PHYSICAL REVIEW E, VOLUME 64, 032901

Blowout bifurcation with non-normal parameters in population dynamics

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(Received 24 November 2000; revised manuscript received 17 April 2001; published 29 August 2001)

Interesting dynamic behaviors have been associated with the transverse stability of an invariant subspace (e.g., riddled basins or on-off intermittency). Recently, these complex behaviors have been generalized to cases of models with non-normal parameters showing that these behaviors might be widespread. In this Brief Report I demonstrate this type of complex dynamics in models of interacting populations for which the invariant subspace is defined by species extinction. In the context of the current biodiversity crisis, implications of these behaviors for population biology are discussed.

DOI: 10.1103/PhysRevE.64.032901 PACS number(s): 87.23.Cc, 05.45.−a, 87.10.+e, 05.45.Tp

Recently, it has been shown that a dynamical system possessing invariant subspaces of topological dimension smaller than the dimension of the full phase space may exhibit surprising dynamics with an exacerbated level of unpredictability [1]. In these systems, several complex attractors coexist and tiny variations in initial conditions induce a random switch between the different asymptotic attractors. Depending on the stability of these invariant subspaces, different behaviors may arise: riddled basins [1–4], intermingled basins [5], attractor bubbling [1,6], and on-off intermittency [1,7].

These phenomena are related to a type of bifurcation called *blowout bifurcation* [1]. This bifurcation is defined in terms of changes in the transverse stability of the invariant subspace. Quantitatively, at the blowout bifurcation point, the largest transverse asymptotic Lyapunov exponent changes its sign. Blowout bifurcation can be understood by considering the distributions of finite time fluctuations in the largest instantaneous Lyapunov exponent for perturbations transverse to the invariant subspace [3]. There exists a spread of the distribution of the transverse instantaneous Lyapunov exponent which accounts for the existence of special dynamics such as riddled basins or on-off intermittency. When the invariant subspace is slightly stable ($\lambda_\perp \lesssim 0$), there are still initial conditions for which the transverse instantaneous Lyapunov exponent becomes positive and trajectories move to another attractor. In this case, one may have basin riddling. Conversely, one can observe on-off intermittency, when this subspace is slightly unstable ($\lambda_\perp \gtrsim 0$). But whether basin riddling or on-off intermittency occurs is also a function of the dynamics away from the invariant subspace.

Riddling and on-off intermittency have received much recent attention [1–7], because they are fairly common in systems with symmetry or in spatiotemporal chaotic systems. This type of complex dynamics has also been found in simple models of interacting populations [8,9]. Competition between different species can be modeled as a dynamical system with an invariant subspace corresponding to the extinction of one (or more) species. The loss of stability of the attractor in the invariant subspace means that the corresponding species can invade and coexist with other species. Thus, this topic appears of major interest for population biology in the context of the current biodiversity crisis associated with a markedly reduced species diversity, a high rate of extinction and invasion, and the puzzle of rare species [10].

Previous investigations of blowout bifurcation focused on the case with normal parameters i.e., parameters leaving the dynamics on the invariant manifold unchanged. However in natural systems, the dynamics more commonly encountered are governed by non-normal parameters, which vary the dynamics inside as well as outside the invariant subspace. Then the dynamics in the invariant subspace is not decoupled from the dynamics in the dimensions transverse to it and the system has a nonskew product structure. Aswhin and coauthors [11] have generalized blowout bifurcation to these systems with non-normal parameters and nonskew product structure. They argued that blowout bifurcation and the associated dynamics could be more pervasive in this case since they can occur regardless of whether the dynamics in the invariant manifold is stable or unstable, nonchaotic or chaotic.

The purpose of this study is to analyze blowout bifurcation with non-normal parameters in models of interacting populations. Chaotic dynamics in population biology is a subject of great debate [12]. In this paper our results do not depend on the presence of chaotic dynamics in the invariant subspace; this leads to several phenomena associated with the blowout bifurcations that might be more likely from an ecological point of view.

To investigate blowout bifurcation with non-normal parameters in the case of interacting populations, I consider three different models. The first model (I) studied is the Franke-Yakubu model [13] for competition between two species affected by both intra- and interspecific competition. This model is known to have riddled basins of attraction [2,8] and reads

$$x(t+1)=x(t)\exp\{r-s[x(t)+y(t)]\},$$

$$y(t+1)=\frac{c_1 y(t)}{c_2+x(t)+y(t)}, \tag{1}$$

where r, c_1 are the intrinsic growth rates and s, c_2 are constants proportional to the carrying capacity of the environment.

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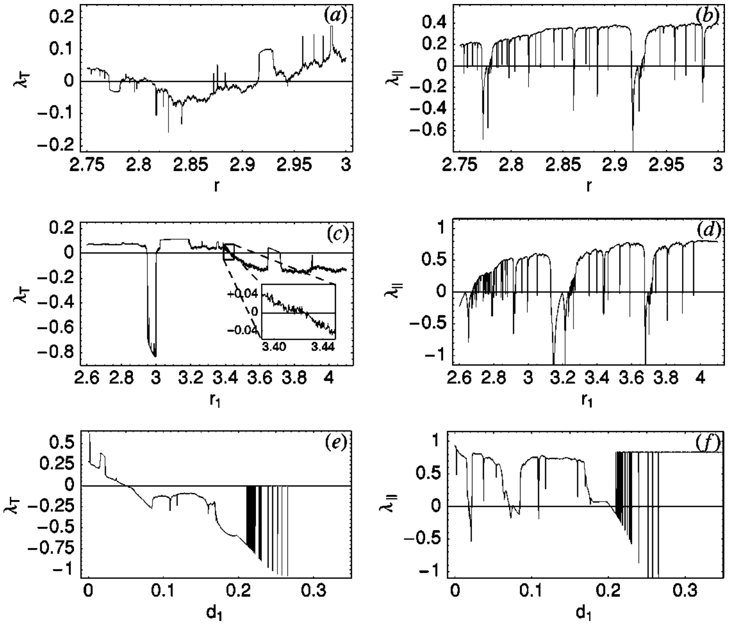

FIG. 1. Blowout bifurcation in models of interacting populations. Estimated transverse ($\lambda_T \equiv \lambda_\perp$) and tangential ($\lambda_\parallel$) Lyapunov exponents computed as functions of non-normal parameter studied for model I (a,b), model II (c,d), and model III (e,f). The parameters used are $s=0.10$, $c_1=20.25$, $c_2=1.20$ for model I, $d_1=0.175$, $k_1=100$, $d_2=0.025$, $r_2=3.50$, $k_2=75$ for model II, and $r_1=4.0$, $a_1=0.10$, $b_1=6.67$, $d_2=0.05$, $r_2=4.0$, $a_2=0.10$, $b_2=6.67$ for model III.

Because ecological systems are unavoidably spatial, analyses of population dynamics require the inclusion of the spatial dimension. I thus analyzed the two-patch model proposed by Holt and McPeek [14] where individuals disperse at a constant rate between the two patches and experience density dependence in each patch. The Holt-McPeek model is given by

$$
\begin{aligned}
x_1(t+1) &= (1-d_x)x_1(t)f_1^l(t) + d_x x_2(t) f_2^l(t),\\
y_1(t+1) &= (1-d_y)y_1(t)f_1^l(t) + d_y y_2(t) f_2^l(t),\\
x_2(t+1) &= (1-d_x)x_2(t)f_2^l(t) + d_x x_1(t) f_1^l(t),\\
y_2(t+1) &= (1-d_y)y_2(t)f_2^l(t) + d_y y_1(t) f_1^l(t), \qquad (2)
\end{aligned}
$$

where x_i and y_i are the two species in patch i, $f_i^l(t) = f^l(x_i(t), y_i(t))$ is the density dependent growth function, and $d_{x,y}$ is the species dependent dispersion rate. The above model (II) assumes that $f_i^l = f_{II}$ following the Ricker model [15]

$$
f_{II}(x_i, y_i) = \exp\left[r_i \left(1 - \frac{x_i + y_i}{k_i} \right) \right] \qquad (3)
$$

with k_i the carrying capacity and r_i the growth rate of patch i.

I have also studied a similar model (III) [16] with another form of density dependence function $f_i^l = f_{III}$:

$$
f_{III}(x_i, y_i) = \frac{r_i}{1 + a_i (x_i + y_i)^{b_i}}, \qquad (4)
$$

where r_i is the intrinsic growth rate, a_i is the inverse of the carrying capacity, and b_i reflects the intensity and the form of the density dependent competition.

For these models, the local dynamics (competition between species) and possible dispersion between different patches determine the ecological dynamics of the community. In this context, the invariant subspace is defined by the extinction of the y or y_i species. The dynamics of such systems may be understood by examining the sign structure of the two largest asymptotic Lyapunov exponents. One of them, the tangential Lyapunov exponent $\lambda_\parallel$, describes the evolution on the invariant subspace. The second, the largest transverse Lyapunov exponent $\lambda_\perp$, characterizes the evolution transverse to the subspace.

As bifurcation parameters, I chose the growth rate (r, r_1) as well as the dispersion rate (d_1) for models I, II, and III, respectively. These non-normal parameters directly influence the dynamics, in the invariant subspace (for r, r_1), and in the full phase space (for d_1). Examples of the evolution of $\lambda_\perp$ and $\lambda_\parallel$ (computed as in [2,8]) with these bifurcation parameters are presented in Fig. 1. These numerical simulations reveal the typical characteristics of the blurred blowout bifurcations with non-normal parameters [11]: (i) continuous but nonsmooth fluctuations through 0 of $\lambda_\perp$ [see the inset Fig. 1(c)]; (ii) numerous windows with a negative $\lambda_\parallel$ value associated with the periodic attractor. This is associated in parameter space with the existence of numerous regions where the attractor within the invariant subspace is periodic and transversely unstable, in contrast to the usual cases with normal parameters [1,2].

An exotic behavior associated with the blowout bifurcations, when $\lambda_\perp$ is slightly positive, is on-off intermittency [1]. These behaviors have been generalized in the cases of non-normal parameters by in-out intermittency [11]. This dynamics is shown in Fig. 2(a,b), where $y(t)$ versus the iteration t is plotted. One sees that there are iteration intervals during which $y(t)$ stays near $y(t)=0$ (the "off" state defined by the extinction of the y species), but there are also intermittent bursts of $y(t)$ (the "on" state defined by the invasion of y species). This is a typical consequence of the

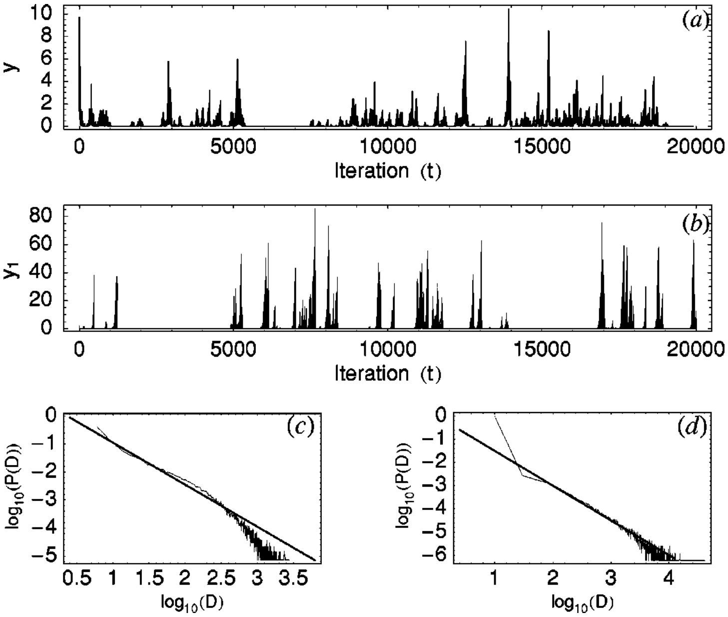

FIG. 2. On-off intermittency in models of interacting populations. (a) and (b) are examples of time series generated with random initial conditions by the models I and II, respectively. (a) $r=2.916$, $s=0.10$, $c_1=20.25$, $c_2=1.20$, and $\lambda_\perp \approx 0.033$; (b) $d_1=0.175$, $r_1=3.414$, $k_1=100$, $d_2=0.025$, $r_2=3.50$, $k_2=75$, and $\lambda_\perp \approx 0.010$. (c) and (d) are the corresponding distributions of the "off" phases (defined by the extinction of the y species) of duration D. The straight line corresponds to the theoretical distribution with slope $\beta=-3/2$.

fact that, despite its positive average, $\lambda_\perp(t)$ has finite time fluctuations that are negative, which makes the invariant subspace locally stable and attracts the trajectory toward the "off" state intermittently. This temporal evolution is repeated in an irregular and aperiodic manner; in the meantime it is characterized by well-defined power laws [7]. In particular, the probability distribution of the "off" phases $P(D)$ depends on their duration D as $P(D) \propto D^\beta$ [17], with $\beta=-3/2$ a universal scaling coefficient [7]. Examples of these relations are shown in Fig. 2(c,d).

Another behavior associated with blowout bifurcations is riddled basins of attraction [1,2]. As the transverse Lyapunov exponent of the invariant subspace is slightly positive, the loss of transverse stability of orbits embedded in that subspace leads to riddled basins [3]. Figure 3 displays the complex fractal boundary between the initial conditions leading to each of the two attractors (defined by the coexistence or the extinction of the y species). In the case of these riddled basins (or partially riddled basins), the basins have fractal boundaries where almost every point is arbitrarily close to a point in the other basin and this behavior persists regardless of the scale examined (Fig. 3). But, in contrast to cases with normal parameters [2], varying a non-normal parameter makes it possible to observe riddled basins, even in the presence of a periodic attractor in the invariant subspace.

These results show that blowout bifurcation and the associated complex dynamics (riddled basins, on-off intermittency) are present in models of interacting population even

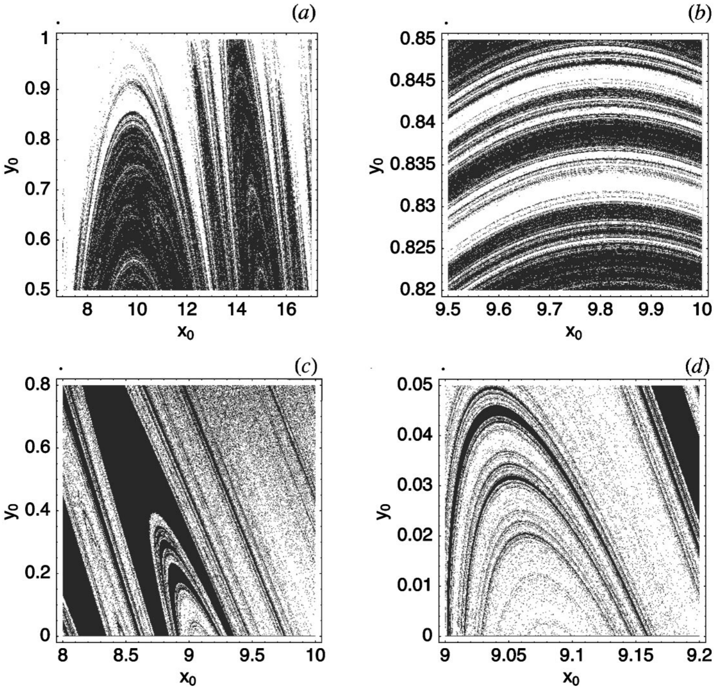

FIG. 3. Riddled basins in models of interacting populations. (a) Basin of attraction in the case of model I with $r=2.86$, $s=0.10$, $c_1=20.25$, $c_2=1.20$, $\lambda_\perp \approx -0.059$, and $\lambda_\parallel \approx -0.219$. White dots correspond to initial conditions attracted by the coexistence attractor; black dots correspond to initial conditions attracted by the attractor defined by the extinction of the y species. (b) Enlargement of (a). (c) Basin of attraction in the case of model III with $d_1=0.225$, $r_1=4.0$, $a_1=0.10$, $b_1=6.67$, $d_2=0.05$, $r_2=4.0$, $a_2=0.10$, $b_2=6.67$, $\lambda_\perp \approx -0.0001$, and $\lambda_\parallel \approx -0.434$. (d) Enlargement of (c).

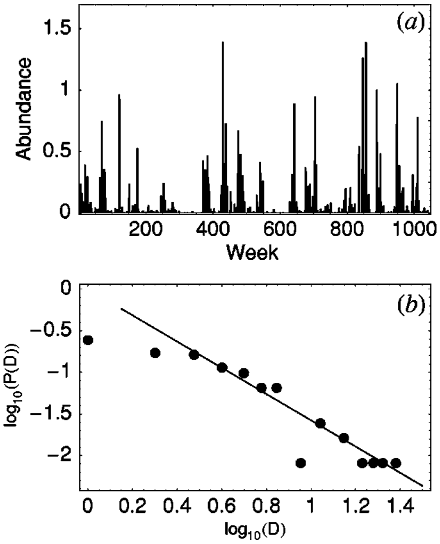

FIG. 4. On-off intermittency in a marine phytoplankton population. (a) Weekly averages of daily counts of diatoms (millions of cells per liter) collected at the Scripps pier (California) between 1920 and 1939 [20]. (b) Distribution of rarity (“off”) phases of duration D. The fitted $\hat{\beta}\approx -1.58$ and the straight line corresponds to the theoretical distribution with slope $\beta=-3/2$

with non-normal parameters. Along the lines suggested by Ashwin and co-authors, this implies that the complex behaviors associated with the blowout bifurcation are more universal in population models since they are not limited to normal parameters.

These results may have important practical consequences [8,9] since these sorts of behaviors are of great interest in population biology, particularly considering the actual biodiversity crisis [10]. All these results are supported by various ecological observations. One of these is the temporal dynamics of rare species involved in intermittent rarity, that is, the alternation of long periods of marked scarcity and short outbreaks of high abundance in a seemingly unpredictable way. This kind of dynamics has been observed in species of great interest to population biologists; however, the mechanisms that underlie intermittent rarity remain poorly understood. One possible explanation could be on-off intermittency. Preliminary results are shown in Fig. 4 for the dynamics of a phytoplankton population. Figure 4(a) displays the observed dynamics and Fig. 4(b) the distribution of rarity (“off”) phases. Despite scanty data, this distribution is remarkably well fitted by the theoretical distribution with the universal scaling coefficient $\beta=-3/2$ [Fig. 4(b)]. On the other hand, dynamics with riddled basins provide a working hypothesis to explain both the differences and the similarities observed among the time series of replicated experiments. For example, different dynamics for various replicates of laboratory cultures have been observed in the case of the flour beetle [18] and in the case of host-parasitoid interactions [19].

The findings reported here stressed that simple deterministic models can have outcomes that are for all practical purposes as stochastic as experimental observations, and one should keep in mind that apparently stochastic variability in the observations of ecological experiments may have deterministic grounds.

I thank Samuele Bottani and Lewi Stone for stimulating discussions and Dany Kaplan who provided me with the diatom data.

[1] E. Ott and J.C. Sommerer, Phys. Lett. A **188**, 39 (1994); P. Ashwin, J. Buescu, and I. Stewart, *ibid.* **193**, 126 (1994); P. Ashwin, J. Buescu, and I. Stewart, Nonlinearity **9**, 706 (1996).

[2] J.C. Alexander, J.A. Yorke, Z. You, and I. Kan, Int. J. Bifurcation Chaos Appl. Sci. Eng. **2**, 795 (1992).

[3] Y.C. Lai, C. Grebogi, J.A. Yorke, and S.C. Venkataramani, Phys. Rev. Lett. **77**, 55 (1996); Y. Nagai and Y.C. Lai, Phys. Rev. E **55**, R1251 (1997).

[4] E. Ott, J.C. Alexander, I. Kan, J.C. Sommerer, and J.A. Yorke, Phys. Rev. Lett. **71**, 4134 (1993); T. Kapitaniak, Y.L. Maistrenko, A. Stefanski, and J. Brindley, Phys. Rev. E **57**, R6253 (1998).

[5] J.C. Sommerer and E. Ott, Phys. Lett. A **214**, 243 (1996); Y.C. Lai and C. Grebogi, Phys. Rev. E **52**, R3313 (1995).

[6] S.C. Venkataramani, B.R. Hunt, and E. Ott, Phys. Rev. E **54**, 1346 (1996).

[7] N. Platt, E.A. Spiegel, and C. Tresser, Phys. Rev. Lett. **70**, 279 (1993); J.F. Heagy, N. Platt, and S.M. Hammel, Phys. Rev. E **49**, 1140 (1994).

[8] B. Cazelles, Chaos, Solitons Fractals **12**, 301 (2001).

[9] M.G. Neubert, J. Theor. Biol. **189**, 399 (1997); R. Ferrière and B. Cazelles, Ecology **80**, 1505 (1999); R.K. Upadhyay, S.R.K. Iyengar, and V. Rai, Chaos, Solitons Fractals **11**, 533 (2000); O. De Feo and R. Ferrière, Int. J. Bifurcation Chaos Appl. Sci. Eng. **10**, 443 (2000).

[10] Nature (London) **405** (2000), special issue on biodiveristy.

[11] E. Covas, P. Ashwin, and R. Tavakol, Phys. Rev. E **56**, 6451 (1997); P. Ashwin, E. Covas, and R. Tavakol, Nonlinearity **9**, 563 (1999); E. Covas, R. Tavakol, P. Ashwin, A. Tworkowski, and J.M. Brooke, Chaos **11**, 404 (2001).

[12] A. Hasting, C.L. Hom, S. Ellner, P. Turchin, and H.C.J. Godfray, Annu. Rev. Ecol. Syst. **21**, 1 (1993); S. Ellner and P. Turchin, Am. Nat. **145**, 343 (1995).

[13] J.E. Franke and A.A. Yakubu, J. Math. Biol. **30**, 161 (1991).

[14] R.D. Holt and M.A. McPeek, Am. Nat. **148**, 709 (1996).

[15] J.W. Ricker, J. Fish. Res. Board Can. **11**, 559 (1954).

[16] M. Doebeli and G. Ruxton, Evolution (Lawrence, Kans.) **51**, 1730 (1997).

[17] For in-out intermittency this power law becomes $P(D) \propto (D^{\beta}e^{\alpha D}+\gamma e^{\delta D})$ [11].

[18] D. Jillson, Nature (London) **288**, 699 (1980).

[19] M. Begon, S.M. Sait, and D.J. Thompson, Nature (London) **381**, 311 (1996); S.M. Sait, W.C. Liu, D.J. Thompson, H.C.J. Godfray, and M. Begon, *ibid.* **405**, 448 (2000).

[20] S. A. Tont, *Diatoms*, Vol. 1 (Scripps Institution of Oceanography, La Jolla, 1986).