J. Math. Biol. (1994) 32:563–572

Journal of
Mathematical
Biology

Strange limits of stability in host-parasitoid systems

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Received 22 February 1993; received in revised form 15 September 1993

Abstract. The classical Nicholson–Bailey model for a two species host–parasitoid system with discrete generations assumes random distributions of both hosts and parasitoids, randomly searching parasitoids, and random encounters between the individuals of the two species. Although unstable, this model induced many investigations into more complex host–parasitoid systems. Local linearized stability analysis shows that equilibria of host–parasitoid systems within the framework of a generalized Nicholson–Bailey model are generally unstable. Stability is only possible if host fertility does not exceed e^4=54.5982 and if superparasitism is unsuccessful. This special situation has already been discovered by Hassell et al. (1983) in their study of the effects of variable sex ratios on host–parasitoid dynamics. We discuss global behaviour of the Hassell–Waage–May model using KAM-theory and illustrate its sensitivity to small perturbations, which can give rise to radically different patterns of the population dynamics of interacting hosts and parasitoids.

Key words: Nicholson–Bailey model – KAM-theory – Birkhoff – Limit cycle

Insect parasitoids (mainly Hymenoptera and Diptera) are an important group of terrestrial and aquatic predators and comprise some 10% of all metazoan species described so far (Waage and Hassell 1982). Synchronized and discrete generations of both host and parasitoid make it easy to formulate the dynamics of such interacting predator–prey populations in terms of simple mathematical models (Hassell 1978). Host–parasitoid models are usually described by a pair of coupled first-order difference equations (Hassell and May 1973; Hassell 1978; May et al. 1981; Murray 1989; Hassell and Anderson 1989; Hassell et al. 1991)

$$
\begin{aligned}
H_{t+1} &= FH_t g(H_t, P_t) \\
P_{t+1} &= cH_t \{1 - g(H_t, P_t)\}\,.
\end{aligned}
$$

H_t and P_t are the number of hosts and parasitoids in generation t. F is the finite rate of increase of the host, and c is the average number of parasitoids emerging from each parasitized host. g is a nonlinear function describing the fraction of hosts escaping parasitism. Assuming randomly searching parasitoids, random distributions of both hosts and parasitoids, and random encounters between the two, this general model reduces to the classical Nicholson–Bailey-model (Nicholson and Bailey 1935; Hassell and May 1973; Hassell 1978; May et al. 1981; Murray 1989; Hassell and Anderson 1989; and Hassell et al. 1991)

$$\begin{aligned} H_{t+1} &= FH_t e^{-aP_t} \\ P_{t+1} &= H_t(1 - e^{-aP_t}). \end{aligned}$$

In the absence of parasitoids the host population grows exponentially with a constant finite rate of increase $F.e^{-aPt}$ (the zero term of a Poisson distribution) is the fraction of the hosts escaping parasitism, whereas the fraction of hosts parasitized exactly k times can be written as $[(aP_t)^k/k!]e^{-aP_t}(k = 1,2,\ldots)$. Only unparasitized hosts develop to adults of the next generation, and setting $c{=}1$ exactly one parasitoid of the next generation emerges from each host parasitized independently of the number of parasitization events. a can be interpreted as area of discovery (Nicholson and Bailey 1935; Hassell and May 1973), or else as per capita searching efficiency (Hassell et al. 1983; Hassell and Anderson 1989).

Linearized local stability analysis shows that the equilibrium point

$$(H_*, P_*) = \left(\frac{F\log F}{a(F-1)}, \frac{\log F}{a}\right)$$

of this model is unstable (Hassell and May 1973; Hassell 1978; Murray 1989). The slightest perturbation away from equilibrium results in diverging oscillations of the population sizes of both host and parasitoid. In real systems this would eventually lead to the extinction of the parasitoid or both parasitoid and host populations. A number of stabilising factors such as spatial heterogeneity, non-random search, density dependent growth of the host, functional responses of the parasitoid, and mutual interference among searching parasitoids were put forward in order to stabilise coexistence in single host-single parasitoid systems (Hassell and May 1973; Beddington et al. 1975, 1978; Hassell 1978; May et al. 1981; Hassell and Anderson 1989; Hassell and Pacala 1990; Hassell et al. 1991).

Starting with the assumptions of the Nicholson-Bailey-model we now assume that k parasitization events (with a single egg being laid each time) on a single host on average result in the emergence of α_k parasitoids of the next generation ($0 \leqq \alpha_k \leqq k$, Nicholson-Bailey: $\alpha_k = 1$ for $k = 1,2,3,\ldots$). Using the auxiliary function

$$\phi(P_t) = \sum_{k=1}^{\infty} \alpha_k \frac{(aP_t)^k}{k!}$$

our generalized model is given by

$$\begin{aligned} H_{t+1} &= FH_t e^{-aP_t} \\ P_{t+1} &= H_t \phi(P_t) e^{-aP_t}. \end{aligned}$$

Setting $H_t = H_{t+1}$ and $P_t = P_{t+1}$ we find its equilibrium at

$$(H_*, P_*) = \left(\frac{F \log F}{a\phi\left(\frac{\log F}{a}\right)}, \frac{\log F}{a} \right)$$

(log: natural logarithm). Stability at equilibrium is impossible whenever $\alpha_k \neq 0$ for one or several $k \geqq 2$ because the Jacobian determinant $\partial(H_{t+1}, P_{t+1})/\partial(H_t, P_t)$ exceeds 1 at (H_*, P_*).

In the phase plane of H and P the trajectory will evolve counterclockwise around the equilibrium, and thus our generalisation has the same dynamic properties as the classical Nicholson–Bailey-model. Such host-parasitoid systems are thus generally unstable and prone to extinction if there are no other stabilising mechanisms, and the only possibly stable solution is given by $\phi(P) = \alpha_1 aP (0 \leqq \alpha_1 \leqq 1)$. We deliberately choose $\alpha_1 = 1$, i.e. we assume that all single parasitization events will lead to the emergence of exactly one parasitoid. This is of no importance to the dynamic properties of the host-parasitoid system considered, and only rescales the H-axis. This particular model was already suggested by Hassell, Waage and May (HWM) in a study of the effects of variable sex ratios on host-parasitoid dynamics (Hassell et al. 1983). The HWM-model ((11)–(14) of Hassell et al. 1983) assumes that superparasitism will lead to the emergence of exclusively male parasitoids, whereas female parasitoids (whose dynamics is described with the difference equation) will emerge from hosts parasitized only once. The equilibrium of the HWM-model (Hassell et al. 1983) is now given by

$$(H_*, P_*) = \left(\frac{F}{a}, \frac{\log F}{a} \right).$$

If we measure host and parasitoid population sizes in terms of multiples of the equilibrium values, and transforming into a log scale (more formally $x = \log(aH/F)$, and $y = \log(aP/\log F)$) we arrive at an equivalent system in x- and y-coordinates of the following form

$$\begin{aligned} x_{t+1} &= x_t + \log F\,(1 - e^{y_t}) \\ y_{t+1} &= x_t + y_t + \log F\,(1 - e^{y_t}). \end{aligned}$$

The equilibrium point (fixed point) is transformed into the origin. This coordinate transformation has the crucial property that our system becomes area-preserving, i.e.

$$\frac{\partial(x_{t+1}, y_{t+1})}{\partial(x_t, y_t)} = 1.$$

Local stability analysis of this transformed system at the origin shows that the fixed point is elliptic for $0 < \log F < 4$, and otherwise still unstable. If $0 < \log F < 4$ we can therefore apply KAM theory (KAM: Kolmogoroff–Arnold–Moser) (Siegel and Moser 1971).

For $0 < \log F < 4$, $\log F \neq 2$ and $\log F \neq 3$ extensive calculations (see Mathematical appendix) prove that we are close to a twist mapping. For $\log F = 2$ and $\log F = 3$, which are unique values in calculating the Birkhoff normal form, resonance occurs and we cannot verify the conditions necessary to apply KAM theory. Numerical results, however, suggest instability. For all other possible values of $\log F$ the dynamics of the system is strongly dependent on its initial conditions, and shows periodicities of different orders, quasi periodical solutions and chaos, as

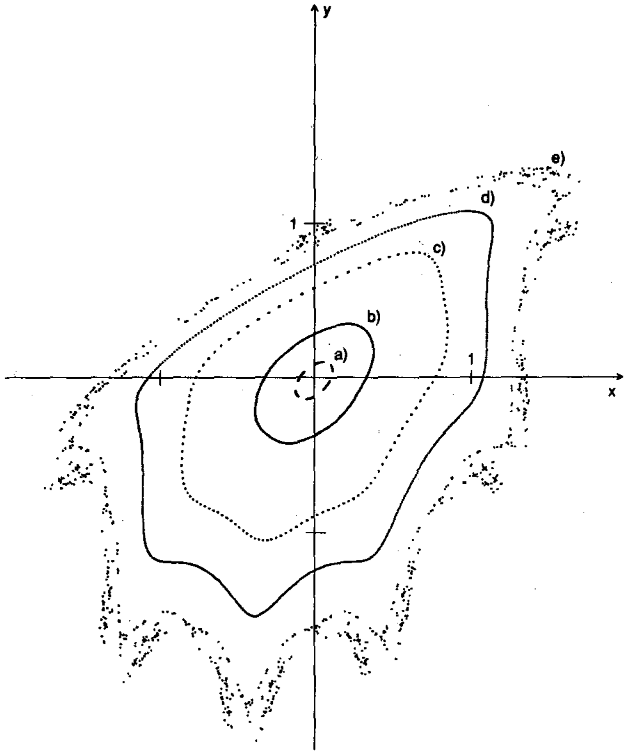

Fig. 1. Phase diagram of the Hassell–Waage–May-model (HWM-model) (x_t, y_t) with $x_{t+1} = x_t + \log F(1 - e^{y_t})$, and $y_{t+1} = x_t + y_t + \log F(1 - e^{y_t})$, $t = 1, 2, \ldots, 1000$, for 5 different initial values (x_0, y_0) with $\log F=1$. *a)* $(x_0, y_0)= (0, 0.1)$: close to equilibrium almost 6-periodicity; *b)* $(x_0, y_0)= (0, 0.3)$: host and parasitoid populations remain on an invariant curve; *c)* $(x_0, y_0)= (0, 0.6)$: (probably) higher periodicity; *d)* $(x_0, y_0)= (0, 0.75)$: (probably) condensation in another curve; *e)* $(x_0, y_0)=(0, 0.9)$: transition to instability and chaos

described by the theorems of KAM theory (Siegel and Moser 1971, §34). Examples for $\log F=1$ are shown in Fig. 1.

As shown in Fig. 2 our transformed system is very sensitive even to small perturbations. The particular perturbation was chosen based on its mathematical simplicity, and its small size at the origin. The fixed point immediately becomes unstable, and bifurcates as predicted by the Hopf theorem (Marsden and McCracken 1976). Because of the term of third degree the trajectories are attracted by a limit cycle around the origin. Different small perturbations and/or other values for $\log F$ can produce amazingly different trajectories in the phase plane. Thus even small changes in the initial conditions or small perturbations (induced either by environmental changes or through evolutionary processes) of the Hassell–Waage–May host–parasitoid system with randomly distributed host and parasitoid individuals and randomly searching parasitoids can give rise to radically different patterns in the population dynamics of both host and parasitoid.

In nature successful superparasitism is a well known phenomenon (Van Alphen and Visser 1990; Van der Hoeven and Hemerik 1990; Speirs et al. 1991). Within the framework of our model, however, successful superparasitism destabilises host–

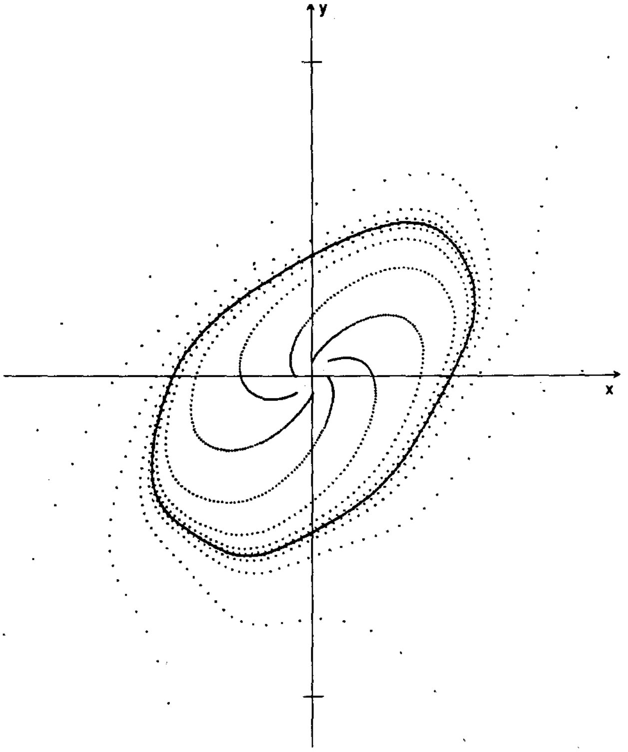

Fig. 2. Phase diagram of the HWM-model (x_t, y_t) with $x_{t+1} = x_t + \log F(1 - e^{y_t})$ and $y_{t+1} = x_t + y_t + \log F(1 - e^{y_t}) + \Delta$ with a small perturbation $\Delta = 0.01\ y_t - 0.05(y_t)^3$ at the origin. Starting with initial values $(x_0, y_0) = (0,\ 0.05)$ and $(x_0, y_0) = (0, 1)$ close respectively far from equilibrium (x_t, y_t) is plotted for t=1, 2,...,5000. The system is attracted by a limit cycle around the origin, the fixed point being unstable

parasitoid systems, and can be considered as a perturbation. Other stabilising counteracting forces are therefore absolutely necessary, and it is worthwhile to investigate patterns as shown in Fig. 2 under the perspective of the Hopf-Bifurcation (Marsden and McCracken 1976; Hassell and May 1989).

Mathematical appendix

We calculate the Birkhoff normal form of

$$\begin{aligned} x_{t+1} &= x_t + f\,(1 - e^{y_t}) \\ y_{t+1} &= x_t + y_t + f\,(1 - e^{y_t}) \end{aligned} \tag{A.1}$$

in order to apply the KAM-theorem to the HWM-model, setting $f = \log F$. We verify that the Jacobian determinant equals one

$$\frac{\partial(x_{t+1}, y_{t+1})}{\partial(x_t, y_t)} = \operatorname{Det}\begin{pmatrix} 1 & -fe^{y_t} \\ 1 & 1 - fe^{y_t} \end{pmatrix} = 1.$$

Thus (A.1) describes an area-preserving map of the x-y-plane onto itself. (A.1) can be written as a real power series and takes the form

$$\begin{aligned} x_{t+1} &= x_t - f\,y_t - f\left(\frac{y_t^2}{2!} + \frac{y_t^3}{3!} + \dots\right) \\ y_{t+1} &= x_t + (1-f)y_t - f\left(\frac{y_t^2}{2!} + \frac{y_t^3}{3!} + \dots\right). \end{aligned} \tag{A.2}$$

The eigenvalues of the linear part of (A.2) are given by

$$\lambda = \left(1 - \frac{f}{2}\right) + \frac{i}{2}\sqrt{f(4-f)}, \qquad \bar{\lambda} = \left(1 - \frac{f}{2}\right) - \frac{i}{2}\sqrt{f(4-f)}. \tag{A.2.a}$$

These eigenvalues reveal that the fixed point (equilibrium point) is parabolic for $f = 0, f = 4$, hyperbolic and therefore unstable for $f < 0$, $f > 4$ and elliptic for $0 < f < 4$. We are interested in the elliptic case where local analysis gives no information on stability, and we thus restrict calculations to $0 < f < 4$.

The reduction of (A.2) into the Birkhoff normal form is done by the following three consecutive coordinate transformations. Calculations are based on Siegel and Moser (1971, §23). We refer to the formulae in Siegel and Moser by using the subscript $(\dots)_{\mathrm{SM}}$.

1) The linear transformation mapping the unit vectors (1, 0), (0, 1) into the eigenvectors $(1-\bar{\lambda}, 1), (1-\lambda, 1)$ yields

$$\begin{aligned} x_{t+1} &= \lambda x_t + c\left(\frac{(x_t+y_t)^2}{2!} + \frac{(x_t+y_t)^3}{3!} + \dots\right) \\ y_{t+1} &= \bar{\lambda} y_t + \bar{c}\left(\frac{(x_t+y_t)^2}{2!} + \frac{(x_t+y_t)^3}{3!} + \dots\right) \end{aligned} \tag{A.3}$$

with

$$c = -\frac{\lambda f}{\lambda - \bar{\lambda}} \tag{A.3a}$$

and $\bar{c}$ the complex conjugate of c. For simplicity we used the same symbols for the transformed coordinates again. The linear terms of (A.3) which corresponds to $(7)_{\mathrm{SM}}$ are already in normal form.

2) To transform the terms up to third degree into normal form we substitute

$$\begin{aligned} x &= \xi + \phi_2(\xi,\eta) + \phi_3(\xi,\eta) \\ y &= \eta + \psi_2(\xi,\eta) + \psi_3(\xi,\eta) \end{aligned} \tag{A.4}$$

with polynomials

$$\phi_k(\xi,\eta) = \sum_{l=0}^{k} a_l^k \xi^{k-l}\eta^l$$

$$\psi_k(\xi,\eta) = \sum_{l=0}^{k} \bar{a}_l^k \xi^l \eta^{k-l}$$

and coefficients a_l^k

$$a_0^2 = \frac{c}{2\lambda(\lambda-1)}, a_1^2 = \frac{c}{1-\lambda}, a_2^2 = \frac{c}{2\lambda(\bar{\lambda}^3-1)},$$
$$a_0^3 = \frac{c}{\lambda(\lambda^2-1)}\left(a_0^2 + \bar{a}_2^2 + \frac{1}{6}\right), a_1^3 = 0,$$
$$a_2^3 = \frac{c}{\lambda(\bar{\lambda}^2-1)}\left(\bar{a}_0^2 + 2\mathrm{Re}a_1^2 + a_2^2 + \frac{1}{2}\right),$$
$$a_3^3 = \frac{c}{\lambda(\bar{\lambda}^4-1)}\left(\bar{a}_0^2 + a_2^2 + \frac{1}{6}\right).$$

In order to avoid $\bar{\lambda}^3=1, \bar{\lambda}^4=1$ in the elliptic case $0 < f < 4$ we have to exclude two additional values $f = 2$ and $f = 3$.

The nonlinear substitution (A.4) transforms (A.3) into normal form up to the third degree

$$\begin{aligned} \xi_{t+1} &= \lambda\xi_t + \alpha_2\xi_t^2\eta_t + O_4 \\ \eta_{t+1} &= \bar{\lambda}\eta_t + \bar{\alpha}_2\xi_t\eta_t^2 + O_4 \end{aligned} \tag{A.5}$$

with

$$\alpha_2 = \frac{c}{2}\left(\frac{c}{\lambda^2-\lambda} + 4\mathrm{Re}\frac{c}{1-\lambda} + \frac{\bar{c}}{\lambda^2-\bar{\lambda}} + 1\right) = \frac{f}{4}\frac{f-2}{f-3}\left(1 + i\frac{f-2}{\sqrt{f(4-f)}}\right).$$

O_4 denotes terms in ξ_t, and η_t of order $\geqq 4$. The second equality is obtained through elementary but longer calculations by substituting (A.2a) and (A.3a) for c and λ and their complex conjugates, respectively.

To check the transformation of (A.3) into (A.5) we first substitute (A.4) in (A.3), and then replace ξ_{t+1} and η_{t+1} by expression (A.5). (A.3) then shows an equality of two power series in ξ_t and η_t up to order 3 with indeed the same coefficients. On the other hand applying $(13)_{\mathrm{SM}}$–$(18)_{\mathrm{SM}}$, we can use this comparison to determine the coefficients $a_l^k (k = 2, 3, 0 \leqq l \leqq k)$ and α_2 recursively.

3) Finally we express (A.5) entirely in terms of real variables r and s by substituting

$$\xi = r + is, \eta = r - is.$$

Separating the real and imaginary parts we get a series, which by comparison of coefficients can be identified up to order 3 with

$$\begin{aligned} r_{t+1} &= r_t\cos(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) - s_t\sin(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) + O_4 \\ s_{t+1} &= r_t\sin(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) + s_t\cos(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) + O_4 \end{aligned} \tag{A.6}$$

where

$$\begin{aligned} \cos\gamma_0 &= \mathrm{Re}\lambda = 1 - \frac{f}{2} \\ \gamma_1 &= -\frac{\mathrm{Re}\alpha_2}{\mathrm{Im}\lambda} = -\frac{1}{2}\frac{f-2}{f-3}\sqrt{\frac{f}{4-f}}. \end{aligned} \tag{A.7}$$

Remember the restrictions $0 < f < 4, f \neq 2, f \neq 3$. (A.6) thus corresponds to $(46)_{\mathrm{SM}}$, and represents the Birkhoff normal form of (A.1). Under the hypothesis $\gamma_1 \neq 0$ and $\gamma_1 \neq \pm\infty$ we can apply the KAM stability theorem to this system (Siegel and Moser, §32).

Interpretation

As outlined above our original HWM-model is transformed into (A.5) with new coordinates r_t, s_t with the restrictions $0 < f < 4$, $f \neq 2$, $f \neq 3$. The coordinates r_t, s_t have no biological meaning. However, by backtransformation they are equivalent to H_t, P_t and x_t, y_t, respectively.

If $f \leqq 0$ ($F \leqq 1$) the system will go extinct because the finite rate of increase of the host is too small. Furthermore, as stated in the main text, for large finite rates of increase i.e. $f \geqq 4$ ($F \geqq e^4 = 54.598$) the fixed point is no longer stable. The slightest perturbation from it leads to increasing fluctuations. We hence restrict to $0 < f < 4$, and discuss three successive approximations.

1) Very close to equilibrium (A.5) can be approximated by

$$\begin{aligned} r_{t+1} &= r_t \cos\gamma_0 - s_t \sin\gamma_0 \\ s_{t+1} &= r_t \sin\gamma_0 + s_t \cos\gamma_0 \end{aligned} \tag{A.8}$$

considering only linear terms in r_t, s_t. This describes a rotation by an angle γ_0, $\cos\gamma_0 = 1 - f/2$, with the origin as centre.

2) Neglecting O_4 we find our system close to

$$\begin{aligned} r_{t+1} &= r_t \cos(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) - s_t \sin(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) \\ s_{t+1} &= r_t \sin(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) + s_t \cos(\gamma_0 + \gamma_1(r_t^2 + s_t^2)) \end{aligned} \tag{A.9}$$

which still can be interpreted in geometrical terms. A given system (r_t, s_t) will remain forever on a circle with radius $\sqrt{r_{t+1}^2 + s_{t+1}^2} = \sqrt{r_t^2 + s_t^2}$, but the rotation angle now depends on the radius. We refer to these circles as invariant circles under (A.8). Obviously we find many different periodicities or quasi periodicities depending on the radius.

3) At last we now include the perturbation terms O_4. As stated earlier the Jacobian determinant of (A.1) equals 1, and according to Siegel and Moser (1971) all transformations that bring (A.1) into the form (A.5) preserve this property. However, this does not guarantee that the iterated states will remain within a bounded distance from the fixed point (origin). Applying KAM-theory it follows that if a system is close enough to a twist mapping (A.6) with rotation angle varying with the radius (i.e. $\gamma_1 \neq 0$), then still infinitely many of the invariant circles of (A.8) survive the perturbation (according to Siegel and Moser 1971, p. 245, the rotation angles $\gamma_0 + \gamma_1(r^2 + s^2)$ of these circles are only badly approximable by rational numbers). Our system is close to a type (A.9) system except for $f \neq 2, f \neq 3$, where calculating the Birkhoff normal form is impossible and we get no information. According to KAM-theory there exist states close enough to the fixed point, which are enclosed by an invariant curve. By continuity arguments the interior of such a closed invariant curve will then map onto itself. The same is true for a state within an annulus enclosed between two such curves. Therefore, if a host–parasite system has its initial state

a) on such an invariant curve
b) on such an annulus

it will remain there forever. Too far from the origin, when the perturbations become too large, the invariant curves decay and the host–parasitoid system may fluctuate in a chaotic way.

A given initial state within an annulus as described can produce many other strange patterns:

- after several generations it can return to the starting point, thus showing periodical behaviour;

- it can be non-periodic and not lie on an invariant circle but come arbitrarily close to every point of the annulus;

- it can iterate the described patterns ad infinitum thus producing sets of annuli, closed curves and chaos around periodical points of successively higher periodicity.

Acknowledgement. We are grateful to R. M. May and M. P. Hassell for their helpful comments on an earlier version of this manuscript. They especially referred us to the paper of Hassell et al. (1983), and their critical comments and propositions improved the final version of the text. The suggestions of an anonymous reviewer improved the final version.

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