Coevolutionary Chase in Exploiter–Victim Systems with Polygenic Characters

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I study the dynamics of a simple quantitative genetic model describing coevolution of two antagonistic species of the victim–exploiter type. In this model, individuals are different with respect to an additive polygenic character that is under direct stabilizing selection and which also determines the strength of within and between species interactions. The model assumes that between species interactions are most intense when the victim's and exploiter's phenotypes match. I show that a cyclic coevolutionary chase is possible under a broad range of conditions. In most cases, the system cycles if the ''victim'' has a stronger incentive to win and/or a larger genetic variance, and is under stronger stabilizing selection than the ''exploiter''. The results presented here provide counter-examples to recent studies that (1) question the applicability of ''Red Queen'' and ''arms race'' metaphors for continuously varying traits; (2) argue for the existence of crucial differences between major and minor loci dynamics; and (3) attribute a stabilizing role to coevolution.

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1. Introduction

Any biological species interacts (directly or indirectly) with many other species. Selection pressure resulting from these interactions is thought to be very strong and evolutionary changes in a certain species are expected to bring about evolutionary changes in species with which it interacts (e.g. Futuyma & Slatkin, 1983; Vermeij, 1987; Thompson, 1994). Antagonistic interactions of the victim–exploiter type, in which one species benefits at the expense of another species, represent an ubiquitous type of between-species interactions. Such interactions can be direct, as in host–parasite and predator–prey systems, or indirect, as in Batesian mimicry systems. One of the most intriguing dynamical consequences of antagonistic between-species interactions is an endless coevolutionary chase between species (Fisher, 1930) commonly referred to in terms of the ''Red Queen'' (Van Valen, 1973) or ''arms race'' (Dawkins & Krebs, 1979) metaphors. In this scenario the victim continuously evolves to decrease the strength of

between species interactions while the exploiter continuously evolves to increase the strength of these interactions. Two different dynamic regimes representing coevolutionary chase have been discussed: ''runaway'' evolution to larger and larger trait values and oscillatory changes of trait values. Permanent cycling is common in genetic models of host-parasite systems (e.g. May & Anderson, 1983; Seger, 1988, 1992) and mimicry systems (Gavrilets & Hastings, 1997) operating in terms of major locus frequencies. In contrast, some genetic models based on continuous variation such as used for describing predator–prey coevolution have seemed to be able to produce mainly ''runaway'' evolution toward infinite size, which is unrealistic, but does not involve cycling (e.g. Shaffer & Rosenzweig, 1978; Seger, 1992).

Continuously varying traits are thought to be very important not only in predator–prey systems, but in mimicry and host-parasite systems as well. The difference in dynamic behavior between existing models based on major loci and on continuous genetic variation has implications for several important theoretical issues. First, since the models predicting runaway evolution for such traits imply conditions

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that seem to be quite restrictive and unrealistic, one can question the generality and applicability of the evolutionary chase scenario (e.g. Rosenzweig *et al.*, 1987; Brown & Vincent, 1992). Second, one can conclude that the mode of inheritance is a very important factor in determining dynamical patterns and that there is a crucial difference between major locus and minor locus dynamics (e.g. Seger, 1992; Thompson, 1994). One can also argue that coevolution has a stabilizing effect on the population dynamics in general (e.g. Saloniemi, 1993). On the other hand, results presented in several recent publications have suggested that coevolutionary cycling may be common (Marrow *et al.*, 1992; Abrams & Matsuda, 1996; Dieckmann *et al.*, 1995; van der Laan & Hogeweg, 1995).

Lack of truly dynamical models that concentrate on the *coevolution* of polygenic systems makes it difficult to assess the generality and plausibility of these arguments. The majority of studies of predator–prey systems with continuous genetic variability, focus on their population dynamics. Another complicating factor is the modeling approach used. Most models are built by introducing genetic variability into an ecological model (usually of the Lotka–Volterra type). As a consequence, the resulting models incorporating both ecology and genetics are very complex, include many parameters and do not admit the analytical analysis of dynamic regimes. All this makes one rely on limited numerical simulations, which restricts the generality of the biological conclusions reached.

Here I present a very simple quantitative genetics model for the coevolution of two antagonistic species of the victim–exploiter type. In developing this model I will assume that population sizes are regulated by factors different from those responsible for changes in the genetic structure of populations. This is a standard population genetic assumption, which is justifiable in many (co)evolving systems. For instance, in many butterfly systems population density is largely controlled at the larval stage, whereas mimicry becomes important at the adult stage. Analytical results in this paper, together with earlier numerical results by Marrow *et al.* (1992), Abrams & Matsuda (1996), Dieckmann *et al.* (1995), and van der Laan & Hogeweg (1995) show that cyclic evolutionary chases are possible for a broad range of conditions.

2. Model

I consider a system of two coevolving species, X and Y. Species X, the "victim", suffers from (possibly indirect) interactions with species Y, while species Y, the "exploiter", benefits from these interactions. I assume that, within each species, individuals differ from one another with respect to an additive polygenic character, x in species X and y in species Y. Characters x and y are under direct (stabilizing) selection and also determine the strength of within and between species interactions. These interactions will be incorporated in the model by assuming that fitnesses of individuals with phenotype x in species X, $W_x(x, p_x, p_y)$, and phenotype y in species Y, $W_y(y, p_x, p_y)$, depend on the phenotypic distributions p_x and p_y i.e. fitnesses are frequency-dependent.

The changes of the mean values $\bar{x}$ ($\equiv \int x p_x \, dx$) and $\bar{y}$ ($\equiv \int y p_y \, dy$) between generations can be approximated by a form of Lande's equations (Lande, 1979)

$$\Delta \bar{x} = G_x \frac{\partial \ln W_x(x, p_x, p_y)}{\partial x} \tag{1a}$$

$$\Delta \bar{y} = G_y \frac{\partial \ln W_y(y, p_x, p_y)}{\partial y} \tag{1b}$$

where G_x and G_y are the corresponding additive genetic variances and the partial derivatives are evaluated at $x = \bar{x}$, $y = \bar{y}$. Equations (1) allow for frequency-dependent selection (Iwasa *et al.*, 1991; Taper & Case, 1992; Abrams *et al.*, 1993a,b). Iwasa *et al.* (1991), Taper & Case (1992) and Abrams *et al.* (1993a,b) state that this approximation is good if genetic variances are small. Because variance has dimension and, thus, can be made small or large by changing the scale of measurement, this claim is misleading. Changing a scale (for instance, from microns to kilometers) should not be important. As apparent from the calculations performed by these authors, eqns (1) are valid if both differences among fitnesses and differences among fitness gradients are small within the population range. If the phenotypic distribution is symmetric, a weaker version of the latter condition is "differences among fitness gradients and their linear approximations are small". I will assume that phenotypic distributions are symmetric and that the conditions just stated are satisfied.

I will assume that three types of selection (stabilizing selection and selection arising from interactions within and between species) operate independently throughout the lifespan of individuals. This allows one to express the overall fitness as a product of three fitness components:

$$\begin{aligned} W_x(x, p_x, p_y) \\ = W_{x,stab}(x) \cdot W_{xx,int}(x, p_x) \cdot W_{xy,int}(x, p_y), \end{aligned} \tag{2a}$$

$$\begin{aligned} W_y(y, p_x, p_y) \\ = W_{y,stab}(y) \cdot W_{yy,int}(y, p_y) \cdot W_{yx,int}(y, p_x), \end{aligned} \tag{2b}$$

where, for example, $W_{x,stab}$, $W_{xx,int}$ and $W_{xy,int}$ describe direct stabilizing selection and selection on x arising from within and between species interactions. Fitness consequences of direct interactions between individuals can be described in the following way (e.g. Roughgarden, 1979; Taper & Case, 1992; Brown & Vincent, 1992). First, one introduces a function $\alpha_{ij}(u, v)$ that measures a fitness component for an individual of species i with phenotype u, which interacts with an individual of species j with phenotype u. To find the fitness component of phenotype u, one then integrates $\alpha_{ij}(u, v)$ over the phenotypic distribution of species j. For example, the fitness component of phenotype x in species X resulting from interactions with species Y is

$$W_{xy,\,int}(x, p_y) = \int \alpha_{xy}(x, y) p_y(y) dy$$

for an appropriate function α_{xy}. If selection is weak, the integral is approximately $\alpha_{xy}(x, \bar{y})$. I will use a Gaussian form for α's (e.g. Roughgarden, 1979; Taper & Case, 1992; Brown & Vincent, 1992) leading to

$$W_{xy,int}(x, p_y) = \alpha_{xy}(x, \bar{y}) = \exp[\beta_x(x - \bar{y})^2], \quad (3a)$$

$$W_{yx,int}(y, p_x) = \alpha_{yx}(y, \bar{x}) = \exp[-\beta_y(y - \bar{x})^2].(3b)$$

Here $\beta_x > 0$ and $\beta_y > 0$ characterize the victim's loss and the exploiter's gain resulting from between species interactions. If species X and Y are a prey and its predator, or a host and its parasite, then x and y can be considered as describing individual size or some other quantitative character. Equation (3) implies that for each predator (or parasite) there is an optimum prey (or host) size (or some other quantitative character). If species X and Y represent a Batesian model–mimic pair, then x and y can be considered as describing coloration patterns. Equation (3) implies that a model loses the least when it is "different" from the modal phenotype of the mimic species, while a mimic gains the most when it is "similar" to the modal phenotype of the model species.

The fitness consequences of within species interactions can be described in a similar way, leading to $W_{xx,int}(x, p_x) = \alpha_{xx}(x, \bar{x})$ and $W_{yy,int}(y, p_y) = \alpha_{yy}(y, \bar{y})$ for appropriate α's. I will assume that within species interactions are the strongest (or the weakest) for individuals with the same phenotype. This implies that $\alpha_{xx}(x, \bar{x})$ considered as a function of x reaches a maximum (or a minimum) at $x = \bar{x}$ and so $\partial W_{xx,int}(x, p_x)/\partial x$ evaluated at $x = \bar{x}$ is zero. Thus, the fitness component $W_{xx,int}(x, p_x)$ does not contribute to the dynamical eqn (1). A similar reasoning can be applied to $W_{yy,int}(y, p_y)$. This means that within the

modeling framework used, the dynamics of the mean values do not depend on within species interactions.

3. Dynamics

In analysing the model dynamics I will make the standard assumption that additive genetic variances G_x and G_y are constant. This is also implied by the weak selection approximation. It is useful to start with a model where stabilizing selection is absent.

NO STABILIZING SELECTION

Let us assume that stabilizing selection is absent ($W_{x,stab} = W_{y,stab} = const$). To derive the dynamic equations below, I approximate the difference eqns (1) by the corresponding differential equations and rescale time to $\tau = 2\beta_x G_x t$. Using dots to represent derivatives with respect to τ, the coevolution is described by

$$\dot{\bar{x}} = \bar{x} - \bar{y}), \quad (4a)$$

$$\dot{\bar{y}} = R(\bar{x} - \bar{y}), \quad (4b)$$

where $R = (\beta_y/\beta_x)(G_y/G_x)$.

The dynamics of (4) are simple. On the phase-plane $(\bar{x}, \bar{y})$, all trajectories are straight lines with slope R. Both $\bar{x}$ and $\bar{y}$ increase (decrease) below (above) the straight line $\bar{x} = \bar{y}$, which represents a line of equilibria. This line is stable if $R > 1$ and is unstable if $R < 1$ (see Fig. 1). Species X wins (i.e. escapes and increases its "distance" from Y as time goes on) if its loss from interactions is bigger than species Y's gain ($\beta_x > \beta_y$) and/or its genetic variance is larger than that of Y ($G_x > G_y$). Otherwise, species Y wins and the mean values for both species coincide after some transient time. One can say that in this model a species with a stronger incentive and/or ability to win wins. This model, however, is unrealistic in that traits can evolve to infinite values. Many quantitative characters are thought to be subject to stabilizing selection (Endler, 1986), which presumably can prevent "runaway" evolution to infinite trait values.

GAUSSIAN STABILIZING SELECTION

A standard choice of a fitness function describing stabilizing selection is Gaussian:

$$W_{x,stab} = \exp[-s_x(x - x_0)^2], \quad (5a)$$

$$W_{y,stab} = \exp[-s_y(y - y_0)^2], \quad (5b)$$

where x_0 and y_0 are "optimum" trait values, and s_x and s_y are parameters characterizing the strength of stabilizing selection. Introducing new variables

$u = \bar{x} - x_0, v = \bar{y} - y_0$, the dynamics are described by

$$\dot{u} = -e_x u + u - v + d, \qquad (6a)$$

$$\dot{v} = R(-e_y v + u - v + d), \qquad (6b)$$

where dimensionless parameters $e_x = s_x/\beta_x$, $e_y = s_y/\beta_y$ characterize the strength of stabilizing selection relative to selection arising from between-species interactions, and $d = x_0 - y_0$ is the difference of the optimum values.

Since this is a linear system, the dynamics of (6) are well understood. In general, the system either evolves towards the only equilibrium (u^*, v^*) with $u^* = de_y/(e_x - e_y + e_x e_y)$, $v^* = de_x/(e_x - e_y + e_x e_y)$ or evolves away from it. What happens depends on R, e_x and e_y, but does not depend on d. If equilibrium (u^*, v^*) is a stable node or focus, the system evolves to this equilibrium. If it is a saddle or an unstable node, both species evolve away from it, with species X increasing its distance from species Y, i.e. species X wins. If this equilibrium is an unstable focus, the system evolves away from it in a spiral manner where periods of close resemblance $(|\bar{x} - \bar{y}| \ll 1)$ and large differences $(|\bar{x} - \bar{y}| \gg 1)$ alternate. Each of these three possibilities can take place. Comparing the dynamics of (4) and (4), one can see that introducing stabilizing selection has resulted in two new features. First, stabilizing selection (even very weak) transforms the line of equilibria into an equilibrium point, which represents a balance between stabilizing selection and between-species interactions. Stabilizing selection can also result in a new regime: an "arms race" where neither species wins. This model, however, remains unsatisfactory in that traits still can evolve to infinite values.

"QUARTIC EXPONENTIAL" STABILIZING SELECTION

Stabilizing selection refers to situations when fitness decreases with deviation from some "optimum" value. There are different ways to choose a specific functional form of a fitness function that describes stabilizing selection. Although a Gaussian function is a popular choice, it is used primarily because of its mathematical convenience. Here, I will use an exponential function of fourth order polynomials (cf. Iwasa & Pomiankovski, 1995)

$$W_{x,stab} = \exp[-s_x(x - x_0)^4], \qquad (7a)$$

$$W_{y,stab} = \exp[-s_y(y - y_0)^4]. \qquad (7b)$$

Stabilizing selection described by (7) is weaker than Gaussian selection near the optimum phenotype but becomes stronger beyond a certain value (see Fig. 2). With stabilizing selection as specified in eqn (7), the dynamic equations for the deviations of the mean values from x_0 and y_0 are

$$\dot{u} = -2e_x u^3 + u - v + d, \qquad (8a)$$

$$\dot{v} = R(-2e_y v^3 + u - v + d), \qquad (8b)$$

(a)

(b)

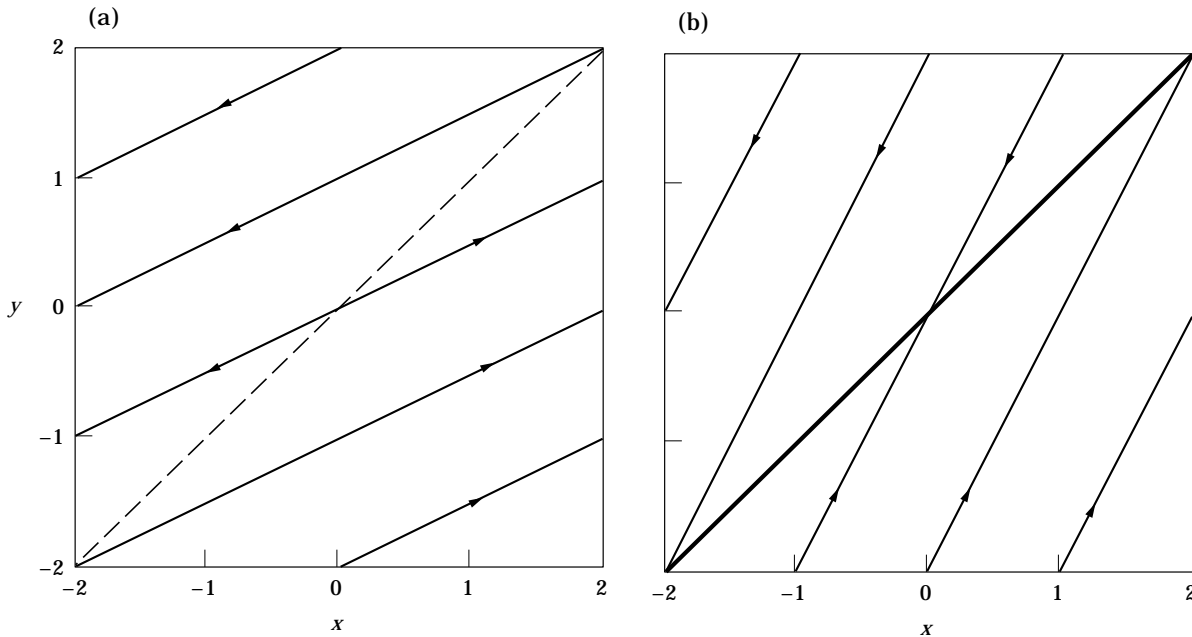FIG. 1. The phase-plane dynamics with no stabilizing selection. (a) $R < 1$ (the line of equilibria $\bar{y} = \bar{x}$ is unstable). (b) $R > 1$ (the line of equilibria $\bar{y} = \bar{x}$ is stable).
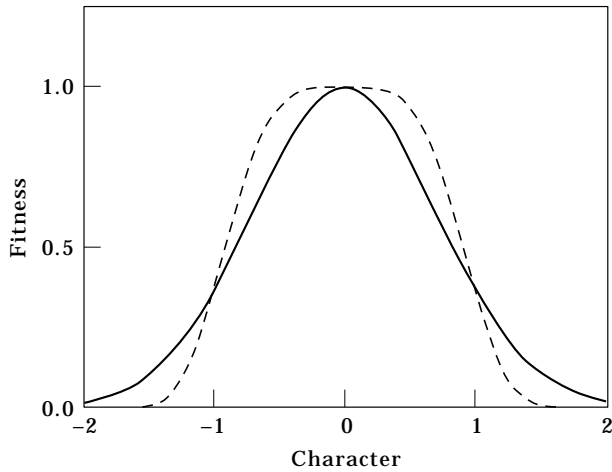
FIG. 2. Comparison of Gaussian fitness function (solid line) and quartic exponential fitness function (dashed line) for $s = 1$, $x_0 = 0$.

FIG. 3. Areas in parameter space (k, R) corresponding to different patterns of existence and stability of equilibria in (8).

where parameters e_x, e_y, R and d are defined by the same formulae as above. Dynamical system (8) can be analyzed using standard methods (e.g. Glendinning, 1994). The rest of this section describes some relevant analytical results.

One of the dynamic possibilities in models with no stabilizing selection and with Gaussian stabilizing selection was continuous evolution to larger and larger absolute values of $\bar{x}$ and $\bar{y}$. In contrast, in model (8) this is not possible: the system stays in a finite neighborhood of $(0, 0)$, which is more realistic. (A simple way to demonstrate this is to transform (8) to polar coordinates, $x = r \cos \theta$, $y = r \sin \theta$, and note that $\dot{r} < 0$ if r is bigger than some critical value.) This is one of the new features introduced by stabilizing selection as described by eqn (7). Let us consider the equilibria of (8). One can easily see that $v = ku$ at equilibrium, where $k = (e_x/e_y)^{1/3}$, and that equilibrium values of u satisfy a cubic $u^3 - pu - q = 0$ with $p = (1 - k)/(2e_x)$, $q = d/(2e_x)$. Let us initially assume that $(q/2)^2 \ll |p/3|^3$; that is equivalent to the condition

$$\frac{d^2}{G_x} \frac{s_x G_x^2}{\beta_x G_x} \ll \frac{1}{27} |1 - k|^3. \tag{9}$$

This condition is satisfied if the difference between the optimum values is small relative to the standard deviation ($d^2 \ll G_x$), and/or stabilizing selection is very weak relative to selection arising from between species interactions ($s_x G_x^2 \ll \beta_x G_x$). In this case, the equilibria of (8) are approximately $(0, 0)$, and $(p^{1/2}, kp^{1/2})$ and $(-p^{1/2}, -kp^{1/2})$. The two latter equilibria are meaningful only if p is positive, that is if $k < 1$. Standard analysis shows that equilibrium $(0, 0)$ is unstable if $R < 1$. If $R > 1$, analysis of the dynamics on a center manifold (e.g. Glendinning, 1994) shows that
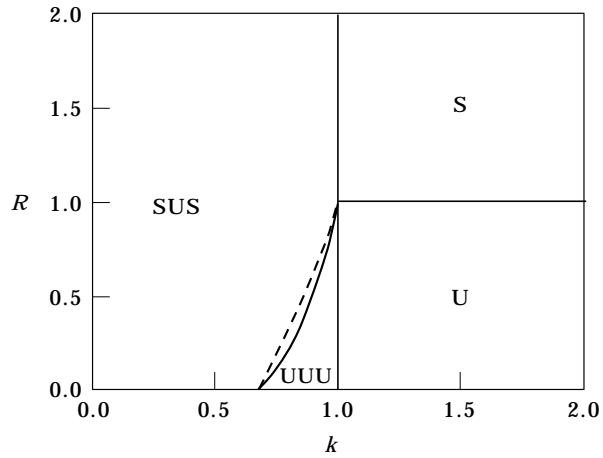
equilibrium $(0, 0)$ is stable if $k > 1$ and is unstable if $k < 1$. The non-trivial equilibria are stable if $R > (3k - 2)k/(3 - 2k)$ and are unstable if the latter inequality is reversed.

Figure 3 shows areas in parameter space (k, R) corresponding to different patterns of existence and stability of equilibria. Each pattern is described by a string of **S**'s (for stable) and **U**'s (for unstable). The middle entry indicates the stability of equilibrium $(0, 0)$, while the remaining entries (if any) indicate the stability of equilibria $(p^{1/2}, kp^{1/2})$ and $(-p^{1/2}, -kp^{1/2})$. If $R > 1$, according to Bendixon's criterion no cycles are possible. Thus, when species Y has a stronger incentive and/or ability to win, system (8) always evolves to an equilibrium. If $R < 1$, the situation is more complicated. In areas marked **U** and **UUU** in Fig. 3 there are no stable equilibria. Hence, at least
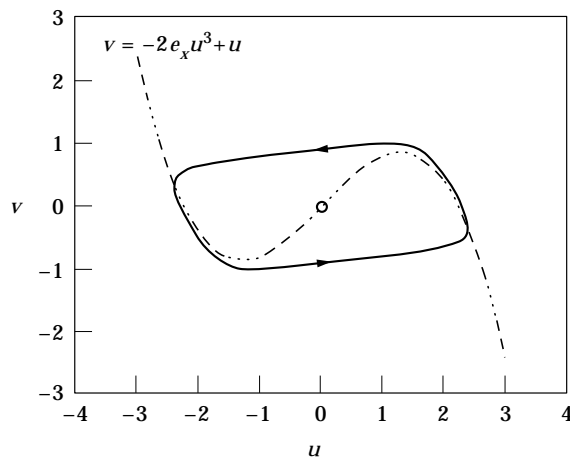

FIG. 4. The limit cycle ("relaxation oscillator") on the phase-plane (u, v) for $k > 1$ and small R. Also shown is the isocline $\dot{u} = 0$.
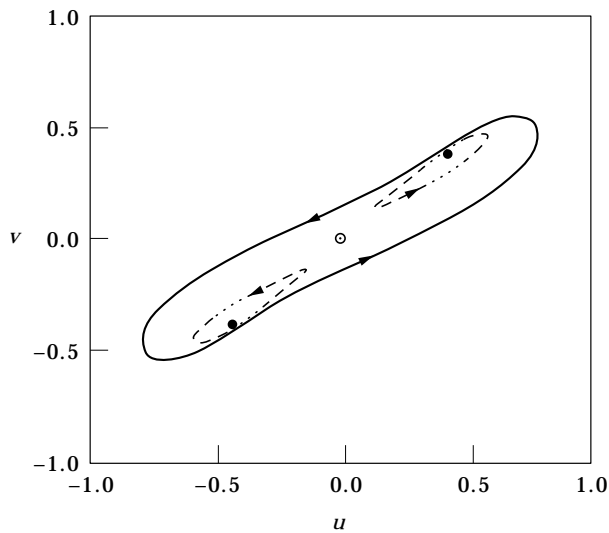
FIG. 5. The phase-plane dynamics with two stable equilibria at $(p^{1/2}, kp^{1/2})$ and $(-p^{1/2}, -kp^{1/2})$ (black circles) surrounded by two unstable limit cycles (dashed lines), which in turn are surrounded by a stable limit cycle (solid line). The white circle represents an unstable equilibrium at $(0, 0)$.

one stable limit cycle is present. Note that since $k^3 = (s_x/s_y)(\beta_y/\beta_x)$, in these areas s_x is sufficiently large relative to s_y, i.e. stabilizing selection acting on X is stronger than that on Y. Numerical analyses show that for $k > 1$ a stable cycle bifurcates from the equilibrium $(0, 0)$ when R becomes smaller than 1. Resulting oscillations can be especially easily understood when R is small. In this case, system (8) resembles a well-known relaxation oscillator. On the phase-plane (u, v) trajectories are attracted to a limit cycle made up of two parts of the curve $v = u - 2e_x u^3$ (at which $\dot{u} = 0$) as shown on Fig. 4, and two almost horizontal pieces where the orbit quickly "falls" off the curve. At the boundary of areas marked **SUS** and **UUU** in Fig. 3 a subcritical Poincaré–Andronov–Hopf bifurcation takes place and, hence, unstable cycles surround stable non-trivial equilibria. An example of a phase portrait with two stable non-trivial equilibria surrounded by two unstable limit cycles, which in turn are surrounded by a stable limit cycle, is given in Fig. 5. Unstable cycles persist for parameter values on the right from the dashed line in Fig. 3. At this line (found numerically) unstable cycles collide with a stable one resulting in mutual annihilation.

Relaxing condition (9), i.e. making stabilizing selection stronger and/or the difference between optimum values larger, causes two effects. First, the area in the parameter space where (8) has three equilibria shrinks (in Fig. 3 the line separating areas with one and three equilibria moves counter-clock-

wise). Second, the area in the parameter space where (8) has a stable equilibrium increases (in Fig. 3 the line separating areas where the only equilibrium is stable and where it is unstable moves down). Both these effects make cycling less and less likely, which corresponds to what biological intuition suggests. In the extreme case when the left and right-hand sides of (9) are exchanged, (8) has the only equilibrium at $(q^{1/3}, kq^{1/3})$. This equilibrium is stable.

4. Discussion

An important conclusion of several recent publications is that coevolutionary cycling may be common in victim–exploiter systems (Marrow *et al.*, 1992; Abrams & Matsuda, 1995; Dieckmann *et al.*, 1995; van der Laan & Hogeweg, 1995). Here I have presented an additional argument in favor of this conclusion. I have considered a simple dynamical model describing the coevolution of two antagonistic species of the victim–exploiter type. In this model the strength of between-species interactions is determined by some quantitative characters that also are subject to natural stabilizing selection. I have shown that a cyclic coevolutionary chase between species is expected under broad conditions. The cycling is brought about by the continuous genetic system rather than by population dynamics. In most cases, the system cycles if the "victim" has a stronger incentive to win and/or a larger genetic variance and is under stronger stabilizing selection than the "exploiter" (see Fig. 3). Victims of antagonistic interactions are often thought to have a stronger incentive to win than their exploiters (Vermeij, 1987) suggesting that some coevolving exploiter–victim systems have a natural tendency to cycle.

Here I assumed that the strength of between species interactions is maximal when the victim's and exploiter's phenotypes match, but declines with the absolute value of the difference between victim's and exploiter's phenotypes. This may be the case for traits such as size (for predator–prey systems) or coloration pattern (for mimicry systems). In contrast, for traits such as speed or ability to detect individuals of other species, the strength of between species interactions should be a monotonic function of the difference between victim's and exploiter's phenotypes. A simple way to model such situations within the present framework is to assume that functions α's are cubic exponentials $\exp[\beta(x - y)^3]$ [cf. eqn (3)]. With this choice of α's, stable cycling does not seem to be possible (cf. Abrams & Matsuda, 1995).

The model of continuously varying traits studied above provides a counter-example to recent studies

questioning the applicability of Red Queen and arms race metaphors for continuously varying traits (Rosenzweig *et al.*, 1987), and arguing for the existence of crucial differences between major and minor loci dynamics (Seger, 1992; Thompson, 1994). The model has a natural tendency to cycle, similar to that in models based on major locus variation (e.g. May & Anderson, 1983; Seger, 1988, 1992; Gavrilets & Hastings, 1997). The model dynamics are complicated. In particular, a stable limit cycle can exist simultaneously with two locally stable equilibria (see Fig. 5). The latter case is especially interesting because approaches based on analyses of (evolutionary stable) equilibria will definitely fail here. Although equilibria are locally stable, for most initial conditions they are irrelevant and the system evolves in a cyclic manner. Cycles in trait values are likely to drive cycles in population densities and can destabilize the population dynamics (Abrams & Matsuda, 1996).

The results presented here highlight the importance of additive genetic variance as a parameter controlling the model dynamics. Changing genetic variances will change parameter k, which can result in a drastic qualitative change in the dynamics. Following such a change the whole system can move from an equilibrium to a cyclic regime or visa versa (cf. Kirkpatrick, 1982; Milligan, 1986; Abrams *et al.*, 1993b; Saloniemi, 1993). In the model studied in this paper, it is the victim that evolves away from phenotypic matching, while the exploiter evolves towards matching. This leads to the conclusion that high genetic variance on the part of the victim is destabilizing. However, it is also possible, depending on the traits in question, that roles are sometimes reversed. A predator may be able to catch prey effectively by using strategies different from what the prey is using, whilst the prey is able to escape if it matches the predator's strategy. This is the case in situations where the defense is immunity against a pathogen. In such a case, the conclusion of the present paper would be reversed, and larger variance for the exploiter would tend to drive cycles. Here genetic variances have been treated as constant, which is justified if selection is weak. One might expect that the dynamics of more general models incorporating changes in genetic variances will be very complex. This paper provides an additional illustration of the sensitivity of quantitative trait dynamics to fine details of the phenotypic fitness function (cf. Nagylaki, 1989; Gavrilets & Hastings, 1994; Matsuda & Abrams, 1994). The graphs of Gaussian and quartic exponential functions are not very different. In contrast, there is a drastic difference in the dynamics of the two models. The model with a Gaussian fitness function allows for (unrealistic) runaway evolution to infinite trait values, while runaway evolution is not possible in the model with a quartic exponential fitness. The approach described here can be generalized in many directions. It is especially interesting to consider coevolution of more than two interacting species. Will incorporation of additional species make the dynamics more complex and perhaps chaotic, or on the contrary will this stabilize the system?

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