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EVOLUTIONARY DYNAMICS OF PREY-PREDATOR SYSTEMS WITH HOLLING TYPE II

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Abstract. This paper considers the coevolution of phenotypes in a community comprising the populations of predators and prey. The evolutionary dynamics is constructed from a stochastic process of mutation and selection. We investigate the ecological and evolutionary conditions that allow for continuously stable strategy and evolutionary branching. It is shown that branching in the prey can induce secondary branching in the predators. Furthermore, it is shown that the evolutionary dynamics admits a stable limit cycle. The evolutionary cycle is a likely outcome of the process, which requires higher evolutionary speed of prey than of predators. It is also found that different evolutionary rates and conversion efficiencies can influence the lengths of evolutionary cycles.

1. **Introduction.** Understanding the origin of new species remains one of the core problems in evolutionary biology. Evolution takes place in an ecological setting that typically involves interactions with other organisms. Prey-predator interactions are ubiquitous in nature [3]. Sometimes the ecological interactions between predator and prey species can be strong enough for the predator to be a major component of the environment in which the prey is evolving, and vice versa. Such interactions have therefore motivated a variety of theoretical models of phenotypic coevolution in prey-predator communities (see, for example, [1]). Of some interest has been the question of whether the phenotypes of predator and prey evolve to an asymptotic equilibrium state, such as an evolutionary stable strategy [21], when the system evolves to a steady state on an ecological timescale. An alternative could be that their interactions prevent the attainment of an equilibrium point and that there is a continuous evolutionary change of their phenotypes. Following Van Valen's Red Queen hypothesis [29], the latter behavior has become known as the Red Queen dynamics. For example, natural selection by the prey on the predator

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favors predator phenotypes best able to consume the prey, whereas selection by the predator on the prey favors prey phenotypes least likely to be killed, which may lead to a cyclic type of "arms race" (see Dawkins and Krebs [7]). Bakker [2] documented changes in mammalian herbivores and carnivores during the Paleocene to the Mid Eocene that could be of the kind suggested by Dawkins and Krebs [7]. Those taxa characteristics of open habitats, where pursuit and flight are critical features of predation, show similar speed-enhancing changes in limb morphology. Dieckmann et al. [8] investigated the coevolution of phenotypes in a community comprising a population of predator and prey. They constructed an evolutionary dynamics from a stochastic process of mutation and selection and concluded that the evolutionary system eventually attains one of the three different evolutionary states: (i) the predator goes extinct; (ii) coevolution leads to constant phenotypes in predator and prey and (iii) the phenotypes in both species undergo coupled and sustained oscillations on a limit cycle corresponding to the Red Queen dynamics. The ecological model they considered was the Lotka-Volterra predator-prey model. However, they did not study the evolutionary branching which occurs when frequency-dependent selection splits a phenotypically monomorphic population into two distinct phenotype clusters and did not consider the saturating effect in the predator-prey interactions. In addition, the stability of evolutionary cycle was not explicitly analyzed. However, the stability of evolutionary cycle is important in determining the evolutionary states to which the prey and predator evolve.

The purpose of this paper is to investigate the ecological and evolutionary conditions that allow for continuously stable strategy and evolutionary branching. We show that the branching in the prey can induce the secondary branching in the predator. Secondly, we show that the evolutionary dynamics admits a stable limit cycle. The population model we consider is the well known Rosenzweig-MacArthur prey-predator model with the functional response of Holling type II. It has most often been used in the past few decades to predict prey and predator abundances at ecological timescale in the absence of mutations. When rare phenotypic mutant populations appear in the resident population, we consider their effects and analyze an evolutionary dynamics. Our approach is based on the theory of adaptive dynamics (see Metz et al. [22], Dieckmann and Law [9]). In this approach, evolutionary dynamics is studied by using the concept of invasion fitness [22].

The organization of this paper is as follows. In the next section, we consider a single phenotypic trait in each species and model an evolutionary dynamics. In section 3, we investigate the properties of the evolutionary singular points and evolutionary branching. In section 4, the Hopf bifurcation is investigated to show that evolutionary cycle is a likely outcome of the process. In section 5, some likely evolutionary states are simulated. A brief discussion is given in section 6.

2. The evolutionary model.

The objective of this section is to construct an evolutionary model. The population model we consider is the well known prey-predator model with the functional response of Holling type II, which considers the saturating effect in the prey-predator interactions. The outcomes of prey-predator interactions often depend on traits which influence or indicate predation ability, such as body size, weight, armament, the running velocity, skin color, or costly signals of strength (see Cohen et al. [4], Simmons and Scheepers [26]). For example, in the case of rabbits and foxes one might imagine that the running velocity for rabbits and foxes might be the most important trait. An increase in the running velocity for rabbits is then an evolutionary advantage to them. In some predator-prey interactions one might imagine that skin color might be the most important trait, but that the color of a prey relative to the environment (not to the predator) might be the important factor. Body size is also an important trait in determining interactions between prey and predator. For simplicity, we focus on a single phenotypic trait in each species and think of these traits as body size, x_1 and x_2, of prey and predator respectively. We consider two important interaction parameters: the predation efficiency α and the carrying capacity K, which depend on these phenotypic traits. Assume that the interaction parameter describing predation efficiency depends on two quantitative traits, one in the prey and the other in the predator. We can specify the effect of the encounter on the birth and death rates of the individuals concerned. In qualitative terms the encounter will most likely lead to an increased risk of mortality in the prey; the predator on the other hand most likely experiences a reduced rate of mortality or, in the longer term, an increased rate of reproduction, or both. The magnitude of the effect on the vital rates depends on the phenotypes of the individuals; any difference in vital rates between co-occurring conspecific individuals with different phenotypes causes natural selection. For instance, a large prey individual is more likely than a small one to defend itself successfully from a predator of intermediate size and, as a result, to gain a selective advantage through a lower risk of death in the encounter. Therefore, the stronger prey-predator interactions are, the more similar prey and predator traits are. As an example, the predation efficiency of a predator with phenotypic trait x_2 on prey individuals with phenotypic trait x_1 is given by

$$\alpha(x_1 - x_2) = \alpha_0 \exp\left(\frac{-(x_1 - x_2)^2}{2\sigma_\alpha^2}\right), \tag{1}$$

which has been previously used in the study of character displacement [27]. It is symmetric about the origin. The asymmetrical predation efficiency $\alpha(x_1 - x_2)$ which has been previously used in the study of character displacement is described as

$$\alpha(x_1 - x_2) = \exp\left(\frac{\sigma_\alpha^2\beta^2}{2}\right)\exp\left(\frac{-(x_1 - x_2 + \sigma_\alpha^2\beta)^2}{2\sigma_\alpha^2}\right),$$

where $\beta \neq 0$ [11]. One can find alternative functions α in [8, 11]. Further, we assume that the resource availability for the prey varies with the phenotypic trait x_1, such that the resource distribution function $K(x_1)$ is of Gaussian form $N(x_0, \sigma_K^2)$ with a maximum at x_0 [10], namely,

$$K(x_1) = K_0 \exp\left(\frac{-(x_1 - x_0)^2}{2\sigma_K^2}\right). \tag{2}$$

For simplicity, we assume that other parameters are not influenced by the quantitative traits x_1 and x_2. As a consequence, the ecological dynamics of monomorphic resident prey and predator populations with traits x_1 and x_2 is given by

$$\begin{aligned} \frac{dN_1(x_1,t)}{dt} &= rN_1(x_1,t)\left(1 - \frac{N_1(x_1,t)}{K(x_1)}\right) - \frac{\alpha(x_1 - x_2)N_1(x_1,t)N_2(x_2,t)}{1 + h\alpha(x_1 - x_2)N_1(x_1,t)}, \\ \frac{dN_2(x_2,t)}{dt} &= N_2(x_2,t)\left(\frac{\theta\alpha(x_1 - x_2)N_1(x_1,t)}{1 + h\alpha(x_1 - x_2)N_1(x_1,t)} - d\right), \end{aligned} \tag{3}$$

where $N_1(x_1, t)$ is the number of the resident phenotypic prey population at time t, $N_2(x_2, t)$ is the number of the resident phenotypic predator population at time

t, $\alpha(x_1 - x_2)$ and $K(x_1)$ are described in (1) and (2), r is the intrinsic growth rate of the prey, h is the predator handling time, θ is the conversion efficiency and d is the death rate of the predator.

To have a meaningful problem, we assume that $\theta > hd$. Otherwise, the predator population can not grow even in the presence of an infinitely abundant prey population. When $\theta > hd$, it follows from [5, 23] that there is a globally stable ecological equilibrium $(N_1^*(x_1, x_2), N_2^*(x_1, x_2))$ in (3), where

$$\begin{aligned} N_1^*(x_1, x_2) &= \frac{d}{(\theta - hd)\alpha(x_1 - x_2)}, \\ N_2^*(x_1, x_2) &= \frac{r\theta}{(\theta - hd)K(x_1)\alpha(x_1 - x_2)}(K(x_1) - N_1^*(x_1, x_2)) \end{aligned} \tag{4}$$

if

$$\frac{rhK(x_1)\alpha(x_1 - x_2) - r}{2hr\alpha(x_1 - x_2)} \le \frac{d}{\alpha(x_1 - x_2)(\theta - hd)} < K(x_1). \tag{5}$$

Note that the strictly positive equilibrium is relevant to the initial resident phenotypic trait values (x_1, x_2).

When rare mutant populations are present in the resident populations, we assume that mutations are sufficiently rare and that there is a separation of ecological and evolutionary timescales, since the ecological dynamics occurs faster than the evolutionary dynamics. Under the assumption (5), we suppose that mutants encounter monomorphic resident populations at their ecological equilibrium (namely, the strictly positive equilibrium). Further, we assume that mutants whose invasion fitness is larger than zero can not only invade (with some probability) but also replace the former resident and thus become the new resident. Under these assumptions, it is possible to study the evolutionary dynamics by analyzing a function $f(y, x)$ describing the invasion fitness of a mutant y in a resident population x. Evolutionary dynamics then follows selection gradients determined by the derivatives of the invasion fitness function $f(y, x)$. As a consequence, the ecological dynamics of rare phenotypic mutant prey y_1 in the resident population is given by

$$\frac{dN_1(y_1, t)}{dt} = rN_1(y_1, t)\left(1 - \frac{N_1^*(x_1, x_2)}{K(y_1)}\right) - \frac{\alpha(y_1 - x_2)N_1(y_1, t)N_2^*(x_1, x_2)}{1 + h\alpha(y_1 - x_2)N_1^*(x_1, x_2)},$$

where $(N_1^*(x_1, x_2), N_2^*(x_1, x_2))$ is the strictly positive equilibrium described in (4), and the functions α and K are given by (1) and (2) respectively. Therefore, the invasion fitness for the prey becomes

$$f_1(y_1, x_1, x_2) = r\left(1 - \frac{N_1^*(x_1, x_2)}{K(y_1)}\right) - \frac{\alpha(y_1 - x_2)N_2^*(x_1, x_2)}{1 + h\alpha(y_1 - x_2)N_1^*(x_1, x_2)}. \tag{6}$$

Similarly, the ecological dynamics of rare phenotypic mutant predator y_2 in the resident population is given by

$$\frac{dN_2(y_2, t)}{dt} = N_2(y_2, t)\left(\frac{\theta\alpha(x_1 - y_2)N_1^*(x_1, x_2)}{1 + h\alpha(x_1 - y_2)N_1^*(x_1, x_2)} - d\right).$$

Then the invasion fitness for the predator becomes

$$f_2(y_2, x_1, x_2) = \frac{\theta\alpha(x_1 - y_2)N_1^*(x_1, x_2)}{1 + h\alpha(x_1 - y_2)N_1^*(x_1, x_2)} - d. \tag{7}$$

The fate of these mutants is determined by the invasion fitness function $f_1(y_1, x_1, x_2)$ and $f_2(y_2, x_1, x_2)$. The quantities that determine the direction of gradual evolutionary change are the selection gradients of $f_1(y_1, x_1, x_2)$ and $f_2(y_2, x_1, x_2)$ with respect to mutant trait values at the resident trait values. By direct calculations, we obtain

$$\begin{aligned} g_1(x_1,x_2) &= \left.\frac{\partial f_1(y_1,x_1,x_2)}{\partial y_1}\right|_{y_1=x_1} \\ &= \frac{rN_1^*(x_1,x_2)K'(x_1)}{K^2(x_1)} - \frac{\alpha'(x_1-x_2)N_2^*(x_1,x_2)}{(1+h\alpha(x_1-x_2)N_1^*(x_1,x_2))^2}, \\ g_2(x_1,x_2) &= \left.\frac{\partial f_2(y_2,x_1,x_2)}{\partial y_2}\right|_{y_2=x_2} = -\frac{\theta\alpha'(x_1-x_2)N_1^*(x_1,x_2)}{(1+h\alpha(x_1-x_2)N_1^*(x_1,x_2))^2}, \end{aligned} \tag{8}$$

where

$$K'(x_1) = \frac{-(x_1-x_0)}{\sigma_K^2}K(x_1), \qquad \alpha'(x_1-x_2) = \frac{-(x_1-x_2)}{\sigma_\alpha^2}\alpha(x_1-x_2),$$

and the functions $\alpha(x_1-x_2)$ and $K(x_1)$ are given by (1) and (2), respectively. More precisely, by Dieckmann and Law [9], if mutations are random and sufficiently small, the evolutionary dynamics of the trait vector $(x_1,x_2)^\top$ is given by

$$\begin{aligned} \frac{dx_1}{dt} &= m_1(x_1,x_2)g_1(x_1,x_2), \\ \frac{dx_2}{dt} &= m_2(x_1,x_2)g_2(x_1,x_2), \end{aligned} \tag{9}$$

where $g_1(x_1,x_2)$ and $g_2(x_1,x_2)$ are the selection gradients described in (8), $m_1(x_1,x_2)$ and $m_2(x_1,x_2)$ are the evolutionary rates of the prey and predator describing how the mutational process influences the speed of evolution; that is,

$$\begin{aligned} m_1(x_1,x_2) &= \frac{1}{2}\mu_1\sigma_1^2 N_1^*(x_1,x_2), \\ m_2(x_1,x_2) &= \frac{1}{2}\mu_2\sigma_2^2 N_2^*(x_1,x_2), \end{aligned} \tag{10}$$

where μ_1 is the probability that the birth event in the prey is a mutant, μ_2 is the probability that the birth event in the predator is a mutant, σ_1^2 and σ_2^2 are the variance of the phenotypic effect of prey and predator mutation respectively.

3. **The properties of the singular points.**

The singular points of the evolutionary dynamics (9) are those points (x_1^*,x_2^*) in trait space for which both selection gradients vanish; that is,

$$\begin{aligned} g_1(x_1^*,x_2^*) &= 0, \\ g_2(x_1^*,x_2^*) &= 0. \end{aligned} \tag{11}$$

By direct calculations, we obtain a unique singular point $(x_1^*,x_2^*) = (x_0,x_0)$. We see that the singular point occurs at the maximum of the resource distribution. Whether the point (x_0,x_0) is an evolutionary attractor or not can be seen from the Jacobian matrix of the evolutionary dynamics (9) at the point (see Marrow et al. [24], Leimar [20]).

The Jacobian matrix J_1 of the evolutionary dynamics (9) at the point (x_0,x_0) is given by

$$J_1 = \begin{bmatrix} m_1(x_1,x_2)\frac{\partial g_1(x_1,x_2)}{\partial x_1} & m_1(x_1,x_2)\frac{\partial g_1(x_1,x_2)}{\partial x_2} \\ m_2(x_1,x_2)\frac{\partial g_2(x_1,x_2)}{\partial x_1} & m_2(x_1,x_2)\frac{\partial g_2(x_1,x_2)}{\partial x_2} \end{bmatrix}_{x_1=x_2=x_0}$$

$$= \begin{bmatrix} m_1(x_0,x_0)\left(-\frac{rN_1^*(x_0,x_0)}{K_0\sigma_K^2} + \frac{\alpha_0 N_2^*(x_0,x_0)}{\sigma_\alpha^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}\right) & A_1 \\ m_2(x_0,x_0)\left(\frac{\theta\alpha_0 N_1^*(x_0,x_0)}{\sigma_\alpha^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}\right) & A_2 \end{bmatrix},$$

where

$$A_1 = m_1(x_0,x_0)\left(-\frac{\alpha_0 N_2^*(x_0,x_0)}{\sigma_\alpha^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}\right),$$

$$A_2 = m_2(x_0,x_0)\left(-\frac{\theta\alpha_0 N_1^*(x_0,x_0)}{\sigma_\alpha^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}\right),$$

$$N_1^*(x_0,x_0) = \frac{d}{\alpha_0(\theta-hd)}, \qquad N_2^*(x_0,x_0) = \frac{r\theta}{K_0\alpha_0(\theta-hd)}(K_0 - N_1^*(x_0,x_0)),$$
$$m_1(x_0,x_0) = \frac{1}{2}\mu_1\sigma_1^2 N_1^*(x_0,x_0), \quad m_2(x_0,x_0) = \frac{1}{2}\mu_2\sigma_2^2 N_2^*(x_0,x_0). \tag{12}$$

If we denote $m_1(x_0,x_0)$ by m_1 and $m_2(x_0,x_0)$ by m_2, we obtain

$$J_1 = \begin{bmatrix} \frac{rm_1}{K_0\alpha_0}\left(\frac{K_0\alpha_0(\theta-hd)-d}{\theta\sigma_\alpha^2} - \frac{d}{\sigma_K^2(\theta-hd)}\right) & -\frac{rm_1(K_0\alpha_0(\theta-hd)-d)}{\theta K_0\alpha_0\sigma_\alpha^2} \\ \frac{m_2 d(\theta-hd)}{\theta\sigma_\alpha^2} & -\frac{m_2 d(\theta-hd)}{\theta\sigma_\alpha^2} \end{bmatrix}.$$

The determinant of the Jacobian matrix J_1 is given by

$$\det(J_1) = \frac{d^2 r m_1 m_2}{\theta K_0\alpha_0\sigma_\alpha^2\sigma_K^2}. \tag{13}$$

Obviously, the determinant of the Jacobian matrix J_1 is always positive. The trace of the Jacobian matrix J_1 is

$$\operatorname{tr}(J_1) = \frac{rm_1}{K_0\alpha_0}\left(\frac{K_0\alpha_0(\theta-hd)-d}{\theta\sigma_\alpha^2} - \frac{d}{\sigma_K^2(\theta-hd)}\right) - \frac{m_2 d(\theta-hd)}{\theta\sigma_\alpha^2}. \tag{14}$$

It can be seen that the trace of the Jacobian matrix J_1 may be positive or negative.

LEMMA 3.1. *The singular point (x_0,x_0) of the evolutionary dynamics (9) is an evolutionary attractor if one of the following conditions is satisfied:*
(1) $\theta > hd$ and $dm_2 \geq rm_1$,
(2) $\theta > hd$ and $K_0\alpha_0\sigma_K^2(\theta-hd)^2 \leq d\theta\sigma_\alpha^2$,
(3) $\theta > hd$ and $K_0\alpha_0\sigma_K^2(\theta-hd)^2 < d(\theta\sigma_\alpha^2 + (\theta-hd)\sigma_K^2)$.

Proof. If one of these conditions holds, it follows from (14) that the trace of the Jacobian matrix J_1 is negative. Note that the determinant of the Jacobian matrix J_1 is always positive. Therefore, both eigenvalues of the Jacobian matrix J_1 have negative real parts, and therefore, the point (x_0,x_0) is an evolutionary attractor. □

Note that in case (1), the stability of the singular point depends on the mutational constants m_1 and m_2. That is, for given selection gradients $g_1(x_1,x_2)$ and $g_2(x_1,x_2)$, a singular point may be an attractor for some values of m_1 and m_2 but not for others [24].

Just as in one-dimensional adaptive dynamics, a singular point (x_1^*, x_2^*) that is an attractor for evolutionary dynamics may not represent the endpoint of the evolutionary process if one or both species find themselves at a fitness minimum at the singular point (x_1^*, x_2^*) (see Geritz et al. [14]). The conditions for fitness minima at a singular point (x_1^*, x_2^*) are those at which the invasion fitness functions have minima with respect to the mutational trait values at this singular point; that is,

$$\begin{aligned} \left.\frac{\partial^2 f_1(y_1, x_1, x_2)}{\partial y_1^2}\right|_{\substack{x_2 = x_2^*,\\ y_1 = x_1 = x_1^*}} &> 0, \\ \left.\frac{\partial^2 f_2(y_2, x_1, x_2)}{\partial y_2^2}\right|_{\substack{x_1 = x_1^*,\\ y_2 = x_2 = x_2^*}} &> 0, \end{aligned} \tag{15}$$

since

$$g_1(x_1^*, x_2^*) = \left.\frac{\partial f_1(y_1, x_1, x_2)}{\partial y_1}\right|_{\substack{x_2 = x_2^*,\\ y_1 = x_1 = x_1^*}} = 0,$$

$$g_2(x_1^*, x_2^*) = \left.\frac{\partial f_2(y_2, x_1, x_2)}{\partial y_2}\right|_{\substack{x_1 = x_1^*,\\ y_2 = x_2 = x_2^*}} = 0.$$

In our model, $(x_1^*, x_2^*) = (x_0, x_0)$. By direct calculations, we obtain

$$\begin{aligned} \left.\frac{\partial^2 f_1(y_1, x_1, x_2)}{\partial y_1^2}\right|_{\substack{x_2 = x_0,\\ y_1 = x_1 = x_0}} &= \frac{r}{K_0\alpha_0}\left(\frac{K_0\alpha_0(\theta - hd) - d}{\theta\sigma_\alpha^2} - \frac{d}{\sigma_K^2(\theta - hd)}\right), \\ \left.\frac{\partial^2 f_2(y_2, x_1, x_2)}{\partial y_2^2}\right|_{\substack{x_1 = x_0,\\ y_2 = x_2 = x_0}} &= -\frac{d(\theta - hd)}{\theta\sigma_\alpha^2}. \end{aligned} \tag{16}$$

Note that $\theta > hd$. Thus

$$\left.\frac{\partial^2 f_2(y_2, x_1, x_2)}{\partial y_2^2}\right|_{\substack{x_1 = x_0,\\ y_2 = x_2 = x_0}} = -\frac{d(\theta - hd)}{\theta\sigma_\alpha^2} < 0.$$

In one-dimensional adaptive dynamics, a fitness minimum at an attracting singular point is sufficient for evolutionary branching [14]. However, in higher-dimensional adaptive dynamics, this need not be true anymore. For example, in adaptive dynamics of two correlated traits in a single species, convergent stable fitness minima alone need not generate evolutionary branching. However, for the present model, if one (or both) of the species are at a fitness minimum at an attracting singular point, then evolutionary branching can occur in one (or both) species. This is because, in our evolutionary model, the two traits belong to the two different species and they are uncorrelated. A timescale separation argument then shows that, at the singular point, each resident phenotypic trait can be considered as a parameter for the evolutionary dynamics of the other species, which in effect reduces the two-dimensional problem at the singular point to the one-dimensional case, where a fitness minimum at an attracting singular point is sufficient for evolutionary branching.

Definition 3.1. *A strategy is a continuously stable strategy (CSS) if it is an attractor of directional evolution; moreover, once it is established, the population cannot be invaded by any nearby strategy.*

THEOREM 3.1. *Assume that $\theta > hd$. Then the singular point (x_0, x_0) of the evolutionary dynamics (9) is a continuously stable strategy if one of the following conditions holds:*

(1) $K_0\alpha_0\sigma_K^2(\theta - hd)^2 < d(\theta\sigma_\alpha^2 + (\theta - hd)\sigma_K^2)$;
(2) $K_0\alpha_0\sigma_K^2(\theta - hd)^2 \leq d\theta\sigma_\alpha^2$.

Proof. Since $\theta > hd$, if (1) or (2) holds, it follows from Lemma 3.1 that the singular point (x_0, x_0) is an evolutionary attractor. Further, by (16) we have

$$\left.\frac{\partial^2 f_1(y_1, x_1, x_2)}{\partial y_1^2}\right|_{\substack{x_2=x_0,\\ y_1=x_1=x_0}} = \frac{r}{K_0\alpha_0}\left(\frac{(K_0\alpha_0(\theta - hd) - d)}{\theta\sigma_\alpha^2} - \frac{d}{\sigma_K^2(\theta - hd)}\right) < 0.$$

Note that

$$\left.\frac{\partial^2 f_2(y_2, x_1, x_2)}{\partial y_2^2}\right|_{\substack{x_1=x_0,\\ y_2=x_2=x_0}} = -\frac{d(\theta - hd)}{\theta\sigma_\alpha^2} < 0.$$

The point (x_0, x_0) is a fitness maximum for both prey and predator. Therefore, the evolutionary attractor (x_0, x_0) is stable against invasion of neighboring phenotypes; that is, the singular point (x_0, x_0) is a continuously stable strategy (CSS) [12]. □

LEMMA 3.2. *If $\theta > hd$, then the singular point (x_0, x_0) of the evolutionary dynamics (9) is not an evolutionary branching point for the predator.*

Proof. If $\theta > hd$, by (16) we have

$$\left.\frac{\partial^2 f_2(y_2, x_1, x_2)}{\partial y_2^2}\right|_{\substack{x_1=x_0,\\ y_2=x_2=x_0}} = -\frac{d(\theta - hd)}{\theta\sigma_\alpha^2} < 0.$$

The predator can not converge to a fitness minimum. Therefore, the singular point (x_0, x_0) is not an evolutionary branching point for the predator. □

THEOREM 3.2. *Assume that $\theta > hd$. The singular point (x_0, x_0) of the evolutionary dynamics (9) is an evolutionary branching point for the prey if we have the following conditions:*

(1) *$rm_1 \leq dm_2$ and*
(2) *$\sigma_K^2(\theta - hd)(K_0\alpha_0(\theta - hd) - d) > d\theta\sigma_\alpha^2$.*

Proof. If (1) holds, from Lemma 3.1, we see that the singular point (x_0, x_0) is an evolutionary attractor. If (2) holds, by (16) we obtain

$$\left.\frac{\partial^2 f_1(y_1, x_1, x_2)}{\partial y_1^2}\right|_{\substack{x_2=x_0,\\ y_1=x_1=x_0}} = \frac{r}{K_0\alpha_0}\left(\frac{K_0\alpha_0(\theta - hd) - d}{\theta\sigma_\alpha^2} - \frac{d}{\sigma_K^2(\theta - hd)}\right) > 0.$$

The point (x_0, x_0) is a fitness minimum for the prey. Therefore, evolutionary branching can occur for the prey, and the singular point (x_0, x_0) is an evolutionary branching point for the prey. □

Note that these conditions are easily satisfied. For example, set $\theta > hd$ and $m_1 \leq m_2$ and $r = d = 1$. Then condition (1) is satisfied. If $K_0\alpha_0(\theta - hd) > d$ and σ_α is small enough, then condition (2) is satisfied [11].

Once the prey has branched, selection pressures for the predator change. Because of the symmetry in the system, the two prey branches are at equal distance δ on the opposite sides of the singular predator trait x_0. Let $N_1(t)$ denote the prey population size at time t

$$\alpha(\delta) = \alpha_0 \exp\left(-\frac{\delta^2}{2\sigma_\alpha^2}\right).$$

Then we have

THEOREM 3.3. *Assume that $\theta > hd$. Then the evolutionary branching in the prey can induce the secondary branching in the predator population if we have the following:*

(1) $rm_1 \leq dm_2$ *and* $\sigma_K^2(\theta - hd)(K_0\alpha_0(\theta - hd) - d) > d\theta\sigma_\alpha^2$ *and*
(2) $h\alpha(\delta)N_1(t) < 2$ *and* $\frac{\delta^2}{\sigma_\alpha^2} > \frac{2+h\alpha(\delta)N_1(t)}{2-h\alpha(\delta)N_1(t)}$.

Proof. If (1) holds, by Theorem 3.2, we see that the prey will split into two different and divergent phenotype clusters. When the prey populations have branched, selection pressures for the predator change. Because of the symmetry in the system, at time t, the growth rate of a rare mutant predator with trait y_2 is given by

$$f_2(y_2, \delta, x_0, t) = -d + \frac{\theta\alpha(x_0 + \delta - y_2)\frac{N_1(t)}{2}}{1 + h\alpha(x_0 + \delta - y_2)\frac{N_1(t)}{2}} + \frac{\theta\alpha(x_0 - \delta - y_2)\frac{N_1(t)}{2}}{1 + h\alpha(x_0 - \delta - y_2)\frac{N_1(t)}{2}}, \tag{17}$$

where the function α is given by (1). Taking the second derivative with respect to mutant trait value y_2 at the resident trait value x_0 reveals whether the predator is located at a fitness minimum after the prey populations have branched. Note that $\alpha(\delta)$ is symmetric about the origin, we obtain

$$\left.\frac{\partial^2 f_2(y_2, \delta, x_0, t)}{\partial y_2^2}\right|_{y_2=x_0} = \frac{\theta N_1(t)\alpha(\delta)(-1 - h\alpha(\delta)\frac{N_1(t)}{2} + \frac{\delta^2}{\sigma_\alpha^2}(1 - h\alpha(\delta)\frac{N_1(t)}{2}))}{\sigma_\alpha^2(1 + h\alpha(\delta)\frac{N_1(t)}{2})^3}. \tag{18}$$

If (2) holds, that is, the two prey branches have moved far away enough from x_0, by (18) we have

$$\left.\frac{\partial^2 f_2(y_2, \delta, x_0, t)}{\partial y_2^2}\right|_{y_2=x_0} = \frac{\theta N_1(t)\alpha(\delta)(-1 - h\alpha(\delta)\frac{N_1(t)}{2} + \frac{\delta^2}{\sigma_\alpha^2}(1 - h\alpha(\delta)\frac{N_1(t)}{2}))}{\sigma_\alpha^2(1 + h\alpha(\delta)\frac{N_1(t)}{2})^3} > 0.$$

In this case, the singular point (x_0, x_0) is a fitness minimum for the predator. Once this happens, the evolutionary branching in the prey can induce secondary branching in the predator. The outcome of the evolutionary process is two prey species, and each prey species is exploited by a special predator. □

Note that these conditions are easily satisfied. For example, if δ is large enough, that is, the two prey branches have moved far away enough from x_0, and the other conditions are the same as those in Theorem 3.2, then conditions (1) and (2) are satisfied.

THEOREM 3.4. *Assume that $\theta > hd$. Then the singular point (x_0, x_0) of the evolutionary dynamics (9) is unstable if*

$$K_0\alpha_0\sigma_K^2(\theta - hd)^2(rm_1 - dm_2) > drm_1(\sigma_K^2(\theta - hd) + \theta\sigma_\alpha^2). \tag{19}$$

Proof. (19) implies that the trace of the Jacobian matrix J_1 is positive. Note that the determinant of the Jacobian matrix J_1 is always positive. Thus, the Jacobian matrix J_1 has eigenvalues with positive real parts, and the singular point (x_0, x_0) is unstable. $\square$

From Theorem 3.4, we can see that there are certain classes of fixed points which are definitely evolutionary repellers, but others could be either repellers or attractors. For example, the ω-limit set is a limit cycle [31]. This can be seen in the next section.

4. **Hopf bifurcation.** The objective of this section is to analyze the Hopf bifurcations and bifurcation directions of the adaptive dynamics. From Lemma 3.1 and Theorem 3.4, we see that the stability of the singular point depends on the mutational constants. Set

$$\begin{aligned} m_1^* &= m_1(x_0, x_0) = \frac{1}{2}\mu_1\sigma_1^2 N_1^*(x_0, x_0), \\ m_2^* &= m_2(x_0, x_0) = \frac{1}{2}\mu_2\sigma_2^2 N_2^*(x_0, x_0), \end{aligned} \tag{20}$$

where $N_1^*(x_0, x_0)$ and $N_2^*(x_0, x_0)$ are described in (12). We obtain

THEOREM 4.1. *Assume that $\theta > hd$. Then*
(1) The singular point (x_0, x_0) of the evolutionary dynamics (9) is an evolutionary attractor if

$$m_2^* > m_1^* \left[\frac{N_2^*(x_0, x_0)}{\theta N_1^*(x_0, x_0)} - \frac{r\sigma_\alpha^2(1 + h\alpha_0 N_1^*(x_0, x_0))^2}{\theta K_0 \alpha_0 \sigma_K^2} \right]. \tag{21}$$

(2) The singular point (x_0, x_0) of the evolutionary dynamics (9) is unstable if

$$m_2^* < m_1^* \left[\frac{N_2^*(x_0, x_0)}{\theta N_1^*(x_0, x_0)} - \frac{r\sigma_\alpha^2(1 + h\alpha_0 N_1^*(x_0, x_0))^2}{\theta K_0 \alpha_0 \sigma_K^2} \right]. \tag{22}$$

Proof. Set

$$A = \frac{N_1^*(x_1, x_2)}{N_1^*(x_0, x_0)}, \quad B = \frac{N_2^*(x_1, x_2)}{N_2^*(x_0, x_0)}.$$

Then, system (9) becomes

$$\begin{aligned} \frac{dx_1}{dt} &= A m_1^* g_1(x_1, x_2), \\ \frac{dx_2}{dt} &= B m_2^* g_2(x_1, x_2), \end{aligned} \tag{23}$$

where $g_1(x_1, x_2)$ and $g_2(x_1, x_2)$ are described in (8).

Set

$$dt = (\sigma_\alpha^2(1 + h\alpha(x_1 - x_2)N_1^*(x_1, x_2))^2)d\tau. \tag{24}$$

If $d\tau > 0$, then $dt > 0$, this is because $\sigma_\alpha^2(1 + h\alpha(x_1 - x_2)N_1^*(x_1, x_2))^2 > 0$. Thus, system (23) is equivalent to

$$\begin{aligned} \frac{dx_1}{d\tau} &= A m_1^* \left(N_2^*(x_1, x_2)(x_1 - x_2)\alpha(x_1 - x_2) - \psi(x_1, x_2) \right), \\ \frac{dx_2}{d\tau} &= B m_2^* \theta N_1^*(x_1, x_2)(x_1 - x_2)\alpha(x_1 - x_2), \end{aligned} \tag{25}$$

where

$$\psi(x_1, x_2) = \frac{r\sigma_\alpha^2 N_1^*(x_1, x_2)(x_1 - x_0)(1 + h\alpha(x_1 - x_2)N_1^*(x_1, x_2))^2}{\sigma_K^2 K(x_1)}.$$

The Jacobian matrix J_2 of system (25) at (x_0, x_0) is given by

$$J_2 = \begin{bmatrix} m_1^*\alpha_0 N_2^*(x_0,x_0) - \frac{m_1^* r\sigma_\alpha^2 N_1^*(x_0,x_0)(1+h\alpha_0 N_1^*(x_0,x_0))^2}{K_0\sigma_K^2} & -m_1^*\alpha_0 N_2^*(x_0,x_0) \\ m_2^*\theta\alpha_0 N_1^*(x_0,x_0) & -m_2^*\theta\alpha_0 N_1^*(x_0,x_0) \end{bmatrix}.$$

The determinant of J_2 is

$$\det(J_2) = \frac{m_1^* m_2^* \theta\alpha_0 r\sigma_\alpha^2 (N_1^*(x_0,x_0))^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}{K_0\sigma_K^2}. \tag{26}$$

Obviously, the determinant of the Jacobian matrix J_2 is always positive. The trace of J_2 is given by

$$\begin{aligned} \operatorname{tr}(J_2) &= m_1^*\alpha_0 N_2^*(x_0,x_0) - m_2^*\theta\alpha_0 N_1^*(x_0,x_0) \\ &\quad - \frac{m_1^* r\sigma_\alpha^2 N_1^*(x_0,x_0)(1+h\alpha_0 N_1^*(x_0,x_0))^2}{K_0\sigma_K^2}. \end{aligned} \tag{27}$$

It follows that (21) implies that $\operatorname{tr}(J_2) < 0$, which means that the singular point (x_0, x_0) is an evolutionary attractor, and (22) implies that $\operatorname{tr}(J_2) > 0$, which means that the point (x_0, x_0) is unstable. □

Let us now verify the existence of a Hopf bifurcation in (9) and determine its direction [32]. Set

$$h_0 = m_1^* \left[\frac{N_2^*(x_0,x_0)}{\theta N_1^*(x_0,x_0)} - \frac{r\sigma_\alpha^2(1+h\alpha_0 N_1^*(x_0,x_0))^2}{\theta K_0\alpha_0\sigma_K^2} \right].$$

THEOREM 4.2. *Assume that* $\theta > hd$.
(1) If $K_0\alpha_0(\theta - hd) > d$ *and* $(\theta - hd)(K_0\alpha_0(\theta - hd) - d) > d(\theta - 2hd)$, *then there is a family of stable limit cycles in (9) if* m_2 *is less than and near* h_0; *that is, a supercritical Hopf bifurcation occurs when* m_2 *passes through* h_0 *from right to left.*
(2) If $K_0\alpha_0(\theta - hd) > d$ *and* $(\theta - hd)(K_0\alpha_0(\theta - hd) - d) < d(\theta - 2hd)$, *then there is a family of unstable limit cycles in (9) if* m_2 *is greater than and near* h_0; *that is, a subcritical Hopf bifurcation occurs when* m_2 *passes through* h_0 *from right to left.*

Proof. As in the proof of Theorem 4.1, system (9) is equivalent to system (25). If $m_2^* = h_0$, then $\operatorname{tr}(J_2) = 0$. Set

$$\omega = \sqrt{\det(J_2)} = \frac{\sigma_\alpha N_1^*(x_0,x_0)(1+h\alpha_0 N_1^*(x_0,x_0))}{\sigma_K}\sqrt{\frac{m_2^* m_1^* r\theta\alpha_0}{K_0}}.$$

Then the eigenvalues of J_2 with $m_2^* = h_0$ are $\lambda_1 = \omega i$ and $\lambda_2 = -\omega i$.

By performing coordinate transformations by $x = x_1 - x_0, y = x_2 - x_0$, system (25) becomes

$$\begin{aligned} \frac{dx}{dt} &= Am_1^*\left(N_2^*(x-y)\alpha(x-y) - \frac{r\sigma_\alpha^2 N_1^* x(1+h\alpha(x-y)N_1^*)^2}{\sigma_K^2 K(x+x_0)}\right), \\ \frac{dy}{dt} &= Bm_2^*\theta N_1^*(x-y)\alpha(x-y), \end{aligned} \tag{28}$$

where τ is represented by t and

$$N_1^* = N_1^*(x+x_0, y+x_0), \ N_2^* = N_2^*(x+x_0, y+x_0), \ A = \frac{N_1^*}{N_1^*(x_0,x_0)}, \ B = \frac{N_2^*}{N_2^*(x_0,x_0)}.$$

Let

$$\begin{aligned} \alpha(x-y) &= \alpha_0 \exp\left(\frac{-(x-y)^2}{2\sigma_\alpha^2}\right), \\ K(x+x_0) &= K_0 \exp\left(-\frac{x^2}{2\sigma_K^2}\right). \end{aligned} \tag{29}$$

Then, system (28) becomes

$$\begin{aligned} \frac{dx}{dt} &= (b-c)x - by + f_0(x,y), \\ \frac{dy}{dt} &= ax - ay + g_0(x,y), \end{aligned} \tag{30}$$

where

$$\begin{aligned} f_0(x,y) &= b\,(x-y)\exp\left(\frac{-(x-y)^2}{2\sigma_\alpha^2}\right) - px\exp\left(-\frac{x^2}{2\sigma_K^2}\right)\left(1+q\exp\left(\frac{-(x-y)^2}{2\sigma_\alpha^2}\right)\right)^2 \\ &\quad + by + cx - bx, \\ g_0(x,y) &= a\,(x-y)\exp\left(\frac{-(x-y)^2}{2\sigma_\alpha^2}\right) + ay - ax, \end{aligned} \tag{31}$$

and

$$b = m_1^*\alpha_0 N_2^*(x_0,x_0), \quad c = \frac{m_1^* r\sigma_\alpha^2 N_1^*(x_0,x_0)(1+h\alpha_0 N_1^*(x_0,x_0))^2}{K_0\sigma_K^2},$$

$$a = m_2^*\theta\alpha_0 N_1^*(x_0,x_0), \quad p = \frac{m_1^* r\sigma_\alpha^2 N_1^*}{K_0\sigma_K^2}, \quad q = h\alpha_0 N_1^*.$$

Set

$$u = x \quad \text{and} \quad v = -\frac{b-c}{\omega}x + \frac{b}{\omega}y. \tag{32}$$

Using $\mathrm{tr}(J_2) = b - c - a = 0$ and $\omega^2 = \det(J_2) = ac$, we obtain

$$\begin{aligned} \frac{du}{dt} &= -\omega v + f(u,v), \\ \frac{dv}{dt} &= \omega u + g(u,v), \end{aligned} \tag{33}$$

where

$$\begin{aligned} f(u,v) &= cu\varphi(u,v) - \omega v\varphi(u,v) - 2pqu\varphi(u,v)\phi(u) - pq^2u\phi(u)(\varphi(u,v))^2 + \omega v, \\ g(u,v) &= \frac{1}{\omega}(-bcu\varphi(u,v) + b\omega v\varphi(u,v) + 2bpqu\phi(u)\varphi(u,v) + bpq^2u\phi(u)(\varphi(u,v))^2 \\ &\quad + c^2u\varphi(u,v) - c\omega v\varphi(u,v) - cpu\phi(u) - 2cpqu\varphi(u,v)\phi(u) + bpu\phi(u) \\ &\quad - cpq^2u(\varphi(u,v))^2\phi(u) + acu\varphi(u,v) - a\omega v\varphi(u,v) - acu), \end{aligned} \tag{34}$$

and

$$\varphi(u,v) = \exp\left(-\frac{(cu-\omega v)^2}{2b^2\sigma_\alpha^2}\right), \quad \phi(u) = \exp\left(-\frac{u^2}{2\sigma_K^2}\right).$$

Let

$$\begin{aligned} \mu &= \frac{1}{16}\left[f_{uuu} + f_{uvv} + g_{uuv} + g_{vvv}\right] \\ &\quad + \frac{1}{16\omega}\left[f_{uv}(f_{uu}+f_{vv}) - g_{uv}(g_{uu}+g_{vv}) - f_{uu}g_{uu} + f_{vv}g_{vv}\right], \end{aligned} \tag{35}$$

which is evaluated at the origin. By some tedious calculations, we obtain

$$\mu = -\frac{3c}{16b\sigma_\alpha^2\sigma_K^2}\left[\sigma_K^2 p(1-q^2) - b\sigma_\alpha^2\right]. \tag{36}$$

When $u = 0$ and $v = 0$, we have

$$p = \frac{m_1^* r\sigma_\alpha^2 N_1^*(x_0, x_0)}{K_0\sigma_K^2}, q = h\alpha_0 N_1^*(x_0, x_0), c = p(1+q)^2, b = m_1^*\alpha_0 N_2^*(x_0, x_0).$$

Substituting p, q, b into (36), we obtain

$$\mu = -\frac{3c}{16\sigma_K^2}\left[\frac{d(\theta - 2hd)}{(\theta - hd)(K_0\alpha_0(\theta - hd) - d)} - 1\right]. \tag{37}$$

Then, $\mu > 0$ if $K_0\alpha_0(\theta - hd) > d$ and $(\theta - hd)(K_0\alpha_0(\theta - hd) - d) > d(\theta - 2hd)$, and $\mu < 0$ if $K_0\alpha_0(\theta - hd) > d$ and $(\theta - hd)(K_0\alpha_0(\theta - hd) - d) < d(\theta - 2hd)$. The conclusion of this theorem follows from [18, Theorem 3.4.2 and formula (3.4.11)]. ☐

As an example, we fix $r = d = 1, \theta = 2.0, h = 1.0, \sigma_\alpha = 0.1, \sigma_K = 0.5, \mu_1 = 0.01, \sigma_1^2 = 0.01^2, \sigma_2^2 = 0.01^2, x_0 = 0.0, \alpha_0 = 0.001, K_0 = 2000.0$. Then, $\theta > hd, K_0\alpha_0(\theta - hd) > d, (\theta - hd)(K_0\alpha_0(\theta - hd) - d) > d(\theta - 2hd)$ and $h_0 = 0.00023$, the first part of Theorem 4.2 shows that there is a stable limit cycle in (9) when m_2 decreases from 0.00023, which is shown in Fig. 1.

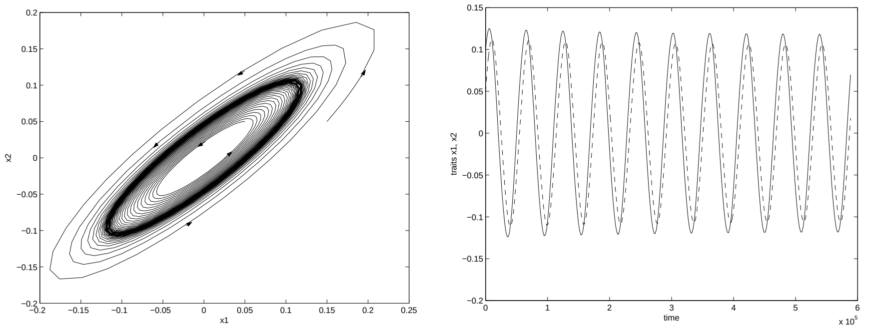

FIGURE 1. The prey and predator evolve to a stable limit cycle. Left graph gives the phase portrait of traits (x_1, x_2) and the right one gives the time series portrait where the solid line is the trait x_1 of prey and the dashed line is the trait x_2 of predator. Parameters: $r = d = 1, \theta = 2.0, h = 1.0, \sigma_\alpha = 0.1, \sigma_K = 0.5, \mu_1 = 0.01, \mu_2 = 0.004, \sigma_1^2 = 0.01^2, \sigma_2^2 = 0.01^2, x_0 = 0.0, \alpha_0 = 0.001, K_0 = 2000.0$.

This is of some biological interest, because it shows that the interactions between prey and predator are sufficient to keep the system evolving infinitely as discussed by Dieckmann et al. [8], and changes in the physical environment are not a prerequisite for continuing evolution. This corresponds to the Red Queen dynamics, in which the selection pressures arising from the prey-predator interactions cause the species to evolve infinitely.

5. **Simulation results.** In this section, we simulate some likely evolutionary states with different conversion efficiencies and evolutionary rates. It is found that different conversion efficiencies and evolutionary rates can markedly influence the dynamical behaviors of (9).

First, we consider the influence of different evolutionary rates. In the last section, we presented Fig. 1 as an example to illustrate that the prey and predator evolve to a stable evolutionary cycle. In that case, the evolutionary rates of the prey and predator are chosen in the ratio 5 : 2, i.e., $\frac{\mu_1\sigma_1^2}{\mu_2\sigma_2^2} = 5:2$. However, if the evolutionary rates of the prey and predator are chosen in the ratio 1 : 1 (i.e., the evolutionary speeds of the prey and predator are the same), then, instead of evolving to a stable evolutionary cycle, the prey and predator evolve to an evolutionary attractor [6]. Therefore, evolutionary cycle requires higher evolutionary speed of the prey than the predator. This is also supported by Fig. 2, where parameters are the same as in Fig. 1 except for $\mu_2 = 0.01$. Furthermore, if the evolutionary rates of the prey and predator are chosen in the ratio 25 : 2 (i.e., the evolutionary speed of the prey is much higher than the evolutionary speed of the predator), then the prey and predator evolve to a stable evolutionary cycle with a longer period of evolutionary cycle (Fig. 3, where the parameters are the same as in Fig. 1 except for $\mu_2 = 0.0008$).

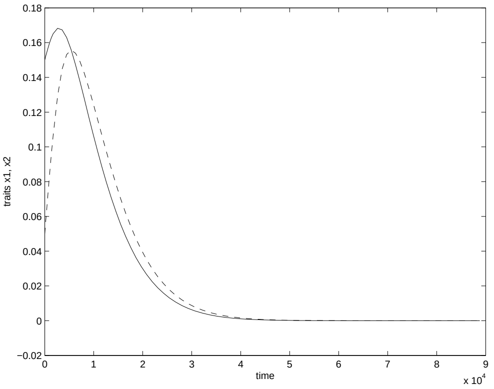

FIGURE 2. The prey and predator evolve to an evolutionary attractor where the parameters are the same as in Fig. 1 except for $\mu_2 = 0.01$.

Second, we consider the influence of different conversion efficiencies. In Fig. 1, with the conversion efficiency $\theta = 2.0$, the prey and predator evolve to a stable evolutionary cycle. However, if $\theta = 2.5$, i.e., the conversion efficiency of the predator is higher, then instead of evolving to a stable evolutionary cycle, the prey and predator evolve to an evolutionary attractor (Fig. 4, where the parameters are the same as in Fig. 1 except for $\theta = 2.5$).

6. **Discussion.** The problem of the coevolution of phenotypes in a community comprising a population of predator and prey has been investigated in this paper. The population model we consider is the well known prey-predator model with the functional response of Holling type II [34]. Following the adaptive dynamics approach [27], we investigate an evolutionary dynamics which is constructed from

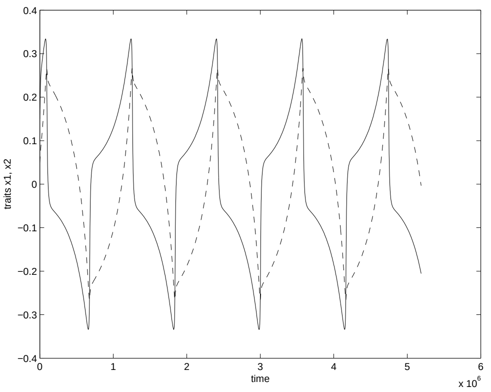

FIGURE 3. The prey and predator evolve to a stable evolutionary cycle with a longer period of evolutionary cycle, where the solid line is the trait x_1 of prey and the dashed line is the trait x_2 of predator. The parameters are the same as in Fig. 1 except for $\mu_2 = 0.0008$.

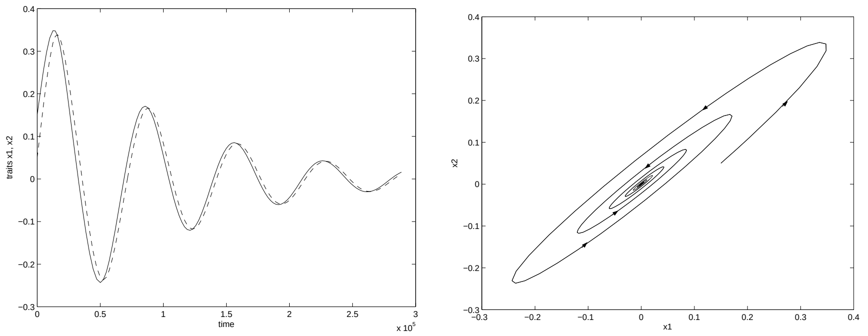

FIGURE 4. The prey and predator evolve to an evolutionary attractor under identical conditions as in Fig. 1 except for $\theta = 2.5$, where the solid line is the trait x_1 of prey and the dashed line is the trait x_2 of predator.

a stochastic process of mutation and selection. The first of two primary results of this paper is that, in investigating the ecological and evolutionary conditions that allow for continuously stable strategy and evolutionary branching, we have shown that the branching in the prey can induce the secondary branching in the predator. Evolutionary branching consists of two phases: in the first, there is a convergence in the phenotype space to an evolutionary attracting fitness minimum, and in the second, the population splits into two different phenotype clusters. The second primary result of this paper is that we have shown that the evolutionary dynamics admits a stable limit cycle. An evolutionary cycle is a likely outcome of the process, which requires higher evolutionary speed of the prey than the predator. There is no general rule in nature to say that phenotypic evolution would lead to a fixed point in the absence of external changes in the environment. The evolutionary cycle corresponds to the Red Queen dynamics, in which the selection pressures arising from the prey-predator interactions cause the species to evolve infinitely. We have also shown that the evolutionary dynamics admits a subcritical Hopf bifurcation. With the aid of computer simulations, we find that different evolutionary rates and conversion efficiencies can influence the dynamical behaviors of (9).

By our analysis of the evolutionary dynamics, we can see that a simple classification of the outcomes of phenotypic evolution can be constructed from three dichotomies: the first depends on whether an attractor exists [28], the second depends on whether the attractor is a fixed point [19, 24] and the third depends on whether the attractor is a fitness minimum for the species. This gives four classes of evolutionary states:

(1) evolution to a continuously stable strategy (CSS) (i.e., evolution to a fixed point with stationary phenotypes which is fitness maxima for the species);
(2) evolution to an evolutionary cycle (i.e., evolution to an attractor that is not a fixed point on which the phenotypes continue to change infinitely);
(3) evolution to an evolutionary branching point and then splitting into different phenotype clusters (i.e., evolution to a fixed point which is fitness minima for the species);
(4) evolution without an attractor, such that the phenotypes take more and more extreme values.

In this paper, we have considered a simple case of coevolution involving two species and two uncorrelated traits which belong to prey and predator respectively. However, in reality, matters are more complicated [15, 30, 13, 33, 25], since it is rare for a predator and prey species to live in isolation from other interactions [17]. Typically, they would be embedded in a food web with other species [16, 32]. Therefore, it will be interesting to study how these larger communities evolve [1]. Secondly, it will be also interesting to consider the asymmetric form of the predation efficiency $\alpha(x_1 - x_2)$ or correlated traits in the species. We leave these as a future work.

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