary of the feasibility set of the parameters. The optimal parameters are calculated as follows. In the feasibility set of the parameters, set the initial parameters of the resident host and randomly choose the invader host whose parameters are close to the resident host's ones. If the invader's parameters satisfy the invasibility criterion and are in the feasibility set of the parameters, then they are replaced with those of the resident host and are plotted in the parameter space. If not, choose the invader's parameter again. Repeating these procedure gives the pathway of the evolution. The three pathways of the evolution are represented by the solid lines in (a) and (c). Each of these converges to the optimal parameter (●). The host–parasitoid dynamics with the optimal parameters obtained in (a) and (c) are shown in (b) and (d), respectively. The dashed and solid lines represent the densities of the host and the parasitoid, respectively. The host and the parasitoid in (b) coexist at a stable positive equilibrium, and the ones in (d) coexist with a sustained oscillation.

evolution has such a property in comparison with the previous one, there is the following qualitatively same property. The higher the parameters above the contour line the resident system has, the harder it is to be invaded, that is, the resident with parameters at the tip of the solid arrows in Fig. 10(a) is more resistant to invasion than the one with parameters at the tail of the arrows. From Fig. 10(a), we see that the host–parasitoid system whose parameters belong to the region (S2)i will be eventually invaded by the host with parameters belonging to the region (S1)i, (S1)ii or (S2)ii. However, remembering the fact that the host with the parameters in (S1)i or

(S1)ii evolves to have the parameters in (S2)i or (S2)ii, we can conclude that the host–parasitoid system eventually becomes unstable without the trade-off of the parameters. An example of the invasions is shown in Fig. 10(b).

Now we assume that there is a trade-off between parameters (Fig. 12). We assumed that along the boundary of the feasibility set of parameters any invader that entails an increase in the finite rate of increase (r) also entails an increase in the vulnerability to the parasitoid (a). The parameters favored by natural selection are given by the point of tangency between the boundary of the feasibility set and the boundary of the
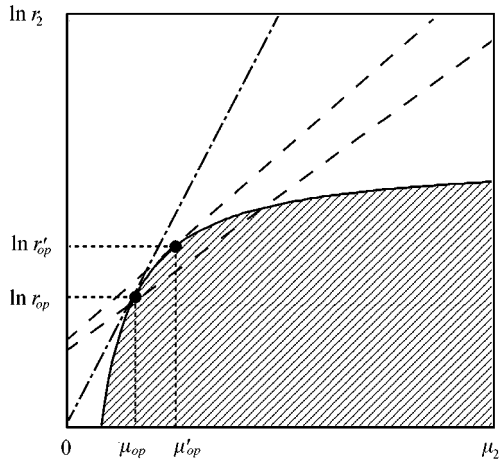
FIG. 9. The μ_2-$\ln r_2$ parameter space. The dot–dashed line represents the boundary of the invasibility in the absence of the parasitoid. The dashed lines represent the boundary of the invasibility to the system composed of 1-host and 1-parasitoid which coexist at a stable cycle. The $(\mu_{op}, \ln r_{op})$ is the point which is favored by natural selection in the absence of a parasitoid. Note that the boundary of the invasibility to the system with the parasitoid intersects the boundary of the feasibility set when the former boundary passes through the point $(\mu_{op}, \ln r_{op})$. The resident host–parasitoid system with the parameters $(\mu_{op}, \ln r_{op})$ is invadable by the host and the $(\mu'_{op}, \ln r'_{op})$ is the point which is favored by natural selection with the parasitoid.

5. Discussion

In this paper, we considered the evolution of host–parasitoid systems and investigated their dynamics which resulted from evolution. We assumed that only the host is allowed to evolve. We considered two cases of the host's evolution. In the first case, we allowed the host's intrinsic growth rate (r) and sensitivity to the density (μ) to evolve. In the second case, the host's intrinsic growth rate (r) and vulnerability to the parasitoid (a) are allowed to evolve. Under these assumptions, we obtained the host–parasitoid system favored by natural selection by using the invasibility criterion of the host to the resident host–parasitoid system without considering
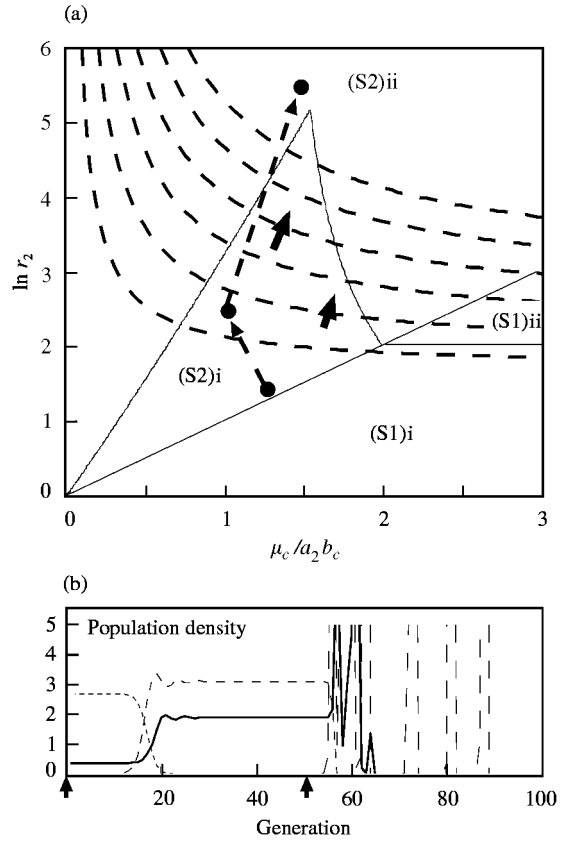

FIG. 10. (a) The $\mu_c/(a_2 b_c)$-$\ln r_2$ parameter space. The dashed lines represent the boundary of the invasibility to the system composed of 1-host and 1-parasitoid which coexist at a stable positive equilibrium. The solid arrows represent the direction of the evolution of the system composed of 1-host and 1-parasitoid which coexist at a stable positive equilibrium. The parameters μ and b are fixed ($\mu_c = 0.5$, $b_c = 1$). The dots ((a, $\ln r$) = (0.4, 1.5), (0.5, 2.5), (0.33, 5.5)) represent the example of the sequence of invasions and a population dynamics shown in (b). (b) The temporal fluctuation of the population densities when the hosts with the parameter values of the dots in (a) invade. The initial host–parasitoid system is at the stable equilibrium. Each invader, whose initial population densities are 0.00001, invades after 50 generations. The first and the second invaders appear at the 0th and 50th generations, respectively, which are represented by arrows. In the final system, the parasitoid goes to extinction and the host has a chaotic oscillation.

invasibility. Hence, we see that according to the shape of the parameter's feasibility set on the above assumption, both the stable and the unstable host–parasitoid systems can be favored by natural selection. Some parameter sets favored by natural selection are calculated for the specific feasibility sets in Fig. 13.

the explicit evolutionary dynamics. As a result, the evolution of the host tends to make the host–parasitoid system unstable. This tendency is different from the one in the single-species system.

The tendency of the host's evolution in the host–parasitoid system to make the host dynamics isolated from the parasitoid unstable in the first case of the evolution is interpreted as follows.
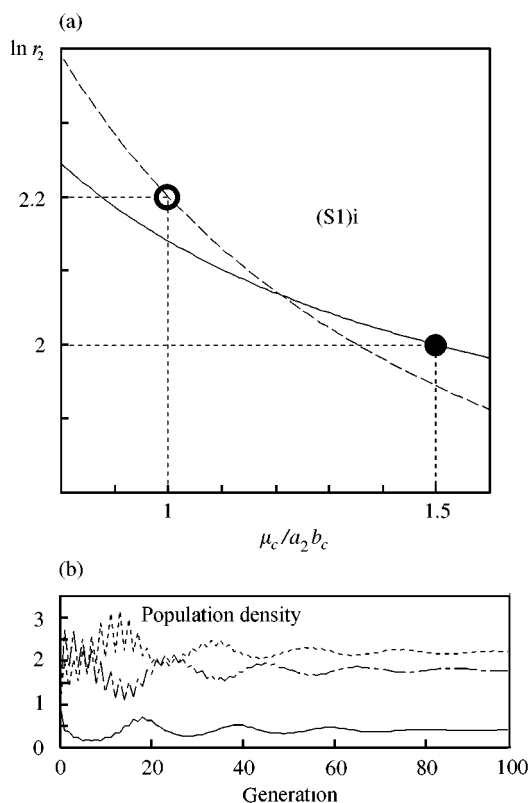
FIG. 11. An example of coexistence of two hosts and a parasitoid. We chose $\mu_c = 0.5$, $b_c = 1$ and two hosts which are characterized by $(a_1, \ln r_1) = (\frac{1}{3}, 1.5)$ and $(0.5, 2.2)$, respectively. Each of these hosts coexists with the parasitoid at a stable equilibrium. The boundaries of the invasibility to the host–parasitoid system with each of these hosts are represented by the solid and the dashed curves, respectively, in (a). From the way of their intersection, we see that these hosts can mutually invade with the help of the parasitoid. The temporal fluctuation of these two hosts' and the parasitoid's population densities is shown in (b). The population dynamics obeys eqn (3) with $(\mu_1, \ln r_1, a_1, b_1) = (0.5, 1.5, \frac{1}{3}, 1)$ and $(\mu_2, \ln r_2, a_2, b_2) = (0.5, 2.2, 0.5, 1)$. The solid line represents the parasitoid's population density. The dashed and dot–dashed lines represent the population densities of the hosts characterized by the dot and the circle in (a).

In general, the existence of the parasitoid depresses the density of the hosts (Beddington *et al.*, 1975), so that the competition between the hosts is relaxed (Comins & Hassell, 1976). Because of this relaxation of the host's competition, the change of the intrinsic growth rate (r) is relatively important when the host evolves in host–parasitoid systems. This implies the increase of the intrinsic growth rate (r). Hence, it means the instability of the host population dynamics isolated from the parasitoid.
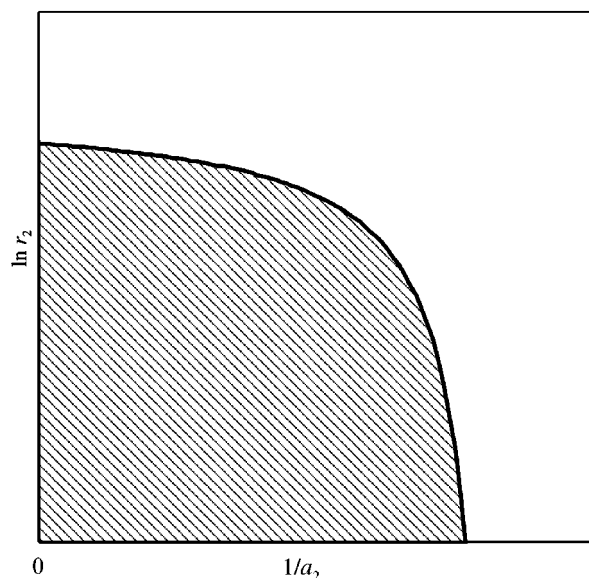

FIG. 12. The feasibility set of the parameters a and $\ln r$. The host can have the parameters in the hatched region. Along the boundary of the feasibility set of the parameters any invader that entails an increase in the intrinsic growth rate (r) also entails an increase in the vulnerability to the parasitoid (a).

There have been some studies about evolution of two-species systems (see Hochberg & Holt, 1995; Abrams & Matsuda, 1997). These studies showed that the evolution affects the stability of the population dynamics as our study did. In Hochberg & Holt (1995) and Abrams & Matsuda (1997), the specific models for the traits dynamics were employed. In this paper, we employed the invasibility criterion of the mutant species to the resident system, instead of assuming the specific models for traits dynamics, so that this paper implicitly assumes that the time scale of evolution is sufficiently larger than the one of population dynamics. Therefore, the evolution considered in this paper corresponds to the evolution with the sufficiently slow traits dynamics. Abrams & Matsuda (1997) considered the evolution of the prey's intrinsic growth rate and vulnerability to the predator in prey–predator systems. In their model, whether the evolution of the traits makes the prey–predator system unstable depends crucially on the assumption about the functional response of the predator. That is, if the functional response of the predator is linear, then the instability is not resulted from the evolution of the prey, but if not, then the instability can occur.
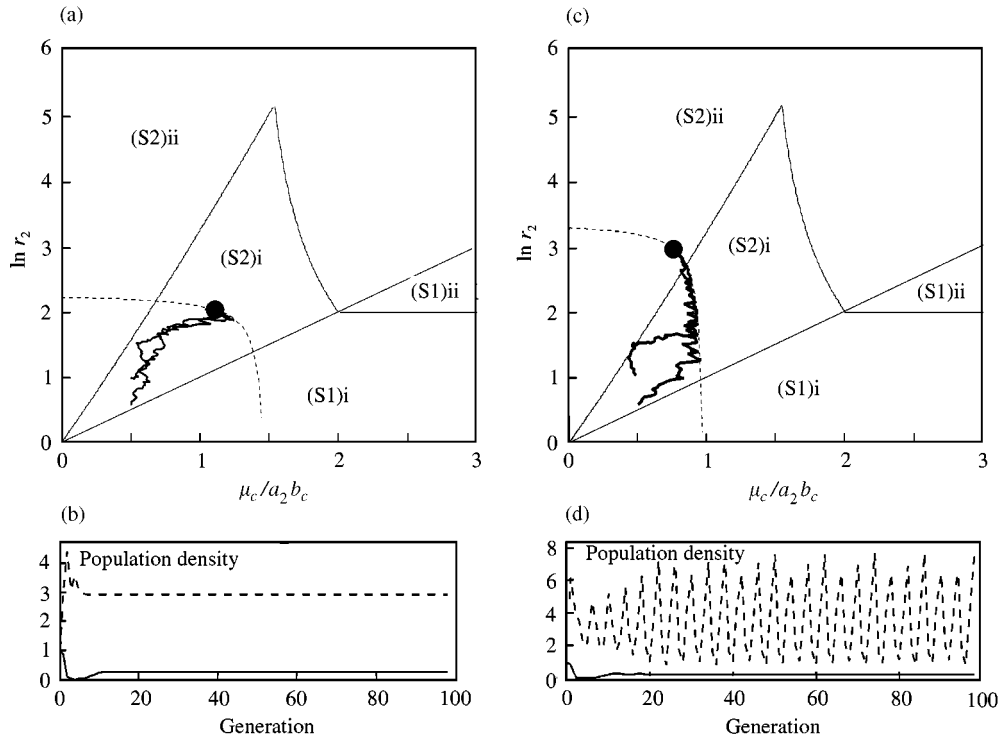
FIG. 13. The example of the calculations of the optimal parameters for the specific feasibility set of the parameters. We chose $\mu_c = 0.5$ and $b_c = 1$. The optimal parameters $(a_{op}, \ln r_{op})$ (●), which are approximately $(0.45, 2.05)$ in (a) and $(0.66, 2.98)$ in (c), are calculated by numerical investigations. The dashed lines, which are $\ln r_2 = 0.1/(\mu_c/(a_2 b_c) - 1.5) + 2.3$ in (a) and $\ln r_2 = 0.1/(\mu_c/(a_2 b_c) - 1) + 3.4$ in (c), represent the boundary of the feasibility set of the parameters. The solid lines represent the pathway of the evolution calculated with a procedure similar to the one in Fig. 8. Each of these converges to the optimal parameter. The host–parasitoid dynamics with the optimal parameters obtained in (a) and (c) are shown in (b) and (d), respectively. The dashed and the solid lines represent the densities of the host and the parasitoid, respectively. The host and the parasitoid in (b) coexist at a stable equilibrium, and the ones in (d) coexist with sustained oscillation.

However, although the functional response of the parasitoid in our model is linear, it can be destabilized by the evolution of the host. One of the reasons for this difference is the property of the discrete-time models that easily have unstable dynamics. Hence, it is expected that population dynamics with non-overlapping generations easily have an unstable dynamics even if traits dynamics are included.

In this paper, we employed the Ricker model as a host population dynamics. But there are many other models which describe a singe-population dynamics. According to Bellows (1981), the following model has a particularly flexible form to describe the density dependence:

$$g[u] = \frac{1}{1 + (\alpha u)^\beta},$$

where $\alpha > 0$ defines sensitivity to the density and $\beta > 1$ determines the types of competition: $\beta \simeq 1$, contest competition; $\beta \gg 1$, scramble competition. To assess the generality of our results, we also employed the above density dependence. As a result, if the competition in the host population is scramble, our results hold, that is the stable host–parasitoid system is eventually invaded by the host which develops unstable dynamics with the parasitoid. But if the competition in the host population is contest, our results do not hold. This difference comes from the property of the Ricker model which does not describe the contest competition. Therefore, it seems that the main results, that is the stable host–parasitoid system is eventually invaded by the host which develops unstable dynamics with the parasitoid, does not depend on the forms of models as long as the host

has a scramble competition. The host–parasitoid model employed in this paper is a simple one, so that it is also expected that if the more realistic models (see e.g. Hochberg & Holt, 1995; Kaitala *et al.*, 1999) are employed, other results can occur. It is a future problem.

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APPENDIX A

Using the Schur–Cohn criterion and the Routh–Hurwitz criterion, we can obtain the following condition for stability of the point E_{++}:

$$\ln r + \mu \ln ru^* - \mu(ab + \mu)u^{*2} > 0,$$

$$1 - (ab + \mu \ln r)u^* + \mu(ab + \mu)u^{*2} > 0, \qquad \text{(A.1)}$$

$$2 - \ln r + (2ab + \mu \ln r)u^* - \mu(ab + \mu)u^{*2} > 0.$$

We show that the first inequality of eqn (A.1) holds as long as the positive equilibrium exists $(\ln r/\mu > 1/(ab))$. We define $h(x)$ as follows:

$$h(x) = 1 - 2ax \exp[-ax] - (\exp[-ax])^2.$$

We see that $h(x) > 0$ for $x > 0$ because the function $h(x)$ has the following properties:

$$h(0) = 0,$$

$$\frac{d}{dx} h(x) = 2a \exp[-ax](-1 + ax + \exp[-ax])$$

$$> 0 \quad \text{for} \quad x > 0.$$

Using the above result, we see that the following inequality holds:

$$\frac{x}{b(1 - \exp[-ax])} > \frac{1}{2b}\left(x + \frac{2}{a}\right) \quad \text{for} \quad x > 0.$$

$$\text{(A.2)}$$

In fact,

$$\lim_{x \to 0} \left[\frac{x}{b(1 - \exp[-ax])} - \frac{1}{2b}\left(x + \frac{2}{a}\right) \right] = 0$$

$$\frac{d}{dx}\left(\frac{x}{b(1 - \exp[-ax])} - \frac{1}{2b}\left(x + \frac{2}{a}\right) \right)$$

$$= \frac{1}{2b(1 - \exp[-ax])^2} h(x) > 0 \quad \text{for} \quad x > 0.$$

Using eqn (A.2) and (2), we see that the following inequality holds:

$$\frac{v^*}{b(1 - \exp[-av^*])} > \frac{1}{2b}\left(v^* + \frac{2}{a}\right),$$

$$u^* > \frac{1}{2b}\left(\frac{\ln r - \mu u^*}{a} + \frac{2}{a}\right),$$

$$u^* > \frac{\ln r + 2}{\mu + 2ab}. \tag{A.3}$$

We see that the following inequality holds:

$$\frac{1}{b}\left(x + \frac{1}{a}\right) > \frac{x}{b(1 - \exp[-ax])} \quad \text{for} \quad x > 0, \tag{A.4}$$

because

$$\lim_{x \to 0}\left[\frac{1}{b}\left(x + \frac{1}{a}\right) - \frac{x}{b(1 - \exp[-ax])}\right] = 0,$$

$$\frac{d}{dx}\left[\frac{1}{b}\left(x + \frac{1}{a}\right) - \frac{x}{b(1 - \exp[-ax])}\right]$$

$$= \frac{\exp[-ax]}{b(1 - \exp[-ax])^2}(-1 + ax + \exp[-ax])$$

$$> 0 \quad \text{for} \quad x > 0.$$

Using eqns (A.4) and (2), we see that the following inequality holds:

$$u^* < \frac{\ln r + 1}{\mu + ab}. \tag{A.5}$$

We define $q(x)$ as follows:

$$q(x) = \ln r + \mu \ln rx - \mu(ab + \mu)x^2.$$

The function $q(x)$ has a maximum value at $x = \ln r/\{2(ab + \mu)\}$, which has the following property:

$$\frac{\ln r}{2(ab + \mu)} < \frac{\ln r + 2}{\mu + 2ab}. \tag{A.6}$$

Using eqns (A.3), (A.5) and (A.6), we see that the following inequalities hold:

$$\frac{\ln r}{2(ab + \mu)} < \frac{\ln r + 2}{\mu + 2ab} < u^* < \frac{\ln r + 1}{\mu + ab}.$$

Then,

$$q(u^*) > q\left(\frac{\ln r + 1}{\mu + ab}\right)$$

$$= \frac{ab\mu}{\mu + ab}\left(\frac{\ln r}{\mu} - \frac{1}{ab}\right) > 0 \quad \text{for} \quad \frac{\ln r}{\mu} > \frac{1}{ab},$$

which shows that the first inequality of eqn (A.1) holds true if E_{++} exists.

APPENDIX B

We obtain the criterion for invasibility, eqn (4), when the resident system corresponds to a stable cycle (equilibrium or periodic oscillation) of period m $\{(u_1(i), v(i))\}_{i=1,\dots,m}$ of system (1). Then $\mathbf{p}(i) = (u_1(i), v(i), 0)$, $(i = 1, 2, \dots, m)$ is the periodic orbit of period m of system (3). To derive the criterion for invasibility, we investigate the stability of the periodic orbit. The Jacobian matrix J of eqn (3) at the periodic orbit is given by

$$J = \begin{pmatrix} \prod_{i=1}^{m} A_i & B \\ 0 & \prod_{i=1}^{m} C_i \end{pmatrix},$$

where

$$A_i = \begin{pmatrix} r_1(1 - \mu_1 u_1(i))\exp[-\mu_1 u_1(i)]\exp[-a_1 v(i)] & -a_1 r_1 u_1(i)\exp[-\mu_1 u(i)]\exp[-a_1 v(i)] \\ b_1(1 - \exp[-a_1 v(i)]) & a_1 b_1 u_1(i)\exp[-a_1 v(i)] \end{pmatrix},$$

$$C_i = r_2 \exp[-\mu_2 u_1(i)]\exp[-a_2 v(i)].$$

B is a suitable 2×1 matrix and 0 is a 1×2 zero matrix. Then the stability of the periodic orbit $\{\mathbf{p}(i)\}_{i=1,2,\ldots,m}$ depends only on the value of $\prod_{i=1}^{m} C_i$, because the resident community corresponds to a stable cycle (the absolute value of eigenvalues of the matrix $\prod_{i=1}^{m} A_i$ is smaller than unity). If

$$\prod_{i=1}^{m} r_2 \exp[-a_2 v(i)] \exp[-\mu_2 u_1(i)] > 1,$$

that is, if

$$\sum_{i=1}^{m} (\ln r_2 - a_2 v(i) - \mu_2 u_1(i)) > 0,$$

the periodic orbit is unstable with respect to u_2-direction and the community (u_1, v) is invadable by the invader u_2. Note that the above is equivalent to eqn (4).

We obtain the necessary condition (5) that system (1) has a periodic orbit of period m. Let $\{(u(i), v(i))\}_{i=1,2,\ldots,m}$ be the periodic orbit. We simply write μ_1, r_1 and a_1 as μ, r and a, respectively. Then we can obtain the following equations by using the first equation of eqn (1):

$$u(2) = ru(1) \exp[-av(1)] \exp[-\mu u(1)],$$

$$u(3) = ru(2) \exp[-av(2)] \exp[-\mu u(2)]$$

$$= r\{ru(1) \exp[-av(1)] \exp[-\mu u(1)]\}$$

$$\times \exp[-av(2)] \exp[-\mu u(2)]$$

$$= r^2 u(1) \prod_{i=1}^{2} \exp[-av(i)] \exp[-\mu u(i)],$$

$$\vdots$$

$$u(m+1) = r^m u(1) \prod_{i=1}^{m} \exp[-av(i)] \exp[-\mu u(i)].$$

Using $u(m+1) = u(1)$ in the above, we obtain eqn (5).

APPENDIX C

We show that the boundaries of the invasibility to host–parasitoid systems which have a stable positive equilibrium do not intersect in $\mu - \ln r$ parameter space if a and b are fixed.

Let (μ_1, r_1, a_c, b_c) and (μ_2, r_2, a_c, b_c) be parameters which belong to the region (S2)i in Fig. 2. System (1) with $u = u_1$, $\mu = \mu_1$, $r = r_1$, $a = a_c$, and $b = b_c$ and the one with $u = u_2$, $\mu = \mu_2$, $r = r_2$, $a = a_c$, and $b = b_c$ have a positive equilibrium (see Section 2). We denote these equilibria as (u_1^*, v_1^*) and (u_2^*, v_2^*), respectively. The values of these equilibria are the roots of the following equations, respectively [see eqn (2)]:

$$u_1^* = \begin{cases} \dfrac{v_1^*}{b_c(1 - \exp[-a_c v_1^*])}, \\[2ex] \dfrac{\ln r_1 - a_c v_1^*}{\mu_1}, \end{cases} \tag{C.1}$$

$$u_2^* = \begin{cases} \dfrac{v_2^*}{b_c(1 - \exp[-a_c v_2^*])}, \\[2ex] \dfrac{\ln r_2 - a_c v_2^*}{\mu_2}. \end{cases} \tag{C.2}$$

Using eqn (6), the boundaries of the invasibility of a host to the community (u_1, v_1) and (u_2, v_2) are given by the following equations, respectively:

$$\ln r = \begin{cases} v_1^* a_c + u_1^* \mu, \\ v_2^* a_c + u_2^* \mu. \end{cases} \tag{C.3}$$

Now we assume that the community (u_1, v_1) is invadable by the host u_2. Then the following inequality holds [see eqn (4)]:

$$\frac{\ln r_2}{\mu_2} > v_1^* \frac{a_c}{\mu_2} + u_1^*.$$

Using the above inequality, the first equation of eqn (C.1) and the two equations of eqn (C.2), we obtain the following inequality:

$$\frac{a_c}{\mu_2} v_2^* + \frac{v_2^*}{b_c(1 - \exp[-a_c v_2^*])}$$

$$> \frac{a_c}{\mu_2} v_1^* + \frac{v_1^*}{b_c(1 - \exp[-a_c v_1^*])}.$$

Since function $(a_c/\mu_2)x + x/\{b_c(1-\exp[-a_c x])\}$ is monotone increasing with respect to $x > 0$, we see that $v_2^* > v_1^*$. Using this inequality and the monotonicity of the function $x/\{b_c(1 - \exp[-a_c x])\}$ we obtain the following inequality:

$$\frac{v_2^*}{b_c(1 - \exp[-a_c v_2^*])} > \frac{v_1^*}{b_c(1 - \exp[-a_c v_1^*])}.$$

Finally, we see $u_2^* > u_1^*$ from the first equations of eqns (C.1) and (C.2). Because $u_2^* > u_1^*$ and $v_2^* > v_1^*$, we see that the boundaries eqn (C.3) do not intersect. In fact,

$$(v_2^* a_c + u_2^* \mu) - (v_1^* a_c + u_1^* \mu)$$

$$= a_c(v_2^* - v_1^*) + \mu(u_2^* - u_1^*) > 0.$$