



Coevolutionary Chase in Two-species Systems with Applications to Mimicry

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We study a general dynamical model describing coevolution of two haploid populations with two alleles at a single locus under weak linear symmetric frequency-dependent selection. A novel and more realistic element of our modeling approach is that both species are allowed to evolve. We analyse conditions for “evolutionary chase” between two phenotypically similar species in which one species evolves to decrease its resemblance with the other species while this other species evolves to increase its resemblance with the first species. We apply our results to a series of simple population genetics models describing classical Müllerian and Batesian mimics as well as intermediate cases. We show that one of the most important factors influencing the plausibility of non-equilibrium dynamics in systems of mimicry is the relationship between the strength of between-species and within-species interactions. This indicates that this relationship should be the focus of both experimental and theoretical work. Our results suggest that systematic studies of frequencies of different mimicry morphs through time may be very useful.

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Introduction

Selection pressure resulting from between species interactions is thought to be very strong and is expected to result in coevolutionary changes in interacting species (e.g. Futuyma & Slatkin, 1983; Vermeij, 1987; Thompson, 1994). Numerous examples of coevolution of competitors, mutualists and victim–exploiter type systems (such as predator–prey and host–parasite systems) have been studied both experimentally and theoretically. Mimicry provides one of the clearest examples of natural selection and coevolution (Thompson, 1994). Mimicry describes a number of phenomena by which a species imitates another one. The most convincing examples are found in butterflies, but mimicry is also known to occur in birds, fish, reptiles, amphibians, mammals, moths, beetles, bugs, flies and snails (Owen, 1980; Pough, 1988) and fungi (Roy, 1993). In Batesian mimicry a palatable species mimics a species (the model) unpalatable to predators. In Müllerian

mimicry two (or more) unpalatable species resemble each other. The standard explanation for the resemblance both between Batesian model and mimic and between Müllerian mimics is natural selection by predation. The Batesian mimic increases its fitness by evolving to a phenotypic pattern that the predator tends to avoid. In the Müllerian case both species improve their protection by evolving to a similar phenotypic pattern that the predator learns to avoid more effectively.

Theoretical studies of the evolution of mimicry driven by predation have been, in general, of two types. One approach concentrates on the (optimal) behavior of the predator (e.g. Huheey, 1976, 1988; Owen & Owen, 1984; Getty, 1985). Another approach, which will concern us here, concentrates on the population dynamics and evolution of mimics and models, using either the standard population ecology framework or the standard population genetics framework. In the ecological framework the system is described in terms of (sub)population sizes (e.g.

Hadeler *et al.*, 1982; Yamauchi, 1993) and the specific dynamic equations are chosen from ecological considerations. In the genetic framework the concentration is on the evolution of genotype frequencies, population sizes are not considered, and all ecological interactions are incorporated into (frequency-dependent) fitness functions (e.g. Matessi & Cori, 1972; Turner, 1980; Mallet & Barton, 1989). This might be justifiable in many butterfly systems, where population density is largely controlled at the larval stage, whereas mimicry becomes important at the adult stage. Here, we will use the genetic approach, which results in simpler and more general mathematical models.

Previous analysis of the mathematical models has confirmed what biological intuition had suggested for maintenance of genetic variability: in classical Batesian mimicry stable polymorphism can be maintained in the mimic (Charlesworth & Charlesworth, 1975), while in classical Müllerian mimicry both species inevitably lose variability. Another interesting dynamical possibility in the Batesian case was described by Fisher (1930) who wrote that “the resemblance which is favorable to the mimic will be . . . disadvantageous to the model. An individual of the model species may suffer from being mistaken for a mimic, and . . . selection will tend to modify the model so as to render it different from the mimic . . .” (p. 148). This can cause an evolutionary chase in which the model flees the mimic while the mimic pursues. This dynamical possibility is not limited to Batesian mimicry. If two unpalatable Müllerian mimics have unequal degrees of unpalatability and/or abundances of species, a “weaker” Müllerian mimic can benefit at the expense of the “stronger” mimic (e.g. Brown & Benson, 1974; Huheey, 1976; Sbordoni *et al.*, 1979; Hadeler *et al.*, 1982; Owen & Owen, 1984). In this case, genetic variability can be maintained (Owen & Owen, 1984) and an evolutionary chase between the “stronger” and the “weaker” Müllerian mimic might be possible (Huheey, 1988).

Surprisingly, the idea of an evolutionary chase between the mimic and the model or between a “weaker” and a “stronger” Müllerian mimic has not received any serious attention. In all previous models of mimicry only a single species was allowed to evolve; in the strict sense in these models *coevolution* of two species was not possible. The lack of interest in the dynamical behavior of mimicry systems reflects the dominant position of the equilibrium paradigm in population genetics. Frequency-dependent selection, which controls the evolution of mimicry systems, has been widely considered in the population genetics

literature as a potentially important mechanism for maintenance of genetic variability in natural populations (e.g. Cockerham *et al.*, 1972; Clarke, 1979; Asmussen & Basnayake, 1990). Frequency-dependent selection also can produce complex dynamical behavior including cycles and deterministic chaos in allele frequencies. The best known examples are models describing coevolution of host–parasite systems (e.g. May & Anderson, 1983; Seger, 1988; Seger & Hamilton, 1988). Complex dynamics are frequent in coevolving predator–prey systems (Seger, 1992) and in coevolving exploiter–victim systems with polygenic characters (Gavrilets, 1997). Cycles, chaos, intermittency and transient chaos arise as well in models of frequency-dependent selection describing a single species (Matessi & Cori, 1972; May, 1979; Hamilton, 1980; Turner, 1980; Altenberg, 1991; Holton & May, 1993; Gavrilets & Hastings, 1995). Unfortunately, the importance of nonlinear phenomena still has not been well recognized within the population genetics community (but see Ferriere & Fox, 1995). One of the reasons seems to be that the single-species models require complex and sometimes unrealistic interactions between different genotypes and very strong selection to produce complex dynamics.

Our first goal here is to formulate and study a general dynamical model describing coevolution of two haploid populations with two alleles at a single locus under weak linear symmetric frequency-dependent selection. Our second goal is to study a class of specific models describing coevolutionary dynamics of mimicry and to demonstrate that evolutionary chase is a likely outcome for a range of interactions of mimics. We will argue that the conclusions of previous authors (e.g. Matessi & Cori, 1972; Turner, 1980) about implausibility of cycling in the evolution of the systems of mimicry are due to the fact that by not allowing the second species to evolve these authors greatly restricted the dynamic behavior. Although our model, like these earlier ones, greatly oversimplifies the description of natural coevolving systems, we argue that the conclusions which do emerge from the simple models reflect general principles that will also govern the behavior of more complex and realistic systems. Our third goal is to contribute to a continuing effort to introduce nonlinear phenomena into population genetics by focusing on a classical system which has been intensively studied since the last century, so the complex dynamics arise naturally from a specific biological process. Additionally, the basic mathematical model describing this system is very simple: two ordinary differential equations. Finally, the

non-equilibrium behavior takes place under a broad range of parameter values not requiring, in particular, overall selection to be strong.

Coevolutionary Model

We consider two haploid populations of different species with non-overlapping generations. We will neglect random genetic drift and initially will neglect mutation. We will concentrate on a single locus with alleles **A** and **a** in species 1 and a single locus with alleles **B** and **b** in species 2. Let w_A , w_a , w_B and w_b be fitnesses (viabilities) of the corresponding morphs, and p_1 and p_2 be the frequencies of morph **A** within species 1 and morph **B** within species 2, respectively. Let $q_i = 1 - p_i$, $i = 1, 2$. The changes in allele frequencies are described by the standard equations

$$\Delta p_1 = p_1 q_1 (w_A - w_a) / \bar{w}_1, \quad (1a)$$

$$\Delta p_2 = p_2 q_2 (w_B - w_b) / \bar{w}_2, \quad (1b)$$

where \bar{w}_i is the mean fitness of the i -th species (for example, $\bar{w}_1 = w_A p_1 + w_a q_1$). We will assume that the fitness of an individual depends on the genetic composition of its own species as well on the genetic composition of the other species, i.e. $w_A = w_A(p_1, p_2)$, $w_a = w_a(p_1, p_2)$ etc. We will make the symmetry assumption that $w_A(p_1, p_2) = w_a(q_1, q_2)$, $w_B(p_1, p_2) = w_b(q_1, q_2)$ and use linear (i.e. the simplest) fitness functions. These assumptions result in the fitnesses

$$w_A = C_1 + ap_1 + bp_2, \quad w_a = C_1 + aq_1 + bq_2, \quad (2a)$$

$$w_B = C_2 + cp_1 + dp_2, \quad w_b = C_2 + cq_1 + dq_2, \quad (2b)$$

Here C_1 and C_2 are positive constants equal to the fitnesses of morphs **A** and **B** (or morphs **a** and **b**) when fixed in the populations. Parameters a and d characterize the strength of (indirect) within-species interactions. Positive values of a (d) imply that individuals of a given morph benefit when they are common. Negative values of a (d) imply that individuals of a given morph benefit when they are rare. Parameters b and c characterize the strength of (indirect) between-species interactions. Positive values of b (c) imply that a given morph benefits when its counterpart in another species is common. Negative values of b (c) imply that a given morph benefits when its counterpart in another species is rare. We will assume that selection is weak (in the sense that $|a|$,

$|b| \ll C_1$, $|c|$, $|d| \ll C_2$) which allows us to describe the dynamics using differential equations:

$$\dot{p}_1 = p_1 q_1 [a(p_1 - q_1) + b(p_2 - q_2)], \quad (3a)$$

$$\dot{p}_2 = p_2 q_2 [c(p_1 - q_1) + d(p_2 - q_2)], \quad (3b)$$

where $\dot{p}_i \equiv dp_i/dt$. Note that parameters a , b and c , d in (3) are different from those in (2) by the factors C_1 and C_2 , respectively. The main reason for all the simplifying assumptions leading to (3) is that they allow us to analyse the system analytically. We will argue below that complicating factors including strong selection, unsymmetric fitnesses, diploidy, spatial structure, etc. will definitely make the dynamics more complex. Before starting to analyse the whole system (3), it is useful to consider two simple partial cases.

ONLY A SINGLE SPECIES IS ALLOWED TO EVOLVE

If only a single species is allowed to evolve, which was the case in all previous models of mimicry systems, the dynamics are described by a single cubic differential equation, say for p_1 assuming that $p_2 = \text{const}$. This equation always has two monomorphic equilibria and can have a polymorphic equilibrium. The allele frequency p_1 monotonically evolves towards one of these equilibria depending on the parameter values, the genetic composition of the second species (characterized by p_2), and initial conditions.

NO WITHIN-SPECIES INTERACTIONS

If fitness of individuals of a species depends only on the genetic composition of another species and does not depend on the genetic composition of its own species (that is if $a = d = 0$), then the solutions of (3) satisfy

$$\frac{(p_2 q_2)^b}{(p_1 q_1)^c} = \text{const.}$$

If parameters b and c have different signs, these solutions are neutrally stable periodic orbits [encircling the polymorphic equilibrium (1/2, 1/2)]; any perturbation moves the system to a different periodic orbit. The dynamic behavior of (3) is similar to the behavior of the classical Lotka–Volterra predator–prey system (e.g. Hofbauer & Sigmund, 1988). If parameters b and c have the same sign, the system evolves to a state with both species monomorphic. The former case represents an appropriate assumption for modeling host–parasite systems (see May & Anderson, 1983; Seger, 1988; Seger & Hamilton, 1988; Andreasen & Christiansen, 1993; Frank,

1993a, b, 1994), while the latter case represents an appropriate assumption for describing coevolving species that compete or cooperate (see Frank, 1997).

Some Results on the Dynamical Behavior of the Coevolutionary Model

In this section we summarize results on the existence and stability of different solutions of the coevolutionary model (3). The corresponding proofs are given in the Appendix. In the following section, we apply these results to the evolution of different mimicry systems. Throughout the paper, $D \equiv ad - bc$.

The dynamical system (3) always has four equilibria with both species monomorphic and an equilibrium with both species polymorphic (at $p_1 = p_2 = 1/2$). There can also be four additional equilibria with one species polymorphic and another monomorphic.

RESULT 1 (EXISTENCE AND LINEAR STABILITY OF EQUILIBRIA)

Equilibria of the coevolutionary model (3) exist and are linearly stable if the corresponding conditions in Table 1 are satisfied.

The next result gives sufficient conditions for the absence of periodic solutions of (3). In this case, the analysis of equilibria as summarized in Result 1 is basically all one needs to understand the dynamics of the system.

RESULT 2 (NON-EXISTENCE OF PERIODIC ORBITS)

The coevolutionary model (3) does not have periodic orbits if the two species have similar effects of each other's fitness (i.e. coefficients b and c have the same sign).

What other behavior besides approach to equilibrium is possible? Chaotic behavior is excluded because the system is two-dimensional, but if the two species have different effects on each other's fitness (e.g. b and c have different signs), periodic orbits are not excluded. Assume that b and c have different signs. Also let $|a/b| < 1$ and $|d/c| < 1$ so consequently (3) does not have equilibria with one species monomorphic and another polymorphic (see Table 1). In this case, all four monomorphic equilibria are saddles. The dynamical system (3) has a heteroclinic cycle. That is the corresponding saddle trajectories ($p_1 = 0, p_2 = 1, p_1 = 1, p_2 = 0$) connect the saddle equilibria in a cyclical way. This cycle is directed clockwise if $b > 0, c < 0$, and is directed anti-clockwise if $b < 0, c > 0$. The next result gives conditions for stability of the heteroclinic cycle and conditions for existence and stability of a periodic orbit bifurcating from this heteroclinic cycle.

RESULT 3 (HETEROCLINIC BIFURCATION)

For definiteness take $b > 0, c < 0$. The heteroclinic cycle is linearly stable if $a/b - d/c > 0$ and unstable if $a/b - d/c < 0$. At the point $a/b - d/c = 0$ a periodic orbit bifurcates from the heteroclinic cycle.

TABLE 1
Conditions for existence and stability of equilibria of the coevolutionary model (3)

Equilibrium (p_1, p_2)	Conditions for existence	Conditions for stability
(0, 0)	Always	$a + b > 0, c + d > 0$
(1, 1)	Always	$a + b > 0, c + d > 0$
(0, 1)	Always	$a - b > 0, d - c > 0$
(1, 0)	Always	$a - b > 0, d - c > 0$
$(\frac{1}{2}, \frac{1}{2})$	Always	$a + d < 0, D > 0$
$(0, \frac{1}{2}(1 + \frac{c}{d}))$	$ c/d < 1$	$d < 0, D < 0$
$(1, \frac{1}{2}(1 - \frac{c}{d}))$	$ c/d < 1$	$d < 0, D < 0$
$(\frac{1}{2}(1 + \frac{b}{a}), 0)$	$ b/a < 1$	$a < 0, D < 0$
$(\frac{1}{2}(1 - \frac{b}{a}), 1)$	$ b/a < 1$	$a < 0, D < 0$

This bifurcation is supercritical (i.e. the periodic orbit exists for $a/b - d/c < 0$ and is stable) or subcritical (i.e. the periodic orbit exists for $a/b - d/c > 0$ and is unstable) depending on whether $a(b + c)/b$ is positive or negative. For the case when $b < 0$, $c > 0$, all the above inequalities should be reversed.

Now consider the polymorphic equilibrium at $p_1 = p_2 = 1/2$. This equilibrium exists always. If $D < 0$, this equilibrium is a saddle. We will assume that $D > 0$. The next result concerns conditions for existence and stability of a limit cycle bifurcating from the polymorphic equilibrium at $p_1 = p_2 = 1/2$.

RESULT 4 (POINCARÉ-ANDRONOV-HOPF BIFURCATION)

The polymorphic equilibrium $(1/2, 1/2)$ is linearly stable if $a + d < 0$ and unstable if $a + d > 0$. At the point $a + d = 0$, a periodic orbit bifurcates from this equilibrium. This bifurcation is supercritical (i.e. the periodic orbit exists for $a + d > 0$ and is stable) or subcritical (i.e. the periodic orbit exists for $a + d < 0$ and is unstable) depending on whether $-a(b + c)/b$ is negative or positive. For small values of $|a + d|$, the period and the amplitude of the periodic orbit are proportional to $2\pi/\sqrt{ad - bc}$ and $\sqrt{|a + d|}$, respectively.

An Application to the Evolution of Mimicry Systems

The two species whose coevolutionary dynamics are described by (3) can be considered as Batesian mimic and model or as two species belonging to the same Müllerian ring. Morph **A** is “similar” to morph **B** and morph **a** is “similar” to morph **b**. Biologically the symmetry assumption means that we include only

the effects of mimicry in our model and no costs or other aspects of fitness. Hence morphs within species are alike in the sense that there is no difference between **A** and **a** (**B** and **b**) except that they look similar to **B** and **b** (**A** and **a**), respectively. Positive values of a and/or d imply that individuals of a given morph benefit when they are common. This is the case when species 1 and/or 2 is unpalatable. Negative values of a and/or d imply that individuals of a given morph benefit when they are rare. This is the case when species 1 and/or 2 is palatable. Parameters b and c characterize the strength of indirect between-species interactions. These interactions are mediated through the “predator” and thereby indirect. Positive values of b and/or c imply that a given morph benefits when its counterpart in another species is common. This is the case when the other species is unpalatable. Negative values of b and/or c imply that a given morph benefits when its counterpart in another species is rare. This is the case when the other species is palatable or it is unpalatable but has a smaller degree of unpalatability (a weaker Müllerian mimic). The plausibility of the latter situations has been demonstrated using theoretical models (Haderl *et al.*, 1982; Owen & Owen, 1984). For related empirical studies see Brown & Benson (1974) and Sbordoni *et al.* (1979). Parameters a , b , c and d can be estimated experimentally by calculating the coefficients of the linear regression of fitness on the frequencies of morphs. See Lindstrom *et al.* (1997) for an appropriate experimental design. Note that Fig. 2 in Lindstrom *et al.* (1997) does suggest that frequency-dependent selection acting in the Batesian case may be adequately described by a linear model.

TABLE 2
Parameter configurations describing different types of mimicry

	Parameter configuration	Interpretation
“Classical” Müllerian mimicry	$a, b, c, d > 0$	Within each species a morph benefits when its own frequency or the frequency of its “counterpart” in the other species increases
“Classical” Batesian mimicry	$a, c < 0, b, d > 0$	Both species 1 (palatable mimic) and species 2 (unpalatable model) benefit from increasing the model frequency and suffer from increasing the mimic frequency
Two unpalatable species have different abundances and/or different degrees of unpalatability	$a, b, d > 0, c < 0$	Within each species a morph benefits when its own frequency increases. Species 1 (the “weaker” mimic) also benefits when the frequency of its “stronger” counterpart (from species 2) increases, but the “stronger” mimic suffers when its weaker counterpart increases in frequency

We now apply the above results on dynamic behavior of (3) to understand the evolutionary dynamics of different mimicry systems. We will consider three different parameter configurations (see Table 2).

“CLASSICAL” MÜLLERIAN MIMICRY

Let $a, b, c, d > 0$, i.e. within each species a morph benefits when its own frequency or the frequency of its “counterpart” in the other species increases. This case corresponds to “classical” Müllerian mimicry where two unpalatable species benefit from convergence to a similar phenotypic pattern. Using Results 1–4, one can show that the dynamics on the phase-plane (p_1, p_2) can only be as shown in Fig. 1. In this figure and in those below allele frequencies p_1 and p_2 change between 0 and 1, and the direction of change is indicated by arrows. Stable equilibria are given by black circles, while unstable equilibria are given by white circles. The results described in Fig. 1 can be summarized as follows.

Conclusion 1

In the classical Müllerian case the system evolves to an equilibrium state with both species monomorphic.

TWO UNPALATABLE SPECIES WITH UNEQUAL DEGREES OF UNPALATABILITY

Let $a, b, d > 0, c < 0$, i.e. within each species a morph benefits when its own frequency increases. Species 1 (the “weaker” mimic) also benefits when the frequency of its “stronger” counterpart (from species 2) increases, but the “stronger” mimic suffers when its weaker counterpart increases in frequency. This parameter configuration can happen when two unpalatable species have different abundances and/or different degrees of unpalatability (cf. Huheey, 1988; Owen & Owen, 1984). Using Results 1–4, one can show that the dynamics can only be as shown in Fig. 2.

For parameter values as used in Fig. 2(a) and 2(b), the heteroclinic cycle is stable and the system quickly

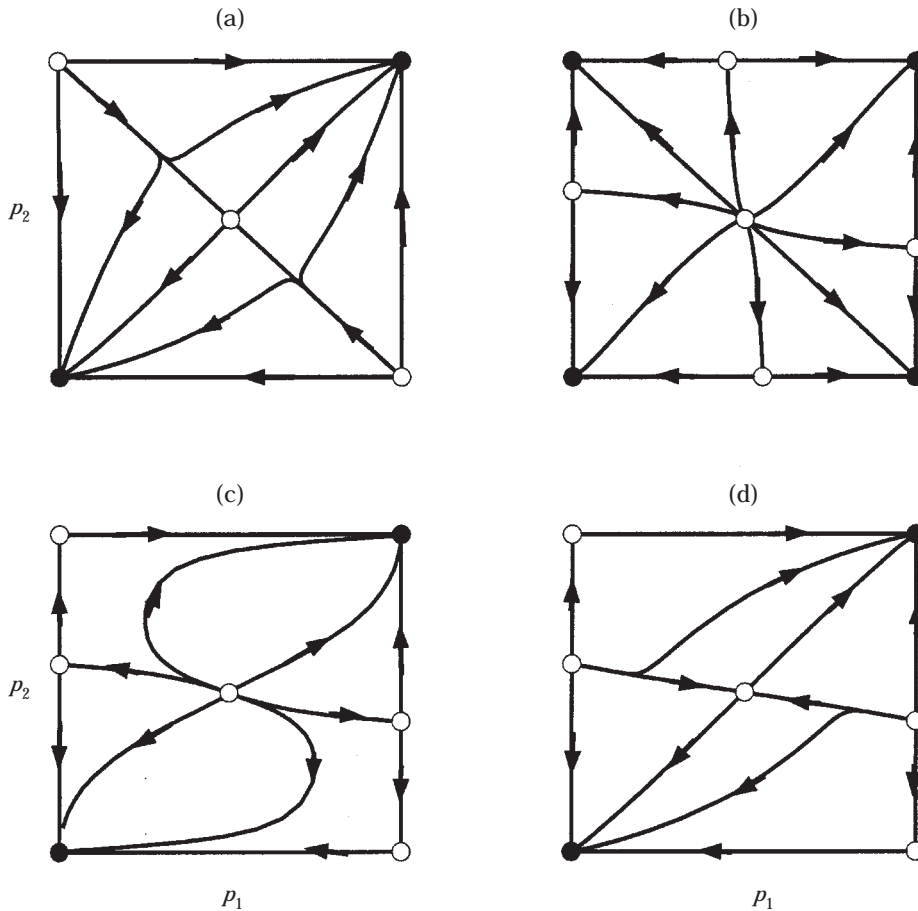


FIG. 1. The phase-plane dynamics of “pure” Müllerian mimicry: (a) $a < b, d < c$ (strong interspecies interactions); (b) $a > b, d > c$ (weak interspecies interactions); (c) $a < b, d > c, ad - bc > 0$; (d) $a < b, d > c, ad - bc < 0$. In cases (c) and (d) the interspecies interactions are stronger than intraspecies interaction for one species.

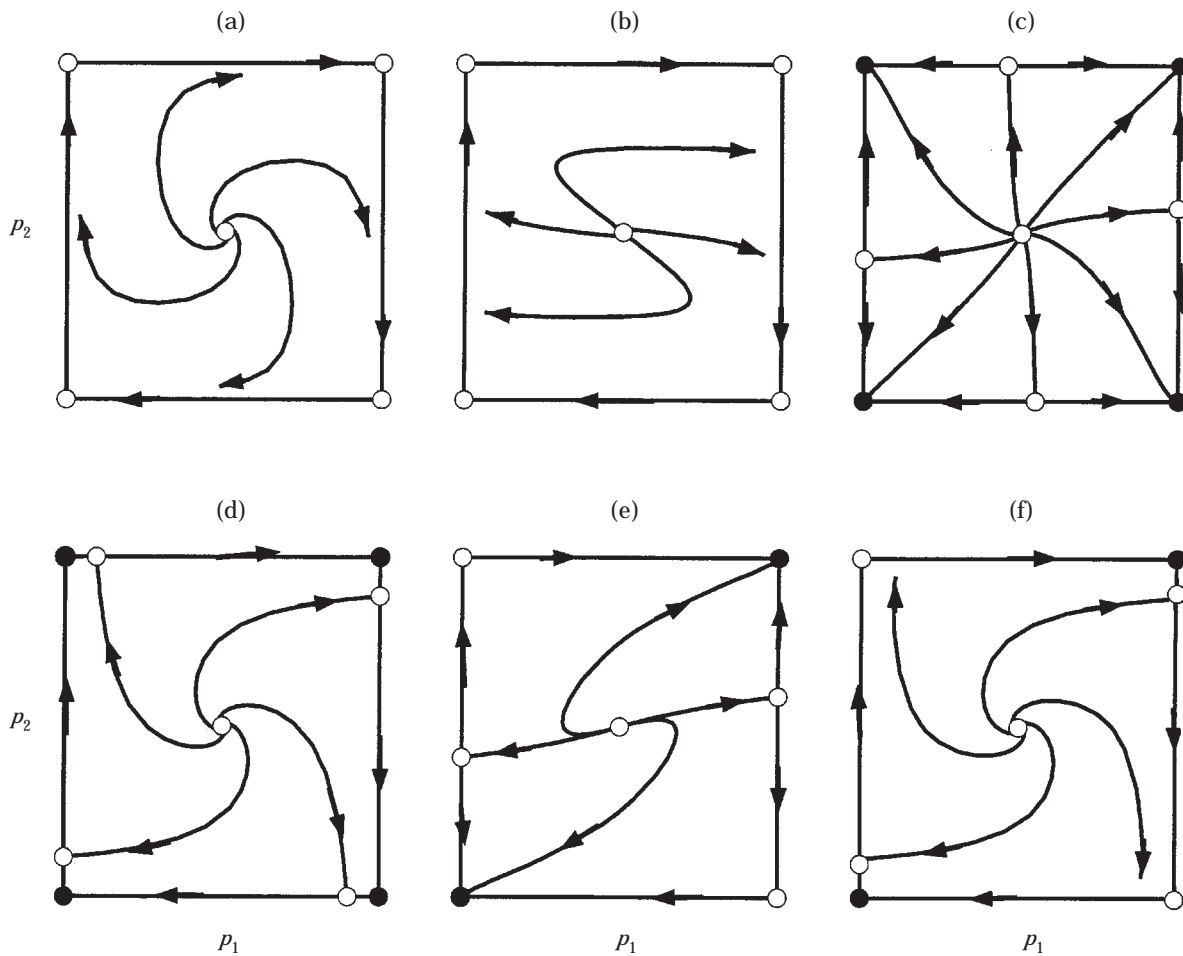


FIG. 2. The phase-plane dynamics for the case of two unpalatable species with unequal degrees of unpalatability: (a) $a < b, d < |c|, (a - d)^2 < 4b|c|$; (b) $a < b, d < |c|, (a - d)^2 > 4b|c|$; (c) $a > b, d > |c|, (a - d)^2 < 4b|c|$; (d) $a > b, d > |c|, (a - d)^2 > 4b|c|$; (e) $a < b, d > |c|, (a - d)^2 < 4b|c|$; (f) $a < b, d > |c|, (a - d)^2 > 4b|c|$. Strong interspecies interactions in (a) and (b), weak interspecies interactions in (c) and (d), and the interspecies interactions are stronger than intraspecies interaction for one species in (e) and (f). The heteroclinic cycle is stable in (a) and (b).

approaches an axis where genetic variability will be completely lost at least in one locus. All the models considered so far have, however, neglected mutation which is a ubiquitous source of new variability. Assuming that forward and backward mutation rates between morphs are the same, mutation can be taken into account by adding terms $\mu_i(q_i - p_i)$ to the right-hand side parts of (3). Here μ_i is the mutation rate for the i -th species, $i = 1, 2$. Introduction of mutation in the model transforms the stable heteroclinic cycle into a stable limit cycle away from the axes (cf. Seger, 1988). The resulting dynamic regime (see Fig. 3), which can be described as mutation-selection balance cycle, corresponds to the evolutionary chase between “weaker” and “stronger” Müllerian mimic. Note that this dynamic regime is characterized by a very small level of genetic variability within at least one species and that through time both the “weaker” and the “stronger” Müllerian

mimics (but only one of them at any given time) can be highly polymorphic. However, most of the time both species will be nearly monomorphic, and then

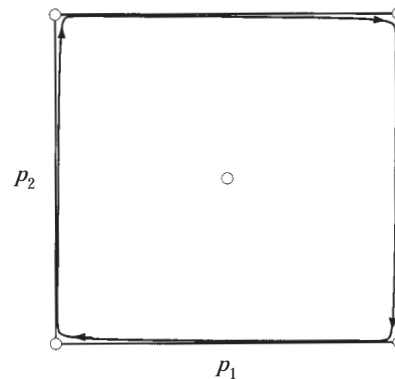


FIG. 3. The mutation-selection balance cycle resulting from a stable heteroclinic cycle in Fig. 2(a).

the system will eventually “jump” close to a new monomorphic equilibrium on a relatively fast time scale. Finally, note that in evolutionary time, mutation is not necessary for the cycle to be observed, as the system will in general wind slowly out to the heteroclinic cycle. The results just presented can be summarized as follows.

Conclusion 2

In the case of two unpalatable species with unequal degrees of unpalatability, the system evolves to an equilibrium state with both species monomorphic if the level of (indirect) between-species interactions is weak. If the level of (indirect) between-species interactions is strong enough (i.e. if $b > a$ and $|c| > d$) and there is mutation, the system evolves towards a mutation-selection balance cycle corresponding to the evolutionary chase between a “weaker” and a “stronger” Müllerian mimic.

“CLASSICAL” BATESIAN MIMICRY

Let $a, c < 0, b, d > 0$, i.e. both species 1 (the mimic) and species 2 (the model) benefit from increasing the model frequency and suffer from increasing the mimic frequency. This parameter configuration will be considered as describing classical Batesian mimicry when the palatable mimic benefits at the expense of the unpalatable model. In this case, Results 1–4 lead to the rich dynamical patterns shown in Fig. 4. As before, introducing mutation transforms stable heteroclinic cycles [as in Fig. 4(a) and 4(d)] into stable mutation-selection balance cycles (similar to the one in Fig. 3).

Conclusion 3

In the classical Batesian case, the system evolves to an equilibrium state with monomorphic model and polymorphic mimic if the level of (indirect) between-species interactions is weak (i.e. if $|a| > b$ and $d > |c|$). If (indirect) between-species interactions are stronger than within-species interactions for at least one species, the spectrum of dynamic behavior is very broad. The possibilities include evolution towards an equilibrium with both species monomorphic, an equilibrium with both species polymorphic, an equilibrium with monomorphic model and polymorphic mimic, and different cycles describing the permanent evolutionary chase between the model and the mimic. The equilibrium with both species polymorphic can be (locally) stable simultaneously with equilibria with both species monomorphic or a mutation-selection balance cycle. In this case, the dynamic behavior depends on initial conditions.

Possible Extensions

Here we have studied a series of simple population genetics models describing coevolution of two species. A novel aspect of our modeling approach is that both species are allowed to evolve. Allowing for the second species to evolve greatly broadens the spectrum of possible dynamic behaviors. In particular, stable limit cycles show up even when the overall selection is weak. We have demonstrated existence of different attractors (equilibria and cycles) with different levels of genetic variability and simultaneous stability of some of them. We have shown that evolutionary chase between Batesian mimic and model or between “strong” and “weak” Müllerian mimic can happen under a range of parameter values. In most cases, a necessary condition for cycling is that between-species interactions are stronger than within-species interactions (that is $|b| > |a|, |c| > |d|$). The periodic solutions of the model equations describing the evolutionary chase can be characterized by large or small levels of genetic variability and can be simultaneously stable with equilibria.

The basic model studied incorporates a number of simplifying assumptions. In the discussion that follows we argue that introducing more realistic (that is complex) assumptions should produce even more complex dynamics and, thus, would only add to the main thrust of this paper. We will consider different additional factors in turn.

UNSYMMETRIC LINEAR FREQUENCY-DEPENDENT SELECTION

One of the assumptions of the basic model was the absence of the difference in fitness between two morphs of a species not related to their frequencies. This assumption led to symmetric fitnesses (2). However, the traits selected by predators (such as a wing tip color trait) can have additional effects on fitness (better thermoregulation or crypticity) resulting in a selection imbalance. Allowing for general linear fitnesses and keeping all other assumptions yields dynamic equations of the form

$$\dot{p}_1 = p_1(1 - p_1)(a + bp_1 + cp_2), \quad (4a)$$

$$\dot{p}_2 = p_2(1 - p_2)(d + ep_1 + fp_2), \quad (4b)$$

where coefficients a, b, c, d, e, f depend on parameters of fitness functions [and are different from those in the dynamical system (3)]. The dynamical system (4) can have a heteroclinic cycle (Hofbauer & Sigmund, 1988, p. 306) and one or even two limit cycles (stable and unstable) encircling a doubly polymorphic equilibrium. Thus, system (4) still has periodic solutions describing the evolutionary chase and its dynamics are more complicated than those of (3).

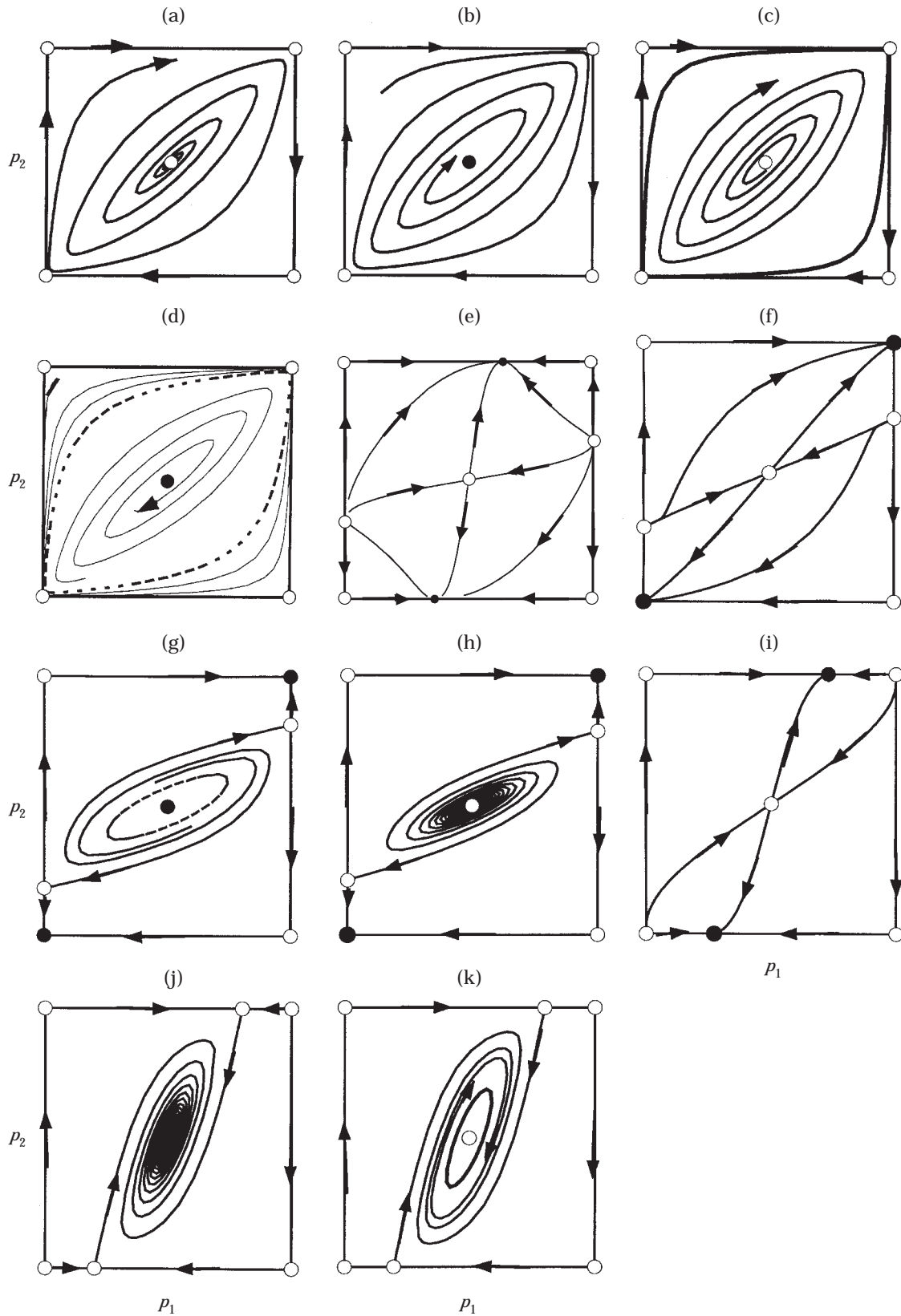


FIG. 4. The phase-plane dynamics of "pure" Batesian mimicry: (a) $|a| < b, d < |c|, a + d > 0, a/b - d/c > 0$; (b) $|a| < b, d < |c|, a + d < 0, a/b - d/c < 0$; (c) $|a| < b, d < |c|, a + d > 0, a/b - d/c < 0$; (d) $|a| < b, d < |c|, a + d < 0, a/b - d/c > 0$; (e) $|a| > b, d > |c|$; (f) $|a| < b, d > |c|, D < 0$; (g) $|a| < b, d > |c|, D > 0, a + d < 0$; (h) $|a| < b, d > |c|, D > 0, a + d > 0$; (i) $|a| > b, d < |c|, D < 0$; (j) $|a| > b, d < |c|, D > 0, a + d < 0$; (k) $|a| > b, d < |c|, D > 0, a + d > 0$. Strong interspecies interactions in (a)–(d), weak interspecies interactions in (e), and the interspecies interactions are stronger than intraspecies interaction for one species in (f)–(k). The heteroclinic cycle is stable in (a), (d), and is unstable in (b) and (c). A limit cycle is stable in (c), (k), and is unstable in (d), (g).

DIPLOID POPULATION

The basic model assumed that populations were haploid. Although this is a valid description of some mimicry systems (Turner, 1980), diploidy is more common. The genes underlying mimicry are typically completely dominant or recessive (Nijhout, 1991). Assuming diploid populations with alleles **A** and **B** completely dominant over alleles **a** and **b** and keeping all other assumptions leads to a model of the form

$$\dot{p}_1 = p_1 q_1^2 [a(1 - 2q_1^2) + b(1 - 2q_2^2)], \quad (5a)$$

$$\dot{p}_2 = p_2 q_2^2 [c(1 - 2q_1^2) + d(1 - 2q_2^2)], \quad (5b)$$

Preliminary results suggest that the dynamics of (3) and (5) are similar. In particular, system (5) can have a heteroclinic cycle and limit cycles can bifurcate from a single doubly polymorphic equilibrium.

STRONG SELECTION

One of the assumptions leading to the model (3) is weak selection. If selection is not weak, the dynamics are better described by difference equations (1). Any complex behavior in a differential equation model will be present in the corresponding difference equation model. Moreover, as is well known, the dynamics of difference equation models in population genetics can be much more complicated than the dynamics of the corresponding differential equations (e.g. Holton & May, 1993; Altenberg, 1991; Gavrillets & Hastings, 1995). Thus, the dynamics of (1) should be significantly more complex, as confirmed by our preliminary numerical results. In particular, the area in the parameter space that corresponds to non-equilibrium behavior becomes broader. For instance, with parameter values as used in Fig. 4(j) where trajectories of (3) converge towards the doubly polymorphic equilibrium, the trajectories of (1) converge to a cyclic attractor (for C_1 and C_2 not extremely large).

MORE ALLELES/LOCI

The model considered here assumes a very simple genetic determination of the phenotypic patterns, a single diallelic locus, which is an obvious oversimplification. For example, the color patterns of *Papilio dardanus*, which is a Batesian mimic, are controlled by a locus with 10 alleles (Nijhout, 1991), while the color patterns of *Heliconius*, which form different Müllerian rings, are controlled by 11 (for *H. melpomene*) or 12 (for *H. erato*) loci with major effects (Sheppard *et al.*, 1985). Introduction of additional alleles and loci into the model would increase the “nonlinearity” of the corresponding dynamic equations and should result in much more compli-

cated dynamics, particularly given the existence of heteroclinic trajectories in the two-variable case. This expectation is supported by Seger’s (1988) numerical results for a host–parasite system under linear symmetric frequency-dependent selection assuming that the fitness of an individual depends only on the frequencies of morphs of another species. He observed “an enormous, almost bewildering, variety of dynamical patterns” in a model with two diallelic loci.

Conclusions

The main biological conclusions of this paper are that the dynamics of systems of two coevolving haploid species can be complex and non-equilibrium, that polymorphism in these systems seems to be likely even if selection does not vary in space and time, and that the coevolutionary chase between species can be common.

What do these conclusions imply for studies of mimicry in natural systems? The mathematical model analysed in this paper predicts that under specific conditions the coevolution of Batesian mimic and model can result in non-equilibrium dynamics. This is consistent with Fisher’s (1930) intuition about mimicry systems. Non-equilibrium dynamics can also be expected in the coevolution of “weaker” and “stronger” Müllerian mimics. This is in accordance with Huheey’s (1988) suggestion. The question of how probable it is that these conditions are satisfied in natural populations remains controversial, especially for the case of Müllerian mimicry (see the critic of Huheey’s 1976, arguments in Turner *et al.*, 1984; Sheppard *et al.*, 1985). This question cannot be answered within the framework used here. To answer this question one needs a model that would map different ecological processes operating in mimicry systems into fitness. The model studied in this paper basically describes two different species in a single location under constant environmental conditions. In mimicry systems observed in nature the number of mimetic species is often more than two (Nijhout, 1991), the populations are subdivided to some degree and climatic changes, presumably, influence fitnesses. All these factors are expected to make the dynamics more complicated. On the other hand, random genetic drift resulting in loss of genetic variability can simplify the dynamics. Without a specific model one can hardly do anything but speculate about effects of population dynamics, nonlinear fitnesses and predator learning which we do not attempt here.

The conclusion that polymorphism is likely is one that has been supported from the earliest systematic

studies of mimicry through almost all current studies. However, these results are almost always static studies—observing the allele frequency at a single point in time, and thus precluding the observation of complex dynamics. One classical set of studies which did look at dynamics of allele frequencies through time, studies of the dynamics of *Biston betularia* (see Berry, 1990) can be thought of as an example of our simplest case where only one species is allowed to evolve. In concordance with the theory, the observation was of a monotonic change in allele frequencies through time. This observation provides a counterpoint to the few studies that have looked at frequencies of different morphs through time. Although the number of systematic studies of frequencies of different mimicry morphs through time has been limited, there are two studies which have begun to look at this question (Brown & Benson, 1974; Smith, 1976). The data are too skimpy to permit a detailed comparison with the theory, but the great variation in time does concord with the theoretical predictions. However, given the paucity of observational or experimental data, the only general conclusion we can draw is that many more studies of the dynamics of mimicry morphs are needed. Our models draw attention to a specific case where allele frequencies are likely to change dramatically through time, analogously to the interaction between diseases of plants and resistance genes in plants. The model shows that one of the most important factors influencing the plausibility of non-equilibrium dynamics is the relationship between the strength of between-species and within-species interactions. This indicates that this relationship should be the focus of both experimental and theoretical work. Our results suggest that systematic studies of frequencies of different mimicry morphs through time may be very useful.

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APPENDIX

Proof of Result 1 is straightforward.

Proof of Result 2

Direct computation shows that $\partial \dot{p}_1 / \partial p_2 = 2bp_1q_1$, $\partial \dot{p}_2 / \partial p_1 = 2cp_2q_2$. Thus, if b and c have the same sign so do $\partial \dot{p}_1 / \partial p_2$ and $\partial \dot{p}_2 / \partial p_1$. Now existence of periodic orbits is excluded by a theorem given in Section 18.7 of Hofbauer & Sigmund (1988) (HS). Note that if b and c are positive, the system is *cooperative*, if b and c are negative, the system is *competitive* (HS). In both these cases the dynamical system evolves towards one of the equilibria which were the concern of Result 1.

Proof of Result 3

Let $b > 0$, $c < 0$. We will directly follow the steps described in Section 29.2 of Hofbauer & Sigmund (1988) (HS) to find the Poincaré map corresponding to a neighborhood of the heteroclinic cycle. This map can be approximated as $g(x) \approx ax^\rho$. As shown in HS, the heteroclinic cycle is stable (unstable) if $\rho > 1$ (< 1) and the heteroclinic bifurcation is supercritical (subcritical) if $\alpha < 1$ (> 1). The problem is to find α and ρ . Let $i = 1, 2, 3, 4$ denote the equilibria (0, 0), (0, 1), (1, 1) and (1, 0), respectively. One can take local coordinates x and y in such a way that near the i -th

saddle point the dynamics are approximated by $\dot{x} = \lambda_i x$, $\dot{y} = -\mu_i y$ (with $\lambda_i, \mu_i > 0$). One can show that

$$\lambda_1 = \lambda_3 = -(c + d), \mu_1 = \mu_3 = a + b$$

$\lambda_2 = \lambda_4 = b + a$, $\mu_2 = \mu_4 = d - c$. Thus, using eqn (29.6) of HS,

$$\rho = \prod_{i=1}^4 \frac{\mu_i}{\lambda_i} = \left(\frac{b+a}{b-a}\right)^2 \left(\frac{c-d}{c+d}\right)^2.$$

The last expression is larger (smaller) than 1, if $a/b - d/c$ is positive (negative). According to eqns (29.3,4,7) of HS,

$$\alpha = \alpha_n \alpha_{n-1}^{\mu_n/\lambda_n} \dots \alpha_1^{\mu_1 \dots \mu_2/\lambda_2 \dots \lambda_2},$$

where

$$\alpha_i = \exp \left(\int_0^1 c_i(x, 0) dx \right)$$

and $c_i(x, 0) = \lim_{y \rightarrow 0} c_i(x, y)$ with

$$c_i(x, y) = \frac{\dot{y}}{yx} + \frac{\mu_i}{\lambda_i} \frac{1}{x} - \frac{\lambda_{i+1}}{\mu_{i+1}} \frac{1}{1-x}.$$

For equilibrium (0, 0), $x = p_2$ and $y = p_1$:

$$c_1(x, 0) = \frac{b(2x-1) - a}{x(1-x)(d(2x-1) - c)} - \frac{a+b}{c+d} \frac{1}{x} + \frac{b-a}{c-d} \frac{1}{1-x} = \frac{4dD}{(c^2 - d^2)(2dx - c - d)}.$$

Integrating the last expression from 0 to 1, we find that

$$\ln \alpha_1 = \frac{2D}{c^2 - d^2} \ln \left(\frac{c-d}{c+d} \right).$$

For equilibrium (0, 1), $x = p_1$ and $y = 1 - p_2$:

$$c_2(x, 0) = \frac{c(2x-1) + d}{x(1-x)(a(2x-1) + b)} - \frac{c+d}{b+a} \frac{1}{x} + \frac{c-d}{a-b} \frac{1}{1-x} = \frac{4dD}{(b^2 - a^2)(a - b - 2ax)}.$$

Integrating the last expression from 0 to 1, we find that

$$\ln \alpha_2 = \frac{2D}{b^2 - a^2} \ln \left(\frac{b-a}{b+a} \right).$$

From the symmetry, $\alpha_4 = \alpha_2$ and $\alpha_3 = \alpha_1$, and

$$\alpha = (\alpha_2 \alpha_1^{\mu_2/\lambda_2} + (\mu_1 \mu_2) / (\lambda_1 \lambda_2)).$$

The heteroclinic bifurcation is supercritical if $\alpha < 1$ (HS), which is equivalent to $\ln\alpha < 0$. The latter is true, if

$$\begin{aligned} \ln\alpha_2 + \frac{\mu_2}{\lambda^2} \ln\alpha_1 &= \frac{2D}{b^2 - a^2} \ln\left(\frac{b+a}{b-a}\right) \\ &- \frac{c-d}{b-a} \frac{2D}{c^2 - d^2} \ln\left(\frac{c-d}{c+d}\right) = \frac{2D}{b-a} \\ &\times \ln\left[\left(\frac{b+a}{b-a}\right)^{1/(b+a)} \left(\frac{c-d}{c+d}\right)^{-1/(c+d)}\right] > 0. \end{aligned}$$

For this to happen, the expression in the square brackets has to be smaller than 1. At the bifurcation point, $a/b = d/c = \xi$, where $|\xi| < 1$. The expression in the square brackets can be represented as

$$\left(\frac{1+\xi}{1-\xi}\right)^{-(b+c)/bc(1+\xi)}.$$

If $\xi(b+c) > 0$, the last expression is smaller than 1, $\alpha < 1$, and the heteroclinic bifurcation is supercritical. If $\xi(b+c) < 0$, the bifurcation is subcritical. This completes the proof.

Proof of Result 4

There are many ways to prove this result. We used a simple and straightforward method developed by Bautin (1938) (see also Bautin & Leontovich, 1976). According to this method, to know the behavior of the system in a neighborhood of a bifurcation point one should know the sign of the so-called first Lyapunov value L_1 . If L_1 is negative, the bifurcation is supercritical, and if L_1 is positive, the bifurcation is subcritical. Using the formulae on p. 207 of Bautin & Leontovich (1976), one finds that $L_1 = -a(b+c)/b$. Alternatively, and to prove the part of Result 4 about the amplitude and period of the bifurcating periodic solution, one can use Theorem 8.6 in Glendinning (1994).