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The effect of emigration and immigration on the dynamics of a discrete-generation population

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Abstract. The recent paper of Sinha and Parthasarathy investigated the effect of modifying the Ricker and logistic population models to simulate the effects of immigration to, and emigration from, the population. Immigration of a fixed number of individuals was shown to reduce the probability of observing chaos in the Ricker model but not the logistic one. Here, isocline analysis is used to investigate why these effects occur. The stabilization effect for the Ricker equation occurs over a wide range of values of the immigration parameter. There are no values of the parameter, however, which increase the stability of the logistic equation substantially. In contrast density-dependent immigration is found to destabilize both the Ricker and logistic models. Density-dependent emigration serves to reduce the propensity of both models to exhibit chaos.

Keywords. Chaos; linked populations; discrete map; cycles.

1. Introduction

It is well known that several discrete-time models which can be used to describe the dynamics of isolated populations display chaotic motion for many parameter values (May 1974, 1975, 1976; May and Oster 1976). Chaotic dynamics have also been predicted by models of interacting populations (e.g., Cavalieri and Kocak 1994) and by continuous time models (e.g., McCann and Yodzis 1994). Whilst chaos has been commonly predicted by population models, it has not been widely observed in field time-series of real populations (Berryman and Millstein 1989; Godfray and Grenfell 1993; Hastings *et al* 1993). This failure to detect chaos in real populations may be due to the difficulties inherent in detecting chaos in population time-series which are typically short and noisy (Morris 1990; Markus 1992; Ellner and Turchin 1995). Another explanation may be that our expectation of the likelihood of chaos in the natural world has been inflated by over emphasis on very simple mathematical models which ignore many factors which are present in real populations. The recent paper of Sinha and Parthasarathy (1994) investigated the effect of adding two of these factors—immigration and emigration—to two of the most commonly used discrete population models: the Ricker and logistic. They observed that adding a constant immigration term reduces the propensity of the Ricker model to exhibit chaos but does not have the same effect on the logistic model. Adding a constant emigration term again was seen to have little effect on the logistic model but to considerably change the dynamics of the Ricker model, driving it to extinction for high values of the intrinsic growth parameter (for which an isolated population would be chaotic). In this paper, this work is re-examined to investigate its robustness against changes in parameter values and variation in the form of the transport term. In particular, the effect of density-dependent migration terms is investigated.

2. The behaviour of the logistic and Ricker maps

The logistic equation defines the population size in one generation (X_{t+1}) in terms of the population size in the previous generation (X_t). The population is commonly scaled to the maximum size that can the sustained (the so-called carrying capacity) to yield an equation.

$$X_{t+1} = r X_t (1-X_t), \tag{1}$$

where r is a constant, commonly called the intrinsic growth rate. The long-term behaviour of the population can be changed by varying the parameter r, as summarized in figure 1a. For values of the growth constant (r) less than 1, the final population size is zero. As r increases, a non-zero stable steady state is reached. However for r values greater than 3·0 the stable equilibrium bifurcates to a two-point cycle. Further increases in r induce a cascade of further period-doubling bifurcations until chaos is observed for high enough values of r. For values of the growth parameter (r) bigger than 4·0, the model might be considered "badly-behaved" in that it can predict negative population values.

The Ricker equation is given by

$$X_{t+1} = X_t \exp(R[1-X_t]), \tag{2}$$

where R is a growth constant. Again, the long-term behaviour of a population governed by this equation is dependent on R, as summarized in figure lb. Low values of the growth parameter (R) produce a stable equilibrium. Increasing (R) beyond 2·0 produces a bifurcation to a two point cycle. Further increases in (R) produce a period-doubling route to chaos. The Ricker map does not suffer from the same unbiological behaviour as the logistic map for any value of the growth rate parameter (R). However, increasing (R) does cause the population to visit lower and lower population levels.

3. The addition of density-independent immigration

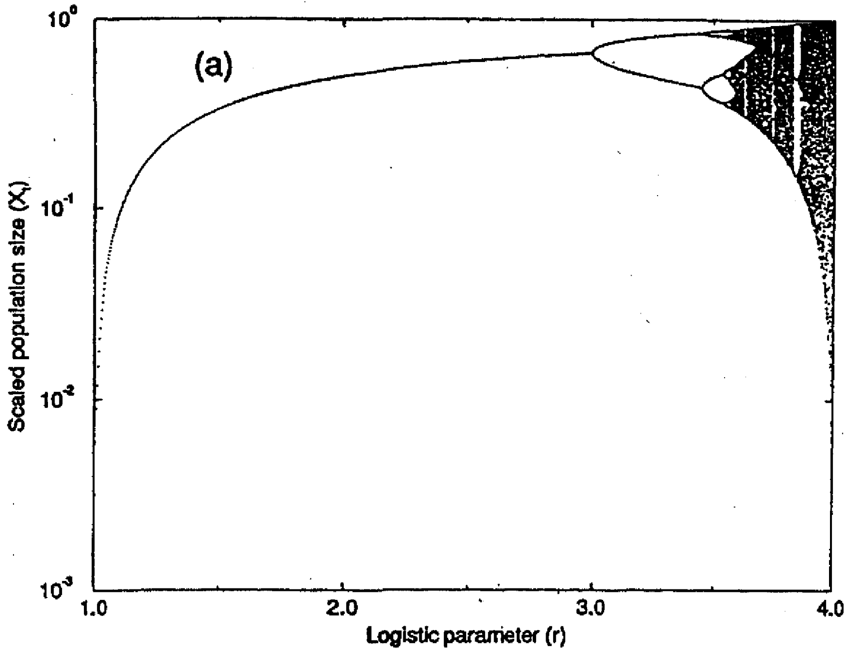
Sinha and Parthasarathy (1994) investigated the effect of adding a constant immigration term to both the logistic and Ricker models. The modified logistic equation is given by

$$X_{t+1} = r X_t (1-X_t) + \lambda, \tag{3}$$

where λ is a constant.

Similarly the modified Ricker equation

$$X_{t+1} = X_t \exp(R[1-X_t]) + \lambda. \tag{4}$$



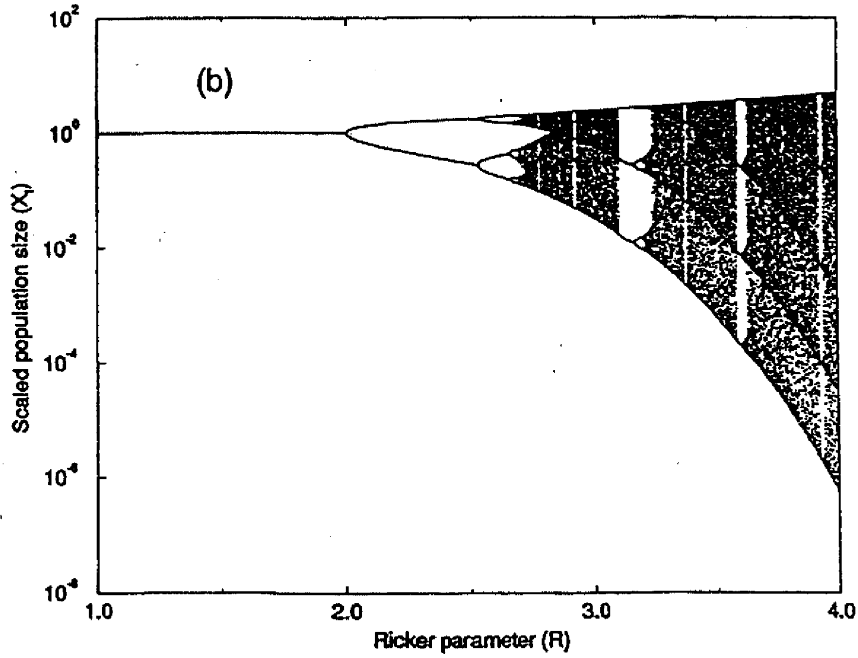


Figure 1. Bifurcation diagrams showing the long-term dynamic behaviour of (**a**) the logistic model of eq 1 and **(b)** the Ricker model of eq 2. For each value of the growth parameter (*r* or *R*), the population is iterated 1000 times from a randomly-chosen initial value, the last 100 points visited are plotted against that value of the growth parameter.

Sinha and Parthasarathy (1994) observed that setting λ to 0·07 causes chaos to disappear for the Ricker map but not for the logistic map. In fact, the stabilizing effect of a constant immigration term on the Ricker map has also been investigated by McCallum (1992) and Stone (1993). A reduction in the propensity to exhibit chaos is apparent even for much lower values of λ than the one considered by Sinha and Parthasarathy.

The difference in the behaviour of the logistic and Ricker maps under constant immigration can be explained as follows. Consider the curves shown in figure 2a. These show the shape of the Ricker function (eq 2) for a variety of R values. The equilibrium value (for a given value of R) can be found graphically as the point where the curve cuts the line $X_{t+1} = X_t$, A period-doubling route to chaos cannot occur unless the slope of the curve at this intersection is both negative and has magnitude greater than one (May 1975, 1976). It can be seen from figure 2a that for R values greater than 1·0, the slope at the intersection point is negative and increases in magnitude (i.e., becomes more steep) with increasing R. Hence increasing R induces chaos. However, observe that at high values of X_t the slope of the curves stay negative but have a magnitude which decreases and approaches zero with increasing X_t. Adding a constant immigration term can be represented graphically as shifting the curves upward (i.e., to higher X_{t+1} values) without altering their shapes. This has the effect of pushing the intersection point to a higher value of X_1 and hence reducing the magnitude of the slope. Thus (regardless of how high R is) increasing the immigration term (λ) will eventually reduce the magnitude of the slope below one and avoid the onset of chaos.

This graphical analysis also explains why the same stabilizing effect does not occur in the logistic model. As figure 2b demonstrates, the magnitude of the slope of the logistic curve does not decrease at high values of X_t in the way the Ricker ones do. Indeed Appendix 1 shows that the slope becomes more steep with increasing X_t. Hence, although the immigration term causes the equilibrium Xt value to increase (see Appendix 1 and figure 2b), this causes the slope of the curve at the equilibrium point to become more negative making chaos rather than less, likely. This holds for all values of the growth parameter r, as demonstrated in Appendix 1.

4. The addition of density-dependent immigration

The effect of adding a density-dependent immigration term to both the logistic and Ricker models will now be investigated. At each generation reproduction occurs according to either the logistic or Ricker equation, then immigration equal to a fraction (β) of the newly produced population occurs before another population census is taken. The modified logistic equation is given by

$$X_{t+1} = (1+ \beta) + rX_t (1-X_t) \qquad (5)$$

Similarly the modified Ricker equation is

$$X_{t+1} =(1+ \beta) X_t \exp (R [1-X_t]). \qquad (6)$$

Equation 5 demonstrates that the immigration term serves simply to increase the effective reproduction rate parameter in the logistic equation. Hence, this has a

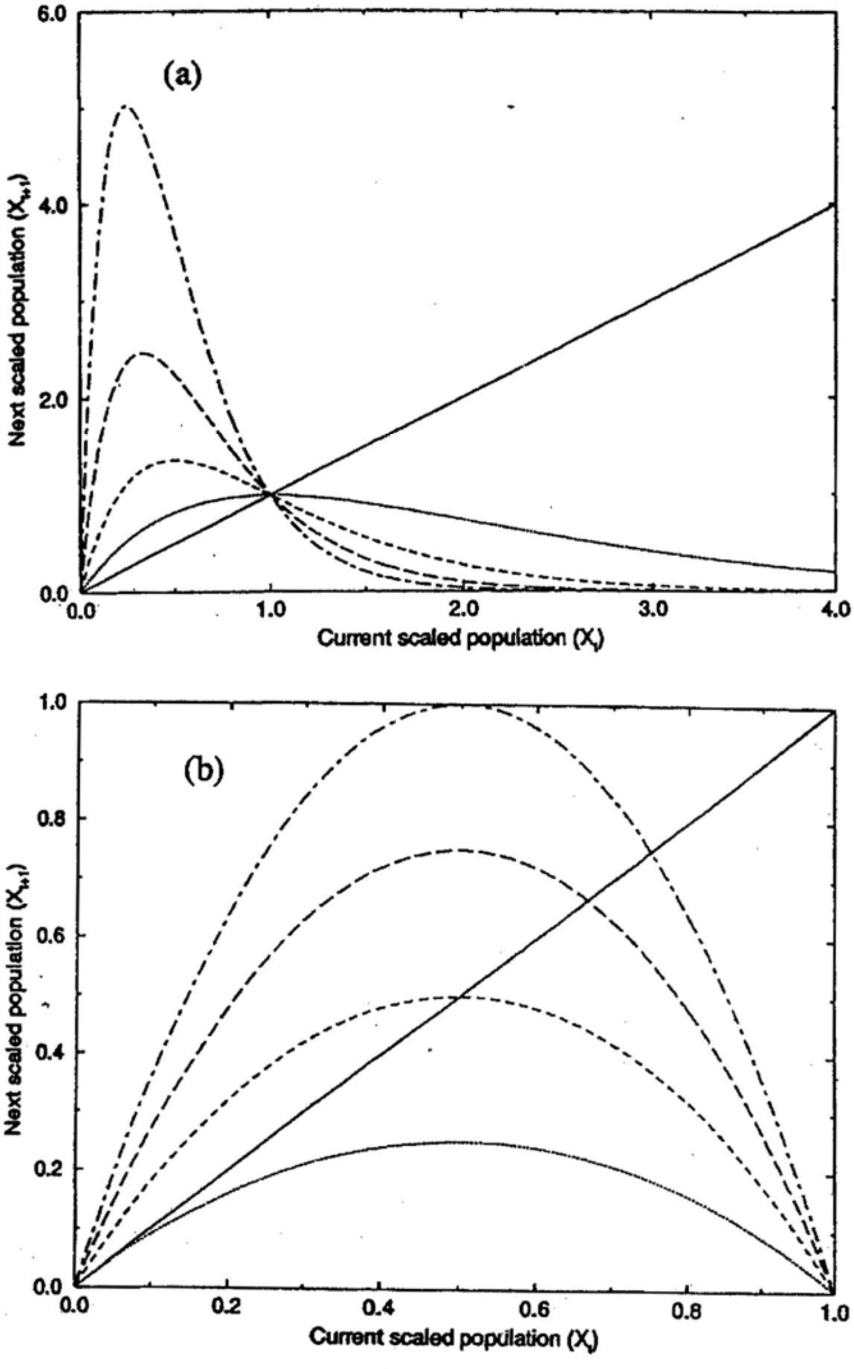


Figure 2. (a) The shape of the Ricker curve (eq 2) for 4 different values of R [1·0 (. . . . .), 2·0 (– – –), 3·0 (– –), 4·0 (–·–)]. The line $X_t = X_{t+1}$ is also shown. **(b)** The shape of the logistic curve (eq 1) for 4 different values of r [1·0 (. . . . .), 2·0 (– – –), 3·0 (– –), 4·0 (– · –)].

destabilizing effect on the population dynamics. This also means that equation 5 will not produce negative populations providing

$$r \leq \frac{4}{1+\beta},$$

hence immigration can cause populations with an r value below 4·0 to exhibit negative values.

For the Ricker eq, simple algebra (analogous to that given in Appendix 1) shows that the slope of the curve at equilibrium is given by

$$1 - R + \ln[1/(1+\beta)],$$

hence increasing the immigration term (β) will make the slope more negative and hence will increase the propensity towards unstable and chaotic dynamics. An example of this effect is shown in figure 3a.

5. Density-independent emigration

Sinha and Parthasarathy (1994) also investigated the effect of assuming that a Fixed number of individuals (λ) leave the population at every generation. They modify the logistic to the form:

$$X_{t+1} = r X_t (1-X_t) - \lambda, \tag{7}$$

and change the Ricker map in a similar way to obtain

$$X_{t+1} = X_t \exp(R[1-X_t]) - \lambda. \tag{8}$$

The main effect of this change is that extinction can now be observed for the Ricker map. As can be seen in figure 1b far a population without emigration, increasing R causes the population to visit lower and lower values. Hence, eventually (with increasing R) the population visits a value lower than λ, the next generation is negative and Sinha and Parthasarathy (1994) considered extinction to have occurred. For similar reasons, extinction is also observed at lower R values (relative to the model of an isolated population) in the logistic map.

6. Density-dependent emigration

I now consider an alternative emigration term, where a fixed proportion (ϕ) of the population emigrates at each generation. This modifies the logistic equation to

$$X_{t+1} = r(1-\phi) X_t (1-X_t), \tag{9}$$

where ϕ is a constant valued between 0 and 1.
The Ricker equation is modified to

$$X_{t+1} = (1-\phi) X_t \exp(R[1-X_t]). \tag{10}$$

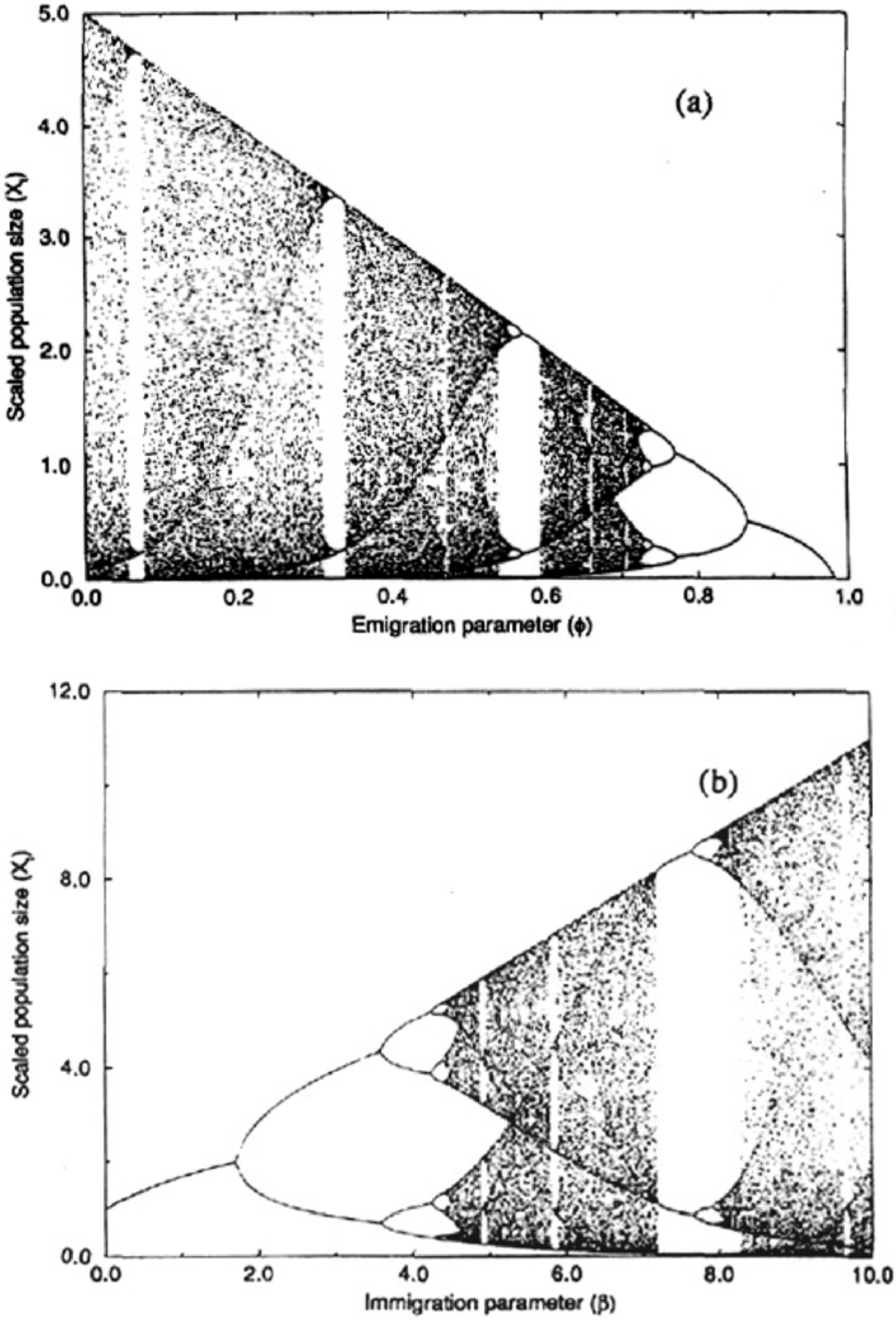


Figure 3. Bifurcation diagrams showing the long term behaviour of the Ricker map with **(a)** immigration to the population at each generation equivalent to a fixed fraction (β) of the current population and R=1·0, and **(b)** a constant fraction (φ) of every generation emigrating from the population and R = 4·0. The population is iterated 1000 times from a randomly-chosen initial value, the last 100 points visited are plotted against the migration parameter.

Equation 9 demonstrates that the emigration term serves simply to decrease the effective reproduction rate parameter in the logistic equation. Hence, this has a stabilizing effect on the population dynamics. This also means that equation 9 will not produce negative populations providing.

$$r \leq \frac{4}{1-\phi},$$

hence emigration can allow populations with an r value above 4·0 to avoid extinction.

It is easy to show that the slope of the modified Ricker map at equilibrium is given by

$$1 - R + \ln[1/(1-\phi)].$$

Hence increasing ö will make the slope less negative and so will be stabilizing, as illustrated in figure 3b. Notice in the figure that extinction eventually occurs at high ϕ , occurring before ϕ = 1·0.

7. Discussion

The paper of Sinha and Parthasarathy (1994) provides interesting examples of the effect of adding constant immigration and emigration terms to the Ricker and logistic models. One of the aims of this paper was to set this work in the context of previous literature. Sinha and Parthasarathy demonstrated that adding a constant immigration term to the Ricker equation causes its propensity to exhibit chaos to be reduced. They add what they consider to be a small fraction of the population carrying capacity at each iteration. McCallum (1992) demonstrates that similar effects can be obtained with an immigration term several orders of magnitude smaller yet. This paper demonstrates that simple analysis (developed by Stone 1993) allow this stabilization effect to be understood in terms of isocline analysis. A small extension of the theory allows one to explain why Sinha and Parthasarathy do not see a similar effect for the logistic equation. Indeed, immigration can actually increase the likelihood of chaos in this model.

A second aim of the paper was to investigate the effect of emigration from the population on dynamics. The effects of the assumption of Sinha and Parthasarathy (1994) that a constant number is removed at each generation are compared to formulations which assume the loss of a constant fraction of individuals. For the logistic, increasing the fraction emigrating will tend to stabilize the resultant dynamics. Further, if the fraction is increased still further, extinction occurs although this happens without negative population sizes being generated. The stabilizing effects of high emigration rates is also demonstrated for the Ricker model, as is extinction. Sinha and Parthasarathy found that density independent immigration and emigration and radically differing effects on the Ricker and logistic models. Here, it is shown that their behaviour when modified to include density-dependent migration to or from the population is generally very similar for the two models.

The effect of linking populations on the propensity to exhibit chaos is an area of considerable current interest. Gonzalez-Andujar and Perry (1993a,b) investigated the effect of adding immigration and emigration simultaneously. In general they found that the expectation of chaos is reduced. This effect is also observed by Ruxton (1994) who briefly also examines the effect of noise. Hastings (1993) showed that the initial conditions can be an important factor in coupled populations even when they are not in isolated ones. Rohani and Miramontes (1995) suggest that the route to chaos has an important bearing on the effect of immigration. Whilst the results presented here may suggest that real populations are less likely to be chaotic than initial mathematical models predicted, we should exercise some care in extrapolating the results presented here. Grenfell (1992) investigated the effect of coupling between sub-populations on the dynamics of the SEIR model, used to describe the epidemiology of infectious diseases, and found that introducing such coupling "does not greatly reduce the propensity for large amplitude fluctuations in the infection coefficient to induce fade-out" of the disease. Indeed, whilst, perhaps, our expectation of chaos should be tempered, we should be careful of over compensation: coupling between model populations has also been suggested under certain circumstances to induce chaos (Ruxton 1993; Bascompte and Sole 1994).

This paper deals with wholly deterministic models. An interesting future extension would be an investigation of how noise through demographic stochasticity or external factors affects the phenomena reported here. Rand and Wilson (1991) and Bolker and Grenfell (1993) both found that the addition of noise can sustain chaotic transients in the SEIR model. Hence, stochastic models may sometimes predict chaos when the analogous deterministic models do not. A similar effect happens in a system of linked Ricker equations (Ruxton 1994). If noise levels are high enough, the system never escapes the influence of a chaotic repeller (Rand and Wilson 1991) and so never settles to the periodic orbit. Even in the absence of noise, the system commonly exhibits a long transient phase. This can be identified as perturbations due to the emigration or immigration hindering the system's escape from the influence of the chaotic repeller.

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Appendix 1

The logistic equation is given by

$$X_{t+1} = f(X_t), \tag{11}$$

where

$$f(X_t) = rX_t\ (1 - X_t). \tag{12}$$

At equilibrium, the population size is equal in consecutive generations: i.e.

$$X_{t+1} = X_t \equiv E. \tag{13}$$

This allows us to form an expression for the equilibrium value.

$$E = rE\,(1 - E). \tag{14}$$

Re-arrangement gives

$$E = 1 - (1/r). \tag{15}$$

The slope of the curve in figure 2b is given by differentiating function *f*.

$$f'(X_t) = r\,(1 - 2X_t). \tag{16}$$

The slope becomes more and more steep with increasing X_t.

The slope of the curve at the equilibrium point is given by

$$f'(E) = 2 - r. \tag{17}$$

Now consider the effect of adding a constant immigration term (λ).

$$X_{t+1} = F(X_t), \tag{18}$$

where

$$F(X_t) = f(X_t) + \lambda. \tag{19}$$

Now, the equilibrium value is given by the same method as before, yielding

$$E = (1/2r)\left[(r-1) + \sqrt{(r-1)^2 + 4r\lambda}\,\right]. \tag{20}$$

Notice that the equilibrium value (E) increases with increasing immigration (λ). The slope of the curve at the equilibrium value is given by

$$F'(E) = 1 - \sqrt{(r-1)^2 + 4r\lambda}. \tag{21}$$

The slope becomes progressively more negative as immigration (λ) increases.

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