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External perturbations and cyclic dynamics in stable populations

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We show that sustained population oscillations do not necessarily stem from the dynamic properties of a population, or from periodic environmental fluctuations. In particular, we demonstrate that population fluctuations may be sustained by random non-cyclic environmental disturbances. These perturbations reduce breeding success in otherwise stable populations with overshootings in their transient dynamics. When the transition phase from non-equilibrium to equilibrium states is slow, as compared with the frequency and strength of the random fluctuations, and includes overshootings, the dynamics may show fluctuating patterns that are hard to tell apart from regular fluctuations. Population dynamics which include overshootings during transient phases are common in a large variety of population models. As a specific example, we consider the effect of delayed density dependence in a Ricker type model. However, to show that the process can be generalized to different types of models, we also use a nonlinear autoregressive model containing density dependence.

1. Introduction

Since 1924 the regular fluctuations shown by many animal populations have occupied a central place in theoretical population ecology (Elton 1924, 1942, Elton & Nicholson 1942, Siivonen 1948, Moran 1952, 1953, Kalela 1962, Keith 1963, Hörnfeldt 1978, Angelstam *et al.* 1984, 1985, Hansson & Henttonen 1985ab, Lindén 1988, 1989, Myers 1988, Ginzburg & Taneyhill 1994). Certainly, the self-repeating dynamics in numbers have a magical spell, as witnessed by the publishing space allocated to analyses of long-term records of snowshoe hare and lynx pelt statistics of the Hudson Bay Company.

The endeavor of the past 50 years has resulted in several hypotheses to account for cyclic dynamics of animal populations. In short, these include such factors as sunspot cycles (Elton 1924), epidemics (MacLulich 1937), predator–prey and host–parasite relationships (Moran 1953, Anderson & May 1978, May & Anderson 1978), lunar cycles (Siivonen & Koskimies 1955), food quality

(Lauckhart 1957), and self-regulation (Chitty 1960). Yet, the causes of periodic population dynamics are one of the persisting mysteries in animal ecology (Royama 1992).

In studies attempting to explain population cycles with environmental disturbances, the perturbation agent has been assumed to continuously affect the target population (e.g. Johnson *et al.* 1986, Townsend *et al.* 1990, Royama 1992). That environmental disturbances need not act continuously is the subject of this study.

With the help of a model containing nonlinear delayed density dependence, we shall demonstrate that random perturbations affecting reproductive success may cause sustained and regular oscillations in otherwise stable populations. We consider delayed density dependence and failures in breeding to be frequent in natural populations, and suggest that rather simple phenomena might frequently be the cause of documented cyclic dynamics. This is exemplified by an excellent match between a simulation model and Black Grouse *Tetrao tetrix* data in south-western Finland between 1897–1930.

2. Delayed density dependence

Consider an animal population in which the density dependence is delayed. Let $x(k)$ denote the population size at time k. The population dynamics is given as (e.g. Turchin 1990)

$$x(k+1) = x(k)F(x(k), x(k-1)) \tag{1}$$

where $F(x(k), x(k-1))$ denotes the density-dependent per capita reproductive success.

We assume here in particular that the population renews itself according to a delayed Ricker-type relationship (Ricker 1954) as follows:

$$F(x(k), x(k-1)) = \exp(r + a_1 x(k) + a_2 x(k-1)) \tag{2}$$

where r is the intrinsic rate of increase, and a_1, a_2 are constant parameters.

The equilibrium population level satisfies $x(k) = x(k-1) = \bar{x}$ for all k. Thus, we have

$$1 = F(\bar{x}, \bar{x}) = \exp(r + (a_1 + a_2)\bar{x}), \tag{3}$$

from which we obtain

$$\bar{x} = -\frac{r}{a_1 + a_2}. \tag{4}$$

Thus, a condition for the positiveness of the equilibrium $\bar{x}$ is

$$a_1 + a_2 < 0. \tag{5}$$

In this paper we consider population dynamics for which the equilibrium population size eq. (4) is locally asymptotically stable (e.g. Edelstein-Keshet 1989). In particular, we show that population dynamics, which would stabilize and ultimately converge to the equilibrium level eq. (4) in the absence of environmental or other disturbances, may show sustained periodic oscillations when reproduction is vulnerable to failure or perturbations of variable intensity at random time intervals. We use autocorrelation analysis to characterize the population cycles and show that the autocorrelation functions may suggest strong periodicity in randomly perturbed populations. The most interesting feature here is that the length of the periods generated by random perturbations may easily extend to years.

The stability properties and the dynamic behavior of the deterministic non-delayed ($a_2 = 0$) Ricker type population dynamics eq. (2) has been analyzed by May (1976). In particular, the population dynamics is stable for $r < 2$, periodic for $2 < r < 2.5$, and double periodic and eventually chaotic for $r > 2.5$. Note that the stability conditions are independent of a_1. The equilibrium level $\bar{x}$ under delayed density-dependent dynamics eq. (1), eq. (2) is locally asymptotically stable if (Appendix A)

$$2 > 1 - a_2\bar{x} > |1 + a_1\bar{x}|. \tag{6}$$

The stability area is illustrated in the (a_1, a_2)-space in Fig. 1 for $r = 0.9$ (for details, see the Appendix A).

3. Random perturbations

We next extend our model to include random perturbations reducing reproductive success of the population at random time intervals. We modify the original population dynamics model eq. (1) by rewriting it as

$$x(k+1) = \mu(k)x(k)F(x(k), x(k-1)), \tag{7}$$

where $\mu(k)$ is a random survival factor at time k. The survival factor is subjected to perturbations characterized as follows. The probability of a perturbation, i.e. $\mu(k)$ being less than one, at time k is denoted as p $(0 < p < 1)$, in which case $\mu(k)$ takes its value from a random distribution. In most of our simulations the probability of such perturbation is $p = 0.05$ meaning that a substantial failure in reproduction occurs, on average, once in 20 years. The values of $\mu(k)$ are evenly distributed on [0.4, 0.6] for each k.

Let us next illustrate the dynamic properties of eq. (7) by simulating the case in which $a_2 = -0.1$, $r = 0.9$, and a_1 obtains different values (but see Kaitala *et al.* 1995). When the value of a_1 increases along the line $a_2 = -0.1$ from $-\infty$ to 0.01, magnitudes of the eigenvalues, characterizing the stability properties of the deterministic dynamics system ($\mu(k) = 1$ for all k), are less than one. This means that the population dynamics system is locally asymptotically stable for all $a_1 \in (-\infty, 0.01)$. For large negative values of a_1 convergence of the population size back to equilibrium level occurs without observable oscillations (Fig. 2A). Specifically, we have $a_1 = -0.4$, and $\bar{x} = 1.8$, and the magnitudes of the complex eigenvalues are $|\lambda_{1,2}| = 0.42$. The convergence after random perturbations back to the equilibrium level occurs quickly. Autocorrelation analysis does not suggest the presence of periodicity in the dynamics (Fig. 2a).

The magnitudes of the eigenvalues remain less than one for all $a_1 < 0.01$ implying that the equilibrium population level is locally asymptotically stable. However, when the non-delayed density dependence becomes weaker and delayed density dependence remains strong, that is, the value of a_1 increases, magnitudes of the eigenvalues become larger, and the convergence to the equilibrium level begins to show signs of oscillations. Fig. 2B illustrates the case in which $a_1 = -0.1$, and $|\lambda_{1,2}| = 0.67$. Visible overshootings are observed during the convergence of the population level after random perturbations. However, autocorrelation analysis does not suggest periodicity in the population dynamics (Fig. 2b).

The next phase is to continue decreasing the stability of the population dynamics (e.g. by increasing further the value of a_1). However, this is done so that the equilibrium population size remains asymptotically stable. Then the convergence back to the equilibrium population level shows increasing patterns of oscillations. In particular, the overshootings become larger and the convergence back to the equilibrium level becomes slower (Fig 2C; $a_1 = 0.005$). The magnitudes of the eigenvalues are $|\lambda_{1,2}| = 0.97$, and convergence of the population level after random perturbations show clear oscillations. Because the frequency of the random fluctuations is high as compared to the rate of convergence, autocorrelation analysis suggests periodicity in the population dynamics (Fig. 2c). In this particular example the statistical analysis shows that the population cycles are 6–7 years.

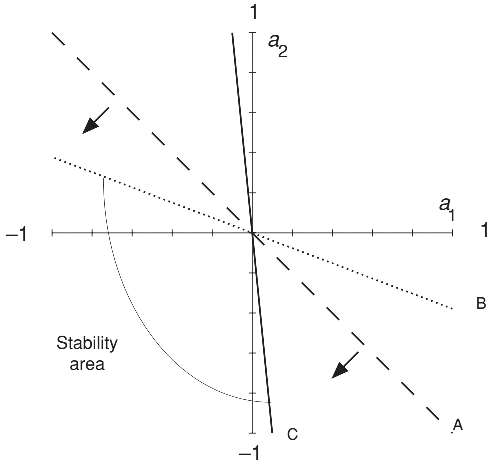

Fig. 1. The arrows below line A denote the area in which the population equilibria levels are positive (see eq. 5). When $r = 0.9$ the stability area in the (a_1, a_2)-space is the sector defined by the conditions:

$$a_2 < -\frac{1.1}{2.9}a_1 \approx -0.38a_1$$

(defined by line B), and $a_2 < -10a_2$ (defined by line C, see the Appendix A).

We next show, for the purposes of comparison, an example of unstable population dynamics. Let $a_1 = 0.015$. Clearly, the pair (a_1, a_2) is now located outside the stability area illustrated in Fig. 1. The magnitudes of the eigenvalues are now $|\lambda_{1,2}| = 1.03$. The patterns of population fluctuations or the autocorrelation results (Fig. 2D) do not seem to differ critically from those presented in Fig. 2C. A closer look at the results reveals, however, some qualitative differences. First, when the population comes close to the equilibrium level, the population shows increasing amplitude fluctuations. This is due to population dynamics converging towards a periodic attractor. Second, the autocorrelation function (Fig. 2d) reveals periodicity slightly stronger than in Fig. 2c. However, it may be very difficult to detect either of these differences in data statistically. Furthermore, this example shows that the qualitative difference between stable and unstable population dynamics may be very faint in the presence of

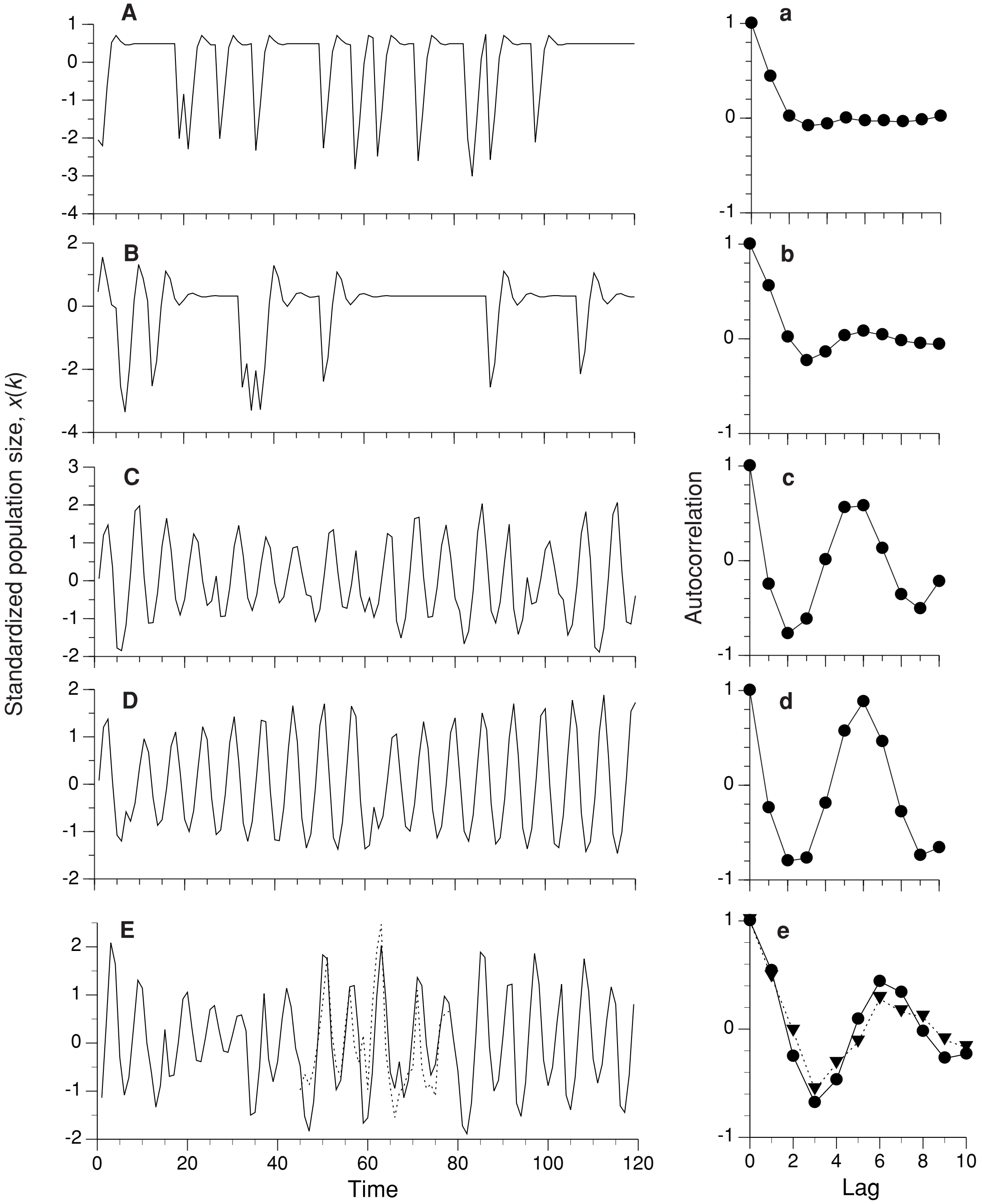

Fig. 2. Population dynamics (graphs A–E) 120 generations (selected at random after at least 3 000 generations of simulations) subject to random perturbations in reproductive success. The small panels (a–e) on the right graph autocorrelation functions for the corresponding time series on the left-hand panels (based on a sample of 500 final generations). Graphs A–D obey eq. (7) with a Ricker-type population model eq. (2). The parameter values are as follows: — A: $r = 0.9$, $a_1 = -0.4$, $a_2 = -0.1$, and the magnitudes of the eigenvalues are $|\lambda_{1,2}| = 0.42$. — B: $r = 0.9$, $a_1 = -0.1$, $a_2 = -0.1$, and $|\lambda_{1,2}| = 0.67$. — C: $r = 0.9$, $a_1 = 0.005$, $a_2 = -0.1$, and $|\lambda_{1,2}| = 0.97$. — D: $r = 0.9$, $a_1 = 0.015$, $a_2 = -0.1$, and $|\lambda_{1,2}| = 1.03$. — E: Simulated population dynamics of eq. (8) subject to random perturbations. The probability of a random perturbation is 0.1, parameter values used were $a_1 = -0.0732$ and $a_2 = -0.8819$. The superimposed data are 1897–1930 Black Grouse dynamics from south-western Finland.

environmental perturbations. Care should be taken when one attempts to tell whether population cycles are due to environmental uncertainty or due to inherently unstable population dynamics.

Relative stability of population dynamics can be further clarified by studying the route from stability to instability. Fig. 3 illustrates the path of the complex eigenvalues as parameter a_1 increases continuously from – 0.4 to 0.01. Note that the corresponding eigenvalues are complex conjugates resulting in two symmetric curves in the complex plane. Clearly, the eigenvalues are all situated within the unit circle in the complex plane indicating that the related population dynamics are locally asymptotically stable. The eigenvalue path crosses, however, the unit circle at $a_1 = 0.01$, and the population dynamics become periodic. The corresponding phase angle, θ, approximates the periodic properties of the population dynamics close to $a_1 = 0.01$. In particular, the length of the period in the population dynamics is 2π/θ, which at $a_1 = 0.01$ is 6.36 units of time. Thus, the transition from stability to instability does not occur here through the "usual" period-doubling route. Instead, the transition from stability to instability occurs through the quasiperiodic route (Rohani *et al.* 1994). In other words, the population dynamics undergo a bifurcation from a stable equilibrium into oscillations in which the period generally differs from two time units.

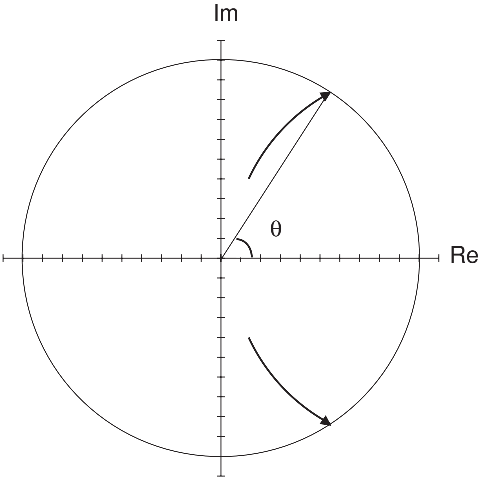

Fig. 3. As parameter a_1 increases along the line $a_2 = – 0.1$ from – 0.4 to 0.01 the eigenvalues change continuously forming a symmetric pair of paths in the complex plane. The eigenvalues are situated within the unit circle implying that the population dynamics are locally asymptotically stable for all a_1 in [0.4,0.01]. The eigenvalue paths cross the unit circle at $a_1 = 0.01$ indicating a transition from stability into instability. The population dynamics becomes periodic and the length of the period in the population dynamics is 2π/θ, which at $a_1 = 0.01$ is 6.36 time units.

4. Grouse dynamics — an example

Recently we have been performing extensive analyses of long-term dynamics in Finnish populations of Capercaillie, Black Grouse and Hazel Grouse (Lindström *et al.* 1995, 1996, Ranta *et al.* 1995). The three species display both cyclic and synchronous fluctuations in Finland. An analysis of the long-term data reveals that the population dynamics in the three species better fits to a second-order nonlinear autoregressive model than to a Ricker type model (Lindström 1996). One such model is:

$$x(k+1) = x(k)\exp\left(1 - \frac{1}{x^{a_1}(k)x^{a_2}(k-1)}\right). \quad (8)$$

This is the eq. (2.20b) by Royama (1992:62) written to be structurally equivalent with the Ricker model eq. (2). For the algebra see Appendix B. With the grouse data (Lindström 1996) it turns out that the fitted values of a_1 and a_2 fall into the region yielding damped cycles. That is, in the initial phases populations obeying eq. (8) with the grouse parameters display cyclic periodicity but the amplitude gradually levels off (Royama 1992). To exemplify that the periodic oscillation (Fig. 2C, D), as achieved by perturbing eq. (2) is not the property associated with the Ricker model only, we merged the eq. (8) into the eq. (7) using grouse parameter values for a_1 and a_2. When the dynamics is perturbed after eq. (7) with $\mu(k)$ from [0.4, 0.6] and $p = 0.1$, a clearly cyclic dynamics (Fig. 2E) is achieved with a period of 6 years (Fig. 2e).

We next superimposed 34 years of data on Black Grouse dynamics between 1897–1930 in south-western Finland. The location of the grouse data was selected by eye for matching synchrony. The original data are from Siivonen (1948) but are detrended here. The match between the two data sets is exceptionally good (Black Grouse $a_1 = – 0.256$, $a_2 = – 0.273$; simulated data for the matching 34 yr. time period $a_1 = – 0.269$, $a_2 = – 0.285$), as also witnessed by almost identical autocorrelation functions derived from the simulated and from the grouse data (Fig. 2e).

Thus, we shall conclude that the process, as described with eq. (8) and eq. (7) is capable producing long-term population dynamics as observed with the Black Grouse.

5. Discussion

We have shown that random perturbations which lower reproductive success may cause and maintain periodic oscillations in otherwise stable populations. This finding is intriguing in its degree of parsimony. Earlier studies concerning perturbations and periodic oscillations have either suggested the external effects occur with random strength, but perpetually (Moran 1953, Townsend *et al*. 1990, Royama 1992) or in a cyclic manner (Elton 1924, Siivonen & Koskimies 1955, Johnson *et al*. 1986, Sinclair *et al*. 1993). Our approach differs from these in two ways. First, our view is that natural populations are adapted to their environment, i.e., they can tolerate a certain amount of external disturbance without this coming an effect in the behavior of the population dynamics. Consequently, we think that the external effects are more likely to seriously affect the reproductive success every now and then than every year. Second, the mechanism leading for cyclic oscillations here, does not call for cyclic perturbations.

Moreover, it has been theoretically shown by Royama (1992) that the order of density dependence is expected to be commonly found as second-order in natural populations, i.e., delayed density dependence. There is also strong empirical evidence arising from different taxa for the existence of delayed density dependence (Turchin 1990, Fryxell *et al*. 1991, Hörnfeldt 1994, Lindström 1996).

Unifying these aspects, random perturbations and delayed density dependence, in population dynamics quite easily leads to sustaining oscillations. This was realized for the first time as early as 1959 by George Leslie (Leslie 1959), but the time lag in the density dependence of his model was achieved by the age structure of the population. Since the time lag also varied from age group to age group, this is rather complicated, and not necessarily biologically intuitive approach, which may explain why Leslie's idea has not been widely recognized. Our results show, however, that the core of the idea is much simpler.

It is important to notice that our characterization of the random perturbation does not lead to the need of identifying the actual perturbation factor in nature. As a matter of fact, we find this kind of attempt largely futile. There is no reason to believe that the factor is — or should be — the same every time. It can be a given weather factor now and predation pressure next time; this kind of list can be extended infinitely. We neither want to exaggerate nor underrate our finding. It would be unrealistic, for instance, to deny the possibility of predator–prey relationship in explaining the origin of periodic oscillations.

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Appendices

Appendix A: Stability analysis of eq. (1), eq. (2)

We characterize here the model parameters a_1, a_2 and r for which the population dynamics (eq. (1), eq. (2)) is locally asymptotically stable. For the purposes of the stability analysis we rewrite (eq. (1), eq. (2)) as

$$x_1(k+1) = x_1(k)F(x_1,x_2), \qquad \text{(a1)}$$
$$x_2(k+1) = x_1(k),$$

where $x_1(k) = x(k)$, $x_2(k) = x(k-1)$, and $F(x_1,x_2) = \exp(r + a_1x_1(k) + a_2x_2(k))$.

The linearized approximation of eq. (1), eq. (2), which determines the local stability properties of the population dynamics, is given as (e.g. Edelstein-Keshet 1989)

$$\begin{pmatrix} N_1(k+1) \\ N_2(k+1) \end{pmatrix} = \begin{pmatrix} a_1\bar{x}+1 & a_2\bar{x} \\ 1 & 0 \end{pmatrix} \begin{pmatrix} N_1(k) \\ N_2(k) \end{pmatrix}, \qquad \text{(a2)}$$

where $x_i(k) = \bar{x} + N_i(k)$, and $N_i(k)$ is the deviation of the ith component from the equilibrium level ($i = 1, 2$). The characteristic equation of eq. (8) becomes (e.g. Caswell 1989)

$$\lambda^2 - (a_1\bar{x} + 1)\lambda - a_2\bar{x} = 0. \qquad \text{(a3)}$$

The eigenvalues are either both real, or complex conjugates of the form $\lambda_{1,2} = \alpha \pm i\beta$.

The equilibrium level $\bar{x}$ is locally asymptotically stable if the magnitudes of both eigenvalues are less than 1. In this case both roots will have magnitude less than 1 if

$$2 > 1 - a_2\bar{x} > |1 + \mathrm{a}_1\bar{x}|. \qquad \text{(a4)}$$

Recall also inequality eq. (5).

The stability conditions eq. (a4) are applied in the case illustrated in Fig. 1 as follows. We have $r = 0.9$. Inequality eq. (5) implies that the parameter values under study are below the line $a_1 + a_2 = 0$. When $r < 1$, condition $1 > -a_2\bar{x}$ is rewritten as:

$$a_2 < \frac{1}{r-1} a_1.$$

Thus, the stability area is restricted by $a_2 < -10\, a_1$. When $1 + a_1\bar{x} > 0$, then $1 - a_2\bar{x} > |1 + a_1\bar{x}|$ is satisfied for all a_1 and a_2 satisfying eq. (5). When $1 + a_1\bar{x} < 0$ the stability area is restricted by:

$$a_2 < \frac{r-2}{r+2} a_1 = -\frac{1.1}{2.9} a_1.$$

As a whole, for $r = 0.9$ the stability area in the (a_1, a_2)-space is the sector defined by the conditions $a_2 < -10a_1$ and

$$a_2 < -\frac{1.1}{2.9} a_1 \approx -0.38a_1.$$

Appendix B: Deriving eq. (8)

The autoregressive time series model used by Lindström *et al.* (1995b) to analyze long-term data on grouse population dynamics in Finland is

$$R(k) = X(k+1) - X(k), \qquad \text{(b1)}$$

where $X(k)$ is the logarithm of the population size and $R(k)$ is the logarithmic growth rate of the population at time k. The nonlinear autoregressive time series model assumes that (Royama 1992)

$$R(k) = 1 - \exp(-\mathrm{a}_1 X(k) - a_2 X(k-1). \qquad \text{(b2)}$$

Denoting $X(k) = \ln x(k)$, we have

$$\begin{aligned} x(k+1) &= x(k)\exp(R(k))) \\ &= x(k)\exp(1 - \exp(-a_1 \ln x(\mathrm{K}) - a_2 \ln x(k-1))) \\ &= x(k)\exp(1 - \exp(-a_1 \ln x(\mathrm{K}) - a_2 \ln x(k-1))) \\ &= x(k)\exp(1 - \exp(\ln(x^{-\mathrm{a}1}(k)x^{-\mathrm{a}2}(k-1))), \qquad \text{(b3)} \end{aligned}$$

which simplifies to eq. (8).