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CHAOS AND COEVOLUTION: EVOLUTIONARY WARFARE IN A CHAOTIC PREDATORY-PREY SYSTEM

J. C. Allen
Department of Entomology and Nematology
University of Florida
Gainesville, Florida 32611-074

ABSTRACT

A model of coevolution in a simple but potentially chaotic predatory-prey system is developed. Coevolution is introduced by making parameters functions of lagged density as if natural selection had affected them. Increasing attack rate and decreasing predator mortality rate were found to be destabilizing, producing more chaos and less phase-locking as revealed by bifurcation diagrams. In general, when the prey was more responsive to natural selection the model was more stable, and when the predator was more responsive to selection, the model was less stable, having more chaotic behavior and less phase-locking. It is concluded that in this simple, phenomenological model that coevolution is not a priori a stabilizing force, and it depends on the circumstances whether coevolution will work for or against chaotic dynamics.

RESUMEN

Un modelo de evolución en un sistema simple, pero potencialmente depredador-presa caótico fue desarrollado. La coevolución fue introducida elaborando funciones parámetro de densidad retardado como si la selección natural las hubiera afectado. Incrementos en la tasa de ataque y de crecimiento en la tasa de mortalidad del depredador tuvieron un efecto desestabilizante, produciendo más caos y menos fase-de-cierre como se reveló por los diagramas de bifurcación. En general, cuando la presa fue más reactiva a la selección natural, el modelo fue más estable, y cuando el depredador fue más reactivo a la selección, el modelo fue menos estable, teniendo mayor comportamiento caótico y menor fase-de-cierre. Se concluyó que en este modelo simple y fenomenológico que la coevolución no es una fuerza a priori, y ella depende de las circunstancias tanto como la coevolución trabajara para o en contra de la dinámica caótica.

Virtually all of the population interactions of animals seem at first glance to be inherently destructive and therefore unstable. Why consumer organisms do not over-
exploit their resources to the point of mutual extinction is one of the great classical questions of ecology (see for example, Elton 1962, or Slobodkin 1964). One might think that natural selection, lacking foresight, would produce ever more efficient consumers thus leading to greater instability and chance of extinction, yet the world is awash with herbivores, predators, parasites and pathogens.

One of the standard answers for why this is so is that the resource species (plants, prey, hosts, etc.) retaliate with defenses against their attackers (Pimentel 1968, Pimental & Soans 1970). Schaffer & Rosenzweig (1978) have argued for the existence of a coevolutionary stable state (CSS) where the rates of victim and attacker evolution are equal but with opposite effects. This idea was originally developed for stable stationary systems, and so it is somewhat uncertain in the context of a cyclic or chaotic system.

The diversity of such defenses was suggested by Witz (1990) in last year's symposium where he found 371 references to antipredator mechanisms in 10 journals from 1969 to 1989 alone. Recent research in chemical and behavioral ecology suggests a mind-boggling web of "communication" between trophic levels: predacious fireflies that lure their firefly prey by mimicking the prey species' flash patterns (Lloyd 1980, 1984, 1990), cricket parasitoids attracted by cricket songs (Cade 1975, Walker 1986), moths that jam bat sonar with ultrasonic pulses (Dunning 1968a, 1968b), host detection by chemically mediated "learning" in parasitic wasps (Lewis & Tumlinson 1988) and plants that summon parasitoids with chemical attractants when they are under attack by the parasitoid's host insect (Turlings et al. 1990, Turlings & Tumlinson 1991).

This paper will investigate the effects of coevolution in a simple (but potentially chaotic) predator-prey model in which the explicit biological details of attack and defense as illustrated in the examples above are modeled only in a phenomenological way. That is, the examples are both numerous and sophisticated enough to assume a priori that the genetics and mechanisms are present for very tightly coupled coevolution to occur between natural enemies. Models of coevolution can easily become entangled in a mass of detail. For example Levin et al. (1990) consider each chemical toxin and detoxifier in a plant-herbivore system explicitly, and Schaffer & Rosenzweig (1978), from a rather small amount of genetic detail, required a large amount of mathematical detail in deriving their CSS for a relatively simple system. A primary consideration of the present paper will be whether an otherwise chaotic system tends to be stabilized by the inclusion of coevolutionary effects between the interacting species. This question is of some importance in the debate on whether chaotic systems would tend to be produced by the effects of natural selection (Allen 1989, Berryman & Millstein 1989, Nisbet et al. 1989, Lomnicki 1989, Mani 1989, Seger 1988).

### A Model of Evolutionary Warfare Between Predator and Prey

We start with a "nongenetic" predatory-prey system similar in spirit to the model discussed in last year's symposium (Allen 1990a) and to the models discussed by Schaffer (1988). The model used here is capable of complex dynamics including chaos, quasiperiodicity, and phase-locking with the forcing cycle. It is given by

\[
\begin{align*}
\dot{x} &= r (1-x) - xyT \\
\dot{y} &= y (x-w) - \mu yT \\
\dot{w} &= (x-w)/\tau_w T
\end{align*}
\]

where: \( \phi = 1 + 8 \cos(2\pi t) \)
and \( T = \) the period of \( \phi \).

which will be referred to as the "no selection" model since it contains no selection effects. \( \phi \) is the forcing cycle which multiples the prey reproductive rate \( \phi = 1 + 8 \cos(2\pi t), 0 > \delta > 1 \). \( f(x) \) is the prey's reproductive function (e.g., \( x(1-x) \) for logistic...
reproduction) and \(g(x)\) is the predator's functional response (Holling 1959, 1965) (e.g., \(x/(1 + x)\) for a type 2 response). \(\dot{x}\) represents the time derivative of \(x\), the model is in dimensionless form, and time is in units of the forcing period, \(T\). This is useful in the analysis to be done below where we sample the system at the forcing period to look for phase-locking with the forcing cycle. In other words, we just sample system (1) at every time unit and "speed-up" (multiply) the whole right-hand-side by \(T\) (in time units/forcing period). This puts the model on a per forcing period time unit thus allowing us to vary \(T\) and still sample every time unit - a much more time-efficient computer method than waiting \(T\) time units to obtain one point. Notice that the numerical response, \(g(w)\), is a function of prey density in the past, \(w\), i.e., that it takes some time for the predator's reproductive rate to respond to an increase in prey density. The mean time lag in this effect is \(\tau_w\). The prey species has a reproductive rate \(r\), the predator has a maximum attack rate, \(\gamma\), and experiences a constant mortality rate, \(\mu\).

We now introduce a kind of "phenomenological" genetics into the above model in which predators exert selection pressure upon prey to develop defenses. We will assume that this is expressed as a reduced attack rate where the attack rate, \(\gamma\), is replaced by \(\gamma e^{-\lambda \tau_w}\) (Fig. 1a) in which \(\dot{y}\) represents lagged predators or predators in the past. The past predators are generated by "pouring" predators through a distributed delay chain as per Macdonald's (1978) "linear chain trick" (see also Manelch 1976). It is further assumed that the prey must pay a proportional reproduction cost for their defense such that \(r\) is reduced to \(r e^{-\lambda \psi}\) (Fig. 1b). The net result of these assumptions is a new model

\[
\begin{align*}
\dot{x} &= (re^{-\lambda \dot{y}})f(x) - \gamma e^{-\lambda \tau_w}g(x)y/T \\
\dot{y} &= (re^{-\lambda \psi}g(w)y - \mu y)/T \\
\dot{w} &= (x-w)/\tau_w T
\end{align*}
\]

(2)

\[
\begin{align*}
\dot{y}_1 &= [3(y_1-y_1)/\tau_y]T \\
\dot{y}_2 &= [3(y_1-y_2)/\tau_y]T \\
\dot{y} &= [3(y_2-y)/\tau_y]T
\end{align*}
\]

which involves selection of increased prey defenses by increased predator density in the past. It should be noted that \(\tau_y\), the mean time lag of the effect, might be thought of as being approximately equal to one prey generation although the effect will be spread over a longer time by the action of the 3-stage delay chain, \(y_i\), and in reality by all sorts of genetic mechanisms which might cause longer time lags. \(\lambda\) can be thought of as a measure of the strength of the selection pressure, and by this parameter we can investigate the effects of selection for prey defenses since, when \(\lambda = 0\), we have system (1) with no selection of defenses.

We now consider a more complete model in which the predator "fights back" by having its attack rate, \(\gamma\), be increased by lower prey densities in the past, i.e., that reduced prey densities put selection pressure on the predator to develop a higher attack rate. (Note that this applies best to a species-specific predator since a generalist predator may simply switch to another prey species when prey are rare.) This effect is introduced by letting \(\gamma\) be replaced by \(\gamma e^{-\lambda \psi}\) (Fig. 1c) so that the highest attack rates result from low prey densities in the past. As with the prey, we assume a cost to the predator such that its mortality is higher for low prey densities in the past due to its investment in a higher attack rate. Thus \(\mu\) is replaced by \(\mu e^{-\lambda \psi}\) (Fig. 1d), in which low prey densities in the past produce a higher current predator mortality rate representing the cost of developing greater prowess. Combining these ideas with the prey selection model, system (2), we obtain
Fig. 1. Illustration of the coevolution functions in the model, eq. (3). (a) Decreasing attack rate as a function of past predator density (prey develop defenses). (b) Cost to the prey of defenses. (c) Increased attack rate for low density of past prey (predators improve their prowess). (d) Cost to predators of increased prowess (higher mortality rate).

\[
\begin{align*}
&\text{(prey)} \quad \dot{x} = \left[ r e^{-\lambda y} f(r) - \gamma e^{-\lambda y} g(x) y \right] T \\
&\text{(predator)} \quad \dot{y} = \left[ \mu e^{-\nu x} g(w) y - \mu e^{-\nu x} y \right] T \\
&\text{(Lagged prey)} \quad \dot{w} = \left[ (x - w) / \tau_w \right] T
\end{align*}
\]

For Selection Purposes

\[
\begin{align*}
&\dot{x}_1 = [3(x-x_1) / \tau_x] T \\
&\dot{x}_2 = [3(x_1 - x_2) / \tau_x] T \\
&\text{(lagged prey)} \quad \dot{x} = [3(x - x_2) / \tau_x] T \\
&\dot{y}_1 = [3(y-y_1) / \tau_y] T \\
&\dot{y}_2 = [3(y_1 - y_2) / \tau_y] T \\
&\ddot{y} = [3(y_2 - y) / \tau_y] T \text{ (lagged predator)}
\end{align*}
\]

which will be called the "coevolution" model since it involves selection effects on prey by high predator densities and on predators by low prey densities. Note that system (1) is just a special case of (3) where \( \lambda \) and \( \nu \) are zero. \( \lambda \) measures the responsiveness of the prey to selection pressure by high predator densities, and \( \nu \) measures the responsiveness of the predator to selection pressure by low prey densities. The delay chains \( x_i \) and \( y_i \) are simply a mathematical trick for generating lagged prey, \( \ddot{x} \), and lagged predators, \( \ddot{y} \). The emergence pattern from the delay chain is determined by the number of stages in the chain (arbitrarily chosen to be three in our case) and the main residence
time in the delay (τx or τy). Narrow emergence patterns are generated by a high number of stages in the delay chain and long time lags by high values of r. Thus the force of natural selection can be given a past distribution whose position and width can be controlled. While these attributes of the selection process can be controlled, this paper will concentrate on the more basic questions of the effect of coevolution itself and the force of natural selection i.e., on the parameters λ and v. The prey reproductive function will be logistic, i.e., \( f(x) = x(1-x) \), and the functional response will be type 2, i.e., \( g(x) = x(1+x) \).

We can also examine two additional areas of interest: the cost associated with increased defenses or prowess and the sensitivity to selection (λ and v). There is an implicit “cost” effect in the model in that the effect of selection increases or decreases at the same rate automatically depending only on past densities. The automatac reversal implies a cost effect else the reversal would not occur. There are, however, the explicit cost effects on reproduction, \( re^{-\alpha y} \) for the prey and the \( \mu e^{-\omega r} \) for the predator in eq. (3) which we might therefore call the “no free lunch” model since there are explicit population level costs associated with selection. As an alternative to this, we can compare a “free lunch” model in which there are no costs for increased defenses or prowess. This model is simply the no free lunch model, eq. (3), with the cost terms missing, i.e.:

\[
\begin{align*}
\dot{x} &= r(x) f(x) - \gamma e^{-\delta x} g(x)y \\
\dot{y} &= \gamma e^{-\delta y} g(y) - \mu y
\end{align*}
\]  

(4)

where the lag equations have been omitted since they are identical to eq. (3).

RESULTS

In the coevolution model, eq. (3), there are 10 parameters: \( r, T, \delta, \tau, \gamma, \mu, \tau_x, \tau_y, \lambda \) and \( v \). Even the no selection model, eq. (1), has 6 parameters: \( r, T, \delta, \tau, \gamma \) and \( \mu \). Since exploration of this total parameter space is a massive computational problem, no attempt will be made here to penetrate this unknown area. Instead attention is focused on a comparison of the no selection model with the coevolution model changing one parameter at a time and looking for differences in stability and the occurrence of chaotic dynamics. Parameters of particular interest are the prey reproductive rate, \( r \), the attack rate \( \gamma \), the predator mortality rate, \( \mu \), and the sensitivity of the prey and predator to selection, \( \lambda \) and \( v \) respectively. The other parameters are judged to be a bit more peripheral to the interaction and will be held at the following constant but seemingly reasonable values: \( T = 15, \delta = 0.5, \tau = 4, \tau_x = 10 \) and \( \tau_y = 10 \).

Viewing the model output at intervals equal to the period of the forcing cycle, \( T \), will reveal if the model is phase-locked with the forcing cycle. If the model is truly periodic, (phase-locked) a repeating point(s) will be observed after transient behavior has died away. If this process is repeated for a range of values of a parameter then (plotting the parameter on the x-axis and the model output on the y-axis) we obtain a plot of model behavior as the parameter changes (a “bifurcation” diagram). At each parameter increment along the x-axis we typically calculate 25 forcing periods and discard them as transients and then plot the model at the next 100 forcing periods. This process is repeated for each computer screen pixel along the x-axis whose scale length is the range of the parameter to be investigated. Phase-locked (periodic) behavior will be revealed as a line or lines where the point(s) are repeating over and over even though 100 have been plotted. For example, 4 lines indicate that over that parameter range there are 4 forcing cycles for each cycle of the population (4 to 1 phase-locking).

Using the method just described, the selection model and the coevolution model are compared in Fig. 2. The parameters \( T, \delta, \tau, \gamma \) and \( \tau \) are held constant at the values
Fig. 2. Comparison of the no selection model (left panels) with the coevolution model (right panels). (a,b) prey reproductive rate, (c,d) predator attack rate, (e,f) predator mortality rate. Lines indicate phase-locking. Diffuse "fuzzy" areas indicate chaos. Banded areas with tight boundaries usually indicate quasiperiodic behavior. Parameters given in text.

given above, and the remaining parameters are $r = 0.5$, $\gamma = 0.5$, $\mu = 0.05$ (except for the one which is being varied). In the coevolution case, $\lambda = 0.2$ and $\nu = 0.5$. In Fig. 2 we first vary the prey reproductive rate (Fig. 2a,b) then the attack rate (Fig. 2c,d) and then the predator mortality rate, (Fig. 2e,f). The no selection model is plotted on the left, and the coevolution model on the right. There appears to be an overall tendency for the coevolution model to phase-lock a bit more with the forcing cycle and to have slightly smaller amplitude oscillations in the predator population. In both models increasing the attack rate tends to produce chaos and larger oscillations, and increasing the predator mortality rate tends to be stabilizing, finally phase-locking one to one with the forcing cycle (Fig. 2e,f). In general it appears that when the predator is doing well (high attack rate, low mortality rate) both the no selection and the coevolution models tend to be destabilized with the effect being somewhat larger for the no selection model.

We now examine the question of costs of defense or increased prowess and the sensitivity of the prey and predator to selection ($\lambda$ and $\nu$ respectively). In Fig. 3 the
Fig. 3. Comparison of prey which are sensitive to selection ($\lambda = 0.2$) (left panels) with prey which are insensitive to selection ($\lambda = 0.02$) (right panels). (a,b) The "no free lunch" model (eq. (3)). (c,d) The "free lunch" model (eq. (4)). The most chaotic behavior occurs in the no free lunch model with insensitive prey and sensitive predator (3b). The x-axis is $u$, the predator's sensitivity to selection. Parameters are the same as Fig. 2.

The full coevolution model (the "no free lunch" model, eq. (3)) is plotted in (a,b) and the "free lunch" version, eq. (4), is plotted in (c,d). In addition, the left panels (a,c) illustrate a prey which is sensitive to selection ($\lambda = 0.2$), and the right panels (b,d) illustrate an insensitive prey ($\lambda = 0.02$). In general, it appears that the "no free lunch" version (a,b) is a little less stable than the "free lunch" model (c,d), the latter having more phase-locking and less chaos. In addition, a prey which is sensitive to selection (a,c) appears to be more stable than one which is not (b,d). In particular, the most chaotic situation is the no free lunch model in which the prey is not very responsive to selection and the predator is responsive (Fig. 3b for the higher values of predator sensitivity).

One interesting question is whether coevolution tends to prevent chaotic dynamics, and increasing the sensitivity of the prey to selection seemed to be stabilizing in Fig. 3. With this in mind and using the no free lunch model (eq. (3)) we increase the prey's sensitivity to selection (f) from 0 to 1, holding other parameters as before (predator sensitivity, $v_r = 0.5$) (Fig. 4). The model is observed to progress from a regime of alternating bands of chaos, bifurcating phase-locking and quasiperiodicity of decreasing amplitude until it finally phase-locks 1 to 1 with the forcing cycle when the prey are highly sensitive to selection. Thus it seems that the model is indeed stabilized if the prey are very sensitive to selection whereas no such effect was noted for the no free lunch model (Fig. 3a,b) when the predator's sensitivity to selection is increased.

**Is this Coevolution? and Does Coevolution Prevent Chaos?**

At this point apologies are extended to readers who would argue that eq. (3) is not a true model of coevolution. At issue is how one defines "evolution" and "coevolution".
Fig. 4. Stabilizing effect of the prey’s sensitivity to selection (λ) on the no free lunch model (eq. (3)). Increasing the predator’s sensitivity to selection (ω) has a tendency to destabilize the model (Fig. 3a,b). Parameters are the same as Fig. 2.

Evolution might be defined as “change in the genetic makeup of a population with time” (Keeton & Gould 1986) or perhaps “a change in gene frequency from generation to generation” (Hickman et al. 1984). Coevolution might be defined as “an evolutionary change in a trait of the individual in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first” (Janzen 1980). Roughgarden (1979) defines coevolution as “the simultaneous evolution of interacting populations.” Schemke (1983) has criticized Janzen for overemphasizing interaction and Roughgarden for underemphasizing it. No attempt will be made here to add another definition to this confusion, and some confusion over such a complicated subject is probably inevitable and may be a good thing. The main point is that the model, eq. (3), is not totally excluded by any of these definitions if one is willing to accept a phenomenological model which avoids genetic details in favor of a lagged density dependence of parameters. Levin et al. (1990) seem to lean strongly in favor of such simplifications. Perhaps another worrisome thing to some readers is the total lack of allowance for mutations or new variants entering the populations. The model is guilty of this. It tacitly assumes that all of the genetic variation to accomplish the observed parameter changes is already in place, and that the changes are simply the result of changes in the frequencies of existing genes by density-dependent selection pressure.

This finally brings us to the question of whether coevolution tends to prevent chaotic dynamics in population interactions. It appears in this model (eq. (3)) that things can go either way: if the prey is more sensitive to selection the model tends to be more stable, but if the predator is more sensitive it tends to be less stable. This suggests that coevolution is not a priori a stabilizing force, i.e., that it can go either way depending on circumstances. One argument which can be applied is the “life-dinner” principle (Dawkins & Krebs 1979). Since the prey is running for its life and the predator only for its dinner, the force of selection is thought to be stronger on the prey. In the present
context, this means that $\lambda > \nu$ which would tend to have a stabilizing influence. There is a flaw in this argument however in that it says nothing about the densities of the prey and predator, i.e., at low predator densities the force of selection on the average prey might be extremely low because predators are rare, while the force of selection on the predator is relatively constant and may then be greater than that on the prey. Thus in the present model it is not really valid to apply the life-dinner idea to say that selection pressure is always greater on the prey since the pressure is time-varying depending on past density. $\lambda$ and $\nu$ represent a time-lagged response to selection spread over several generations and as such say very little about a single encounter. Over a longer time it is just as important to the predator's survival to obtain its dinner as it is for the prey to escape.

Finally, one additional point needs to be made clear. That is that self-destructive systems (by definition) do not last long. Thus, wildly chaotic populations that go to extremely low densities may have a high extinction rate, killing all the members of the population. Extinction of wildly chaotic systems has nothing to do with biology, genetics or natural selection in that reproduction is not a necessary part of the process. There is much evidence that the solar system was once a much more chaotic system than it is now (Wisdom 1989), but no one would argue that it was stabilized by Darwinian selection. Neverthess the same mechanism probably operates on ecological systems, eliminating chaotic systems which go to extremely low densities, and this process can be “stabilizing” without involving Darwinian selection (Allen 1990b). It would seem that there is some danger of confusing the results of this process with the results of ordinary natural selection and attributing them to natural selection. In view of this and the result here that coevolution may be indifferent to dynamics, it seems relevant to ask: Is the occurrence of chaos independent of natural selection except for coincidental effects which can be either positive or negative?

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