

Are ecological systems chaotic? – An enquiry into population growth models

Somdatta Sinha

Centre for Cellular and Molecular Biology, Uppal Road, Hyderabad 500 007, India

The discovery of quasiperiodic and chaotic behaviour of deceptively simple discrete population models is a major unexpected development of the last few decades. While these complex phenomena are relatively well accepted and understood in physical sciences, the biological significance of complex dynamics (chaos) is still not acknowledged fully. Indeed field data of biological populations has often been thought to somehow avoid the predictions of the mathematical models. Ecologically realistic reformulation of these models has now begun to suggest that chaos is not biologically unrealistic and that ecological processes such as migration of individuals between populations can appear to suppress complex oscillations.

Eyesight should learn from reason.

– Johannes Kepler

IN an otherwise descriptive experimental science of biology, mathematical models have been used extensively to study population growth processes in ecology. The prime reason being the need to be able to predict the future course of events for necessary manipulation/intervention. These models have been applied to diverse fields such as, demography, economics of natural resource management, health and conservation studies. It has been used for predicting guidelines for harvesting policies, vaccination regimen, and growth and spread of infectious diseases¹⁻⁵.

Living systems show two types of growth – continuous and discrete. In many organisms such as humans, reproduction (growth) continues throughout most of their lifetime, and, more than one generation can overlap at any period of time. This is not the case with many others such as, annual plants and insects, where generations do not overlap and thus growth is discrete. The mathematics used for modelling are different in these two cases. Single populations of organisms with non-overlapping generations are modelled using one-dimensional discrete equations (maps), and continuously growing organisms are modelled using ordinary differential equations.

A variety of biotic and abiotic factors contribute to population growth. Thus the time series data from different systems (shown in Figure 1), incorporates the resultant of all relevant factors to the population size.

Controlling or even having knowledge of all the contributing deterministic and stochastic factors is almost impossible in field experiments, but can be attempted in the laboratory. Therefore, single population models described by few parameters such as, the intrinsic growth rate of the species and carrying capacity of the environment are highly idealized. Many ecological factors contributing to a population's growth such as, predation, dispersal and competition are assimilated in the growth rate and the carrying capacity, thus retaining the essence of biological details. In spite of being simple, these models have been found to be quite useful in describing the temporal pattern of growth and are used regularly in ecology^{6,7}.

The commonly used density-dependent, single population, continuous models can either show exponential growth, stabilize to the saturation value (carrying capacity of the environment), or die depending on its intrinsic growth rate and the carrying capacity. Some of the factors that may induce regular or erratic oscillations (as shown in Figure 1) are environmental noise, time lag, growth rate regulation, and interactions with other species (predator-prey, host-parasite, etc.). On the other hand, the density-dependent single population models for discrete growth exhibit a variety of dynamics depending on the intrinsic growth rate R and other density-dependent factors. These models can show a range of dynamics such as, equilibrium, periodic (including higher period oscillations), and irregular, aperiodic oscillations or chaos^{1,8,9}. Thus these models have complex dynamics intrinsic to them and can show erratic fluctuations even in the absence of stochastic environmental factors.

The predominant perception in population dynamics has been that of *homeostasis*. The concept of 'balance of nature' is well-entrenched in biological thought and a stable, equilibrium world is considered to be normal. The erratic fluctuations observed in population size over a span of time (as seen in Figure 1) have been generally considered to reflect stochastic factors such as weather conditions. There have been voices of dissent¹⁰ to this view where the fluctuations have been attributed to factors inherent to the system. Thus there has been a continuing debate between the biotic and the climatic schools over the relative importance of deterministic versus stochastic forces in controlling ecological popu-

lations^{11,12}. This debate has taken new meaning with the concepts of chaos and complex dynamics in ecology.

Other than the philosophical argument against chaos, there exists an evolutionary argument also. Chaos is associated with violent oscillations with very low minimum. Some feel¹³⁻¹⁵ that this property of chaotic oscillation increases the risk of extinction and, hence, chaos must be evolutionarily selected against. It is common sense and supported by many field studies^{16,17} that a small population indeed has a higher risk of extinction under any sudden environmental perturbation. Violent oscillations also have high risk because they may stress

the environment with very high numbers and then create sudden lows for even not-so-significant environmental factors to act against it.

Thus having equations showing chaotic oscillations do not necessarily justify the presence of chaos in natural ecological systems. Are these models realistic for natural populations? A study¹³, that has been quoted extensively in discrete population literature, collected life table data for twenty-four field populations and four laboratory populations of insects which show discrete growth (Table 1). This data was fitted to a single-species, discrete model developed based on detailed biological considerations¹⁸. The results showed that all natural populations have population parameters lying in the region of stable dynamics. This study, based on a large data set, strengthened the perception that equilibrium dynamics is normal in nature and not chaos. The insect populations studied in the controlled conditions of the laboratory came closest to true single-species situation and showed regular or erratic oscillations in their growth dynamics. Thus it was concluded that the equations are realistic but only in the confines of the laboratory.

In this paper we enquire into the possible reasons of absence of periodicity or chaos in natural populations by considering the above-mentioned mathematical model¹⁸. We show that simple ecological processes like density-independent migration, can act to suppress oscillations or fluctuations (chaos) in a population with unstable population parameters and thus exhibit stable dynamics. We also reason against the evolutionary argument and show that chaos *per se* may not increase the risk of extinction even under regular emigration or depletion. Thus the results on natural populations¹³ neither argue against chaos in evolution, nor do they have negative implications about the realism of the single species discrete growth models in ecology.

In the following sections, we first describe the model and its dynamics during free growth; then study the dynamics of the model under migration; and finally, discuss the implications of our results.

The model and its dynamics

There are two different kinds of intraspecific competition – ‘scramble’ and ‘contest’ – that contribute to population growth. ‘Scramble’ involves equal partitioning of resources and either all individuals survive and reproduce or the population goes extinct when resource is insufficient. In the case of ‘contest’, some successful individuals get all they require whereas some get insufficient for survival and reproduction¹⁹. These two are the extreme forms and usually the situation is always mixed – there is some contest likely because some individuals will be more successful than others. The model proposed by Hassell¹⁸ is based on the mortality and natality data of

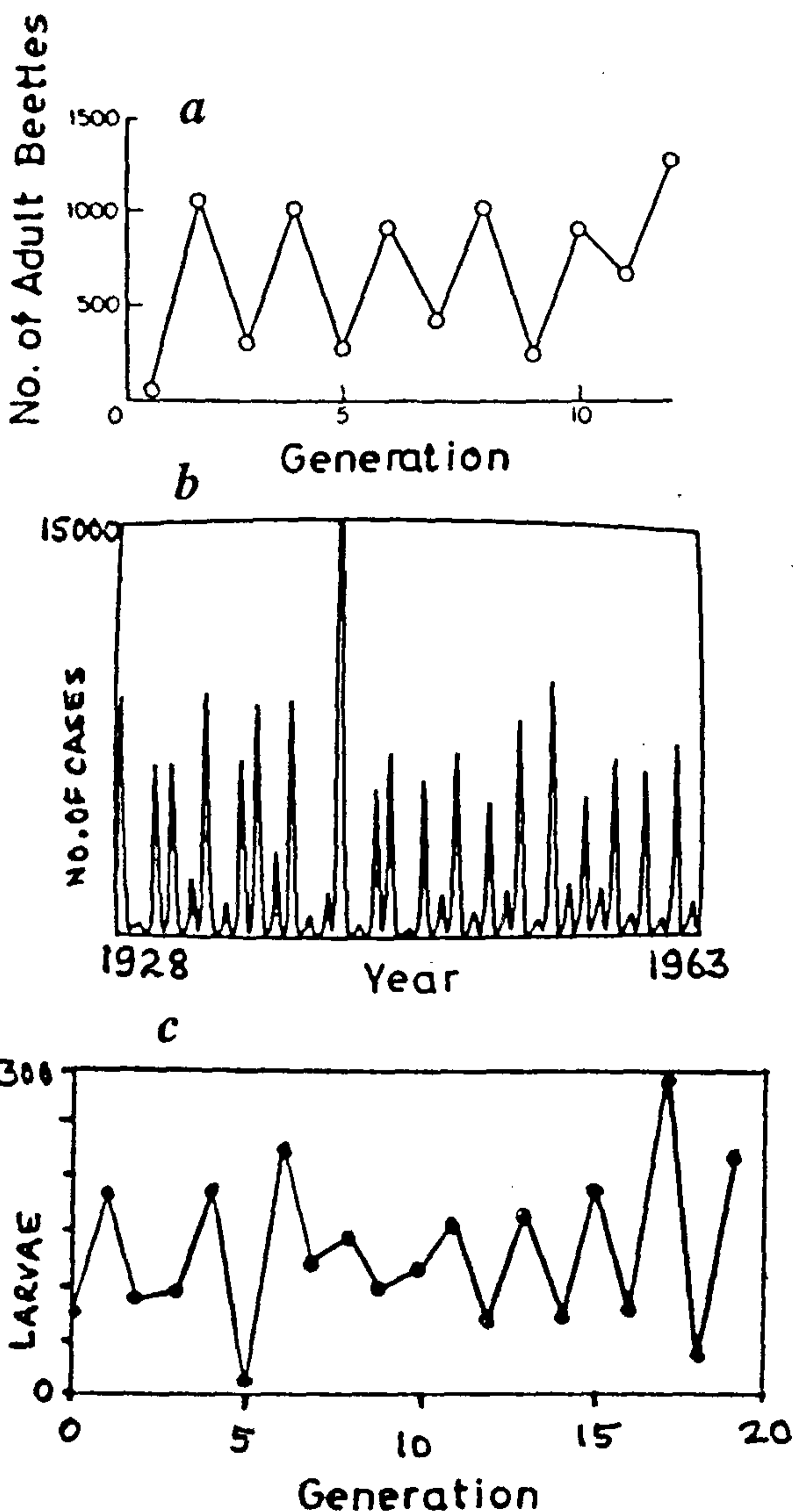


Figure 1. Time series data representing population size variation for three organisms: a, Laboratory culture of a stored-product beetle *C. maculatus*^{34a}. b, Number of cases of measles reported in New York between 1928 to 1963 (ref. 36b). c, Number of larvae of a strain of flour beetle *T. castaneum* over several generations^{36c}.

a number of insects (see Table 1) which show density-dependent relationship due to intraspecific competition. The one-dimensional discrete equation representing the population size (N) at any two consecutive generations (t and $t + 1$) in this model is

$$N(t + 1) = [R(1 + a.N(t))^{-b}] N(t),$$

where R is the intrinsic growth rate, and a and b are constants defining the density-dependent feedback terms. On scaling $X = a.N$, the dimensionless form of the equation becomes

$$X(t + 1) = [R(1 + X(t))^{-b}] X(t). \quad (1)$$

This two-parameter equation (called Hassell model henceforth) has been used for all theoretical studies in this work. Varying values of b describe intraspecific competition for resources – with $b = 1$ for pure ‘contest’, and $b = \infty$ for pure ‘scramble’. For $0 < b < 1$, competition is only through different degrees of contest. All intermediate values of b , i.e. $1 < b < \infty$ signify varying combinations of scramble and contest in population growth.

The return map²⁰ ($X(t)$ versus $X(t + 1)$) plot of equation (1), like most other realistic single population discrete growth models^{21,22}, has a single-hump growth function with a ‘tail’ extending to infinity as shown in Figure 2. The gradient of the hump at the equilibrium point (where $f(X) = X$) becomes progressively higher as b increases for all $b > 1$ (Figure 2a). The effect of increasing R for a fixed b is also similar (Figure 2b), and both these parameters contribute towards increasing

Table 1. Estimates of b and R from the analysis of insect life table data (from ref. 13)

Species	b	R
Moth: <i>Zeiraphera diniana</i> Gn.	0.1	1.3
Bug: <i>Anthocoris confusus</i> (Reuter)	0.5	1.6
Beetle: <i>Phytodecta olivacea</i> (Forst)	0.3	1.7
Moth: <i>Hyphantria cunea</i> Drury	1.5	1.7
Scale: <i>Parlatoria oleae</i> (Colvee)	0.7	2.2
Bug: <i>Leptoterna dolobrata</i> (L.)	2.1	2.2
Moth: <i>Erannis defoliaria</i> (Clerk)	0.4	3.0
Moth: <i>Bupalus piniarius</i> L.	0.5	3.1
Parasitoid fly: <i>Cyzenis albicans</i> (F)	0.5	3.2
Fly: <i>Erioischia brassicae</i> (L.)	1.0	3.3
Moth: <i>Cadra cautella</i> Walk.	0.3	3.3
Bug: <i>Nezara viridula</i> L.	0.7	4.3
Moth: <i>Operophtera brumata</i> (L.)	0.3	5.5
Bug: <i>Nephotettix cincticeps</i> Uhler	0.2	6.1
Moth: <i>Erannis progemmaria</i> (Hb.)	0.5	6.3
Moth: <i>Anagasta kuehniella</i> (Zell.)	0.5	8.6
Bug: <i>Neophilaenus lineatus</i> (L.)	0.4	9.2
Mosquito: <i>Aedes aegypti</i> (L.)	1.9	10.6
Moth: <i>Tyria jacobaeae</i> L.	0.4	10.7
Moth: <i>Erannis leucophaearia</i> (Schiff.)	0.2	11.2
Moth: <i>Acleris variana</i> Fern.	0.2	13.0
Bug: <i>Succarosydne saccharivora</i> (Ww.)	0.4	13.5
Parasitoid wasp: <i>Bracon hebetor</i> Say	0.9	54.0
Beetle: <i>Leptinotarsa decemlineata</i> (Say)	3.4	75.0

the instability in the system. Figure 3 shows the stability boundaries (solid lines) between different dynamical regions (stable, damped oscillatory, periodic, chaos) for variations of the density-dependent parameter b and the population growth rate R for this model. The broken line separates the stable limit cycle region from the region with higher period oscillations. Thus at low b , the system tends to be stable for a large range of growth rates, whereas at higher values of b , it can exhibit a range of dynamics from stability to chaos through period doubling bifurcations.

In a study¹³, the abundance of twenty-four different insect populations in the field was considered (see Table 1), and the life table was constructed to evaluate the population parameters b and R . Similar study was done on three laboratory populations of insects also. The pairs of b and R values for each population were plotted with a circle on the stability graph of the model (Figure 3) where filled circles and open circles represented field and laboratory populations respectively. As can be seen, most field populations tend to have b and R values clustering in the region of stable dynamics. These results generated the following views:

- Some of the types of dynamical behaviour that are possible in theory, in fact, rarely occur in real, single-species populations;

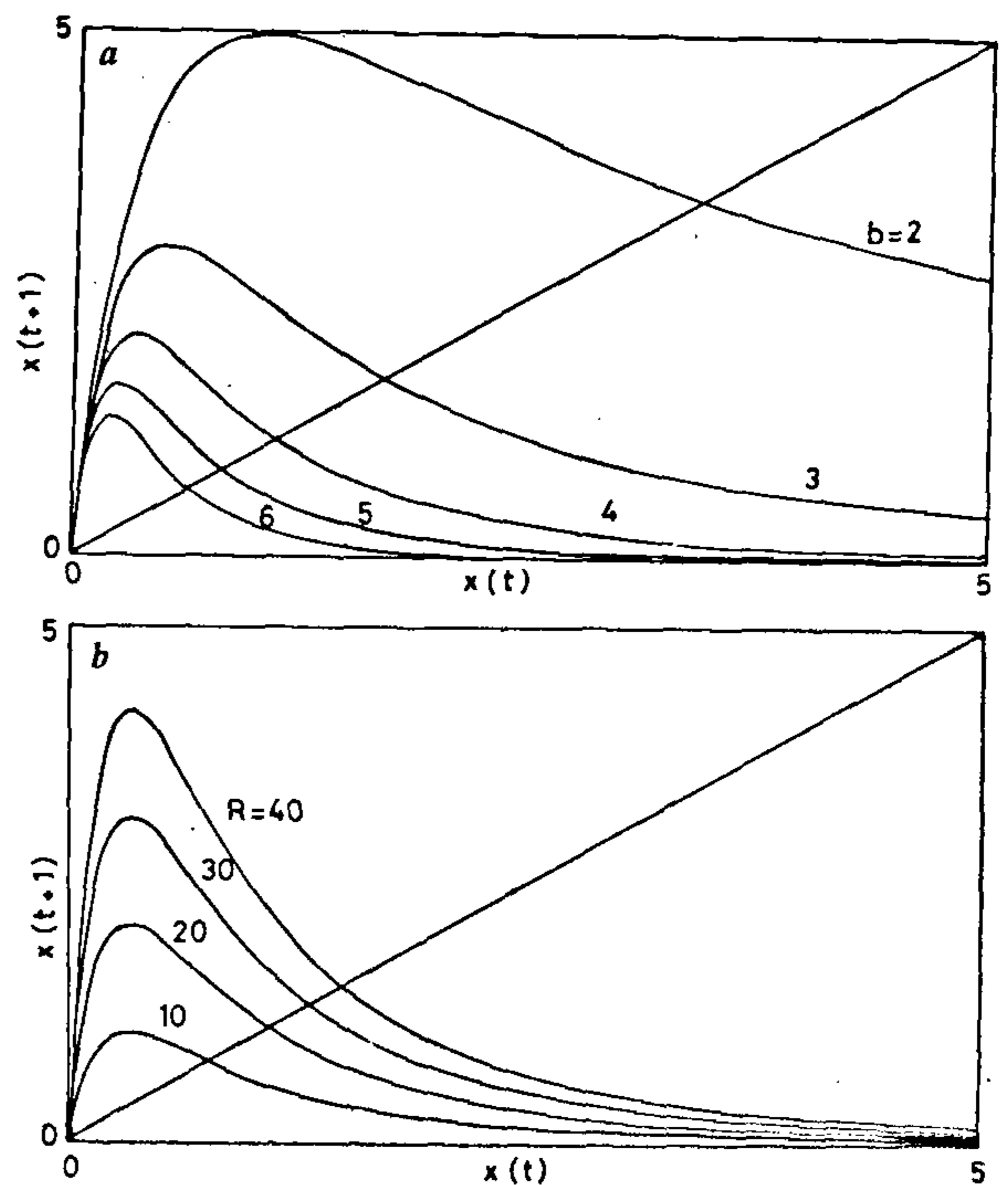


Figure 2. Return maps showing the one-hump nature of the Hassell model for (a) $R = 20$ and $b = 2, 3, 4, 5, 6$; (b) $b = 4$ and $R = 10, 20, 30, 40$.

- High order limit cycles and chaos appear to be a relatively rare phenomenon in *naturally occurring* single-species populations;
- Evolutionary considerations suggest that extreme fluctuations are unlikely because the population would need to be very abundant or agile to persist.

The laboratory populations, on the other hand, showed unstable dynamics and were viewed to be the result of internal dynamics as is expected from their tendency to scramble for resources in close confinement and for the general absence of density-independent mortalities.

Population dynamics under migration

In reality, population in an area does not live in isolation but interacts through different spatiotemporal connectivities with other population patches (metapopulation). One of the ecological processes that contributes in a major way in determining population size, persistence and even its genetic composition is migration. Immigration can increase the size or aid in forming 'refuge' or 'founder' populations, whereas emigration can lead to population extinction or loss of diversity. Some related processes that act in a similar manner are recruitment, harvesting, vaccination, etc. These play significant roles in determining the spatiotemporal dynamics of the metapopulation. Considerable amount of work has been done to elucidate the effect of density-dependent migration between two subpopulations with simple discrete models of single populations^{17,23-25}. Here we study the effect of density-independent migration on the dynamics of the Hassell model. We consider the case where the model

population undergoes a fixed amount of migration (L) at every generation after growth has taken place. The model equation (1) then takes the form

$$X(t+1) = [R(1 + X(t))^{-b}] X(t) + L, \quad (2)$$

where $L > 0$ at immigration, and $L < 0$ at emigration. The effect of $+L$ on the return maps (Figure 2a & b) is to elevate the hump above the X -axis, and that of $-L$ is to push it down, thereby shortening the 'tail' of the hump. In the following sections, we show the effects of a small amount of constant immigration and emigration ($\pm L$) on the dynamics of population growth in the Hassell model.

All our results on the long-term dynamics of the Hassell model are shown through bifurcation diagrams²⁰ where the population size (X) for a large number of generations is plotted for variation of the parameter of interest (e.g., R , b , or L) after discarding initial 1000 generations. In these diagrams, a population at equilibrium is shown as one point representing its stable size. When the population size repeats every second generation, it is represented by two points and is called a P-2 oscillation. Similarly for higher period oscillations such as, P-4, P-8, etc., population size repeats every 4th and 8th generations. When the size varies irregularly without repeating itself, it is quasiperiodic or chaotic. At chaos the population attains many sizes at different generations and the regions in the bifurcation diagram get filled up with many points. Thus these diagrams give a clear idea of the dynamics exhibited by the model for a range of parameter values.

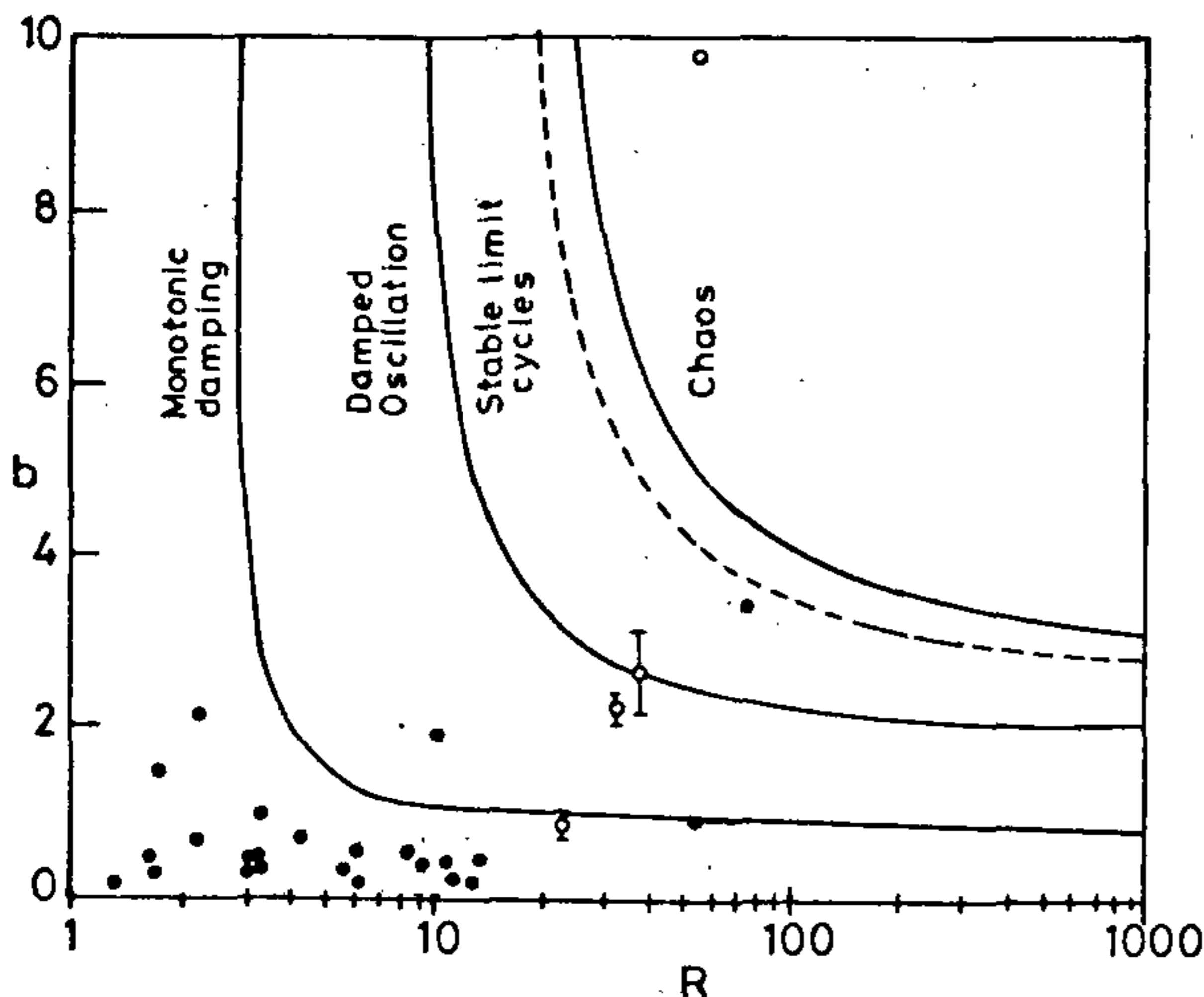


Figure 3. Stability boundaries in the R - b parameter space of the Hassell model¹³. The solid lines separate the regions of different dynamics and the broken line separates the stable limit cycle region from higher periodic region. The closed circles correspond to data from Table 1 and the open circles for laboratory population data.

Effect of small migration on the dynamics of the model with increasing growth rate

It is known that population dynamics in this model becomes increasingly complex as the growth rate R is increased for $b > 1$. Figures 4 and 5 show bifurcation diagrams for two cases ($b = 4$ & 6) where the population undergoes a small amount ($L = 0.05$) of immigration and emigration during growth with varying intrinsic growth rates ($0 < R < 70$). The dynamics of free growth for $b = 4$ (Figure 4b) changes from stable to P-2 and P-4 as R increases. The changes in the dynamics towards suppression of higher order oscillations under small immigration (Figure 4a), and towards more complex dynamics under emigration (Figure 4c) are clear. Similar results are observed for the case of $b = 6$ (Figure 5). In this case, during free growth (Figure 5b) the population goes through a range of dynamics from equilibrium to oscillatory to chaos complete with periodic windows²⁰ as R increases. But there is complete suppression of chaos under immigration (Figure 5a) and early onset of higher order oscillations and chaos under emigration

(Figure 5 c). In addition to the above, the population is also unable to balance even such small amount of fixed emigration at every generation and goes extinct (Figure 5 c) at a much lower growth rate compared to the case with $b=4$ (Figure 4 c). The major results from this study are:

- A small amount of constant immigration increases stability and emigration enhances instability in dynamics at all growth rates.
- Ability to balance small emigration reduces considerably at higher growth rates for higher b .

Effect of migration on the dynamics of the model with increasing b

Higher b indicates increased amount of scrambling in intraspecific competition and it also induces instability in the system. Figures 6 and 7 are the bifurcation diagrams showing the effect of increasing b in the dynamics of free growth and for populations undergoing migration at a low ($R=10$, in Figure 6) and a high ($R=50$, in Figure 7) growth rate. Figure 6 shows that slower-growing organisms ($R=10$) exhibit only equilibrium and P-2 dynamics at free growth (Figure 6 b) in the range of b studied here. A relatively high rate of immigration and emigration ($L=0.3$) induces stability

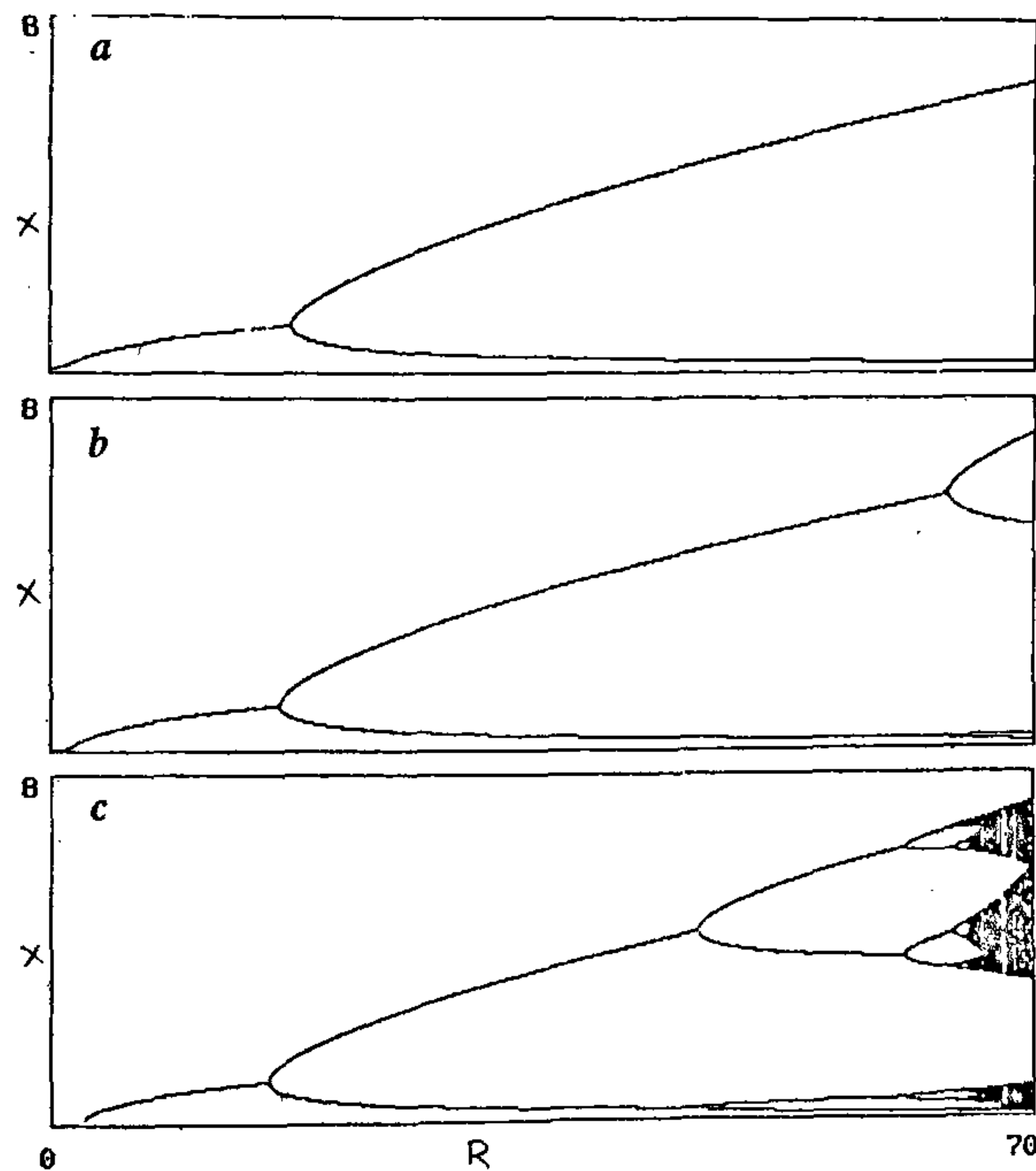


Figure 4. Dynamics of the model population ($b=4$) with increasing growth rate during (a) immigration $L=0.05$, (b) free growth, and (c) emigration $L=0.05$.

(Figures 6 a & c), but extinction occurs under emigration. For a faster-growing population ($R=50$) exhibiting the full range of period doubling dynamics and chaos (Figure 7 b), a much smaller immigration rate ($L=0.02$) completely suppresses chaos (Figure 7 a). But in contrast to Figure 6 c, in this case emigration enhances unstable dynamics (Figure 7 c) and extinction occurs at a lower b . The main results from this study are:

- There is complete suppression of chaos under small amount of constant immigration for a large range of b .
- The dynamic response to emigration for increasing b is growth rate dependent—stable at lower R , but induce early instability at higher R .
- There are two modes of population extinction under emigration—(a) preceded by large amplitude chaotic oscillations, and (b) while exhibiting stable dynamics.

Effect of increasing migration on the dynamics of the model with different b

To show the effect of increasing amounts of migration on the dynamics of populations having different b , we choose a population ($R=20$) which shows stable and P-2 dynamics for $2 < b < 5$ during free growth. The three bifurcation diagrams for $b=2, 3$ and 4 in Figure 8 a exhibit the growth dynamics of such a population undergoing increasing levels of emigration. As is observed earlier, Figure 8 a also shows that populations with higher b can balance less emigration and extinction

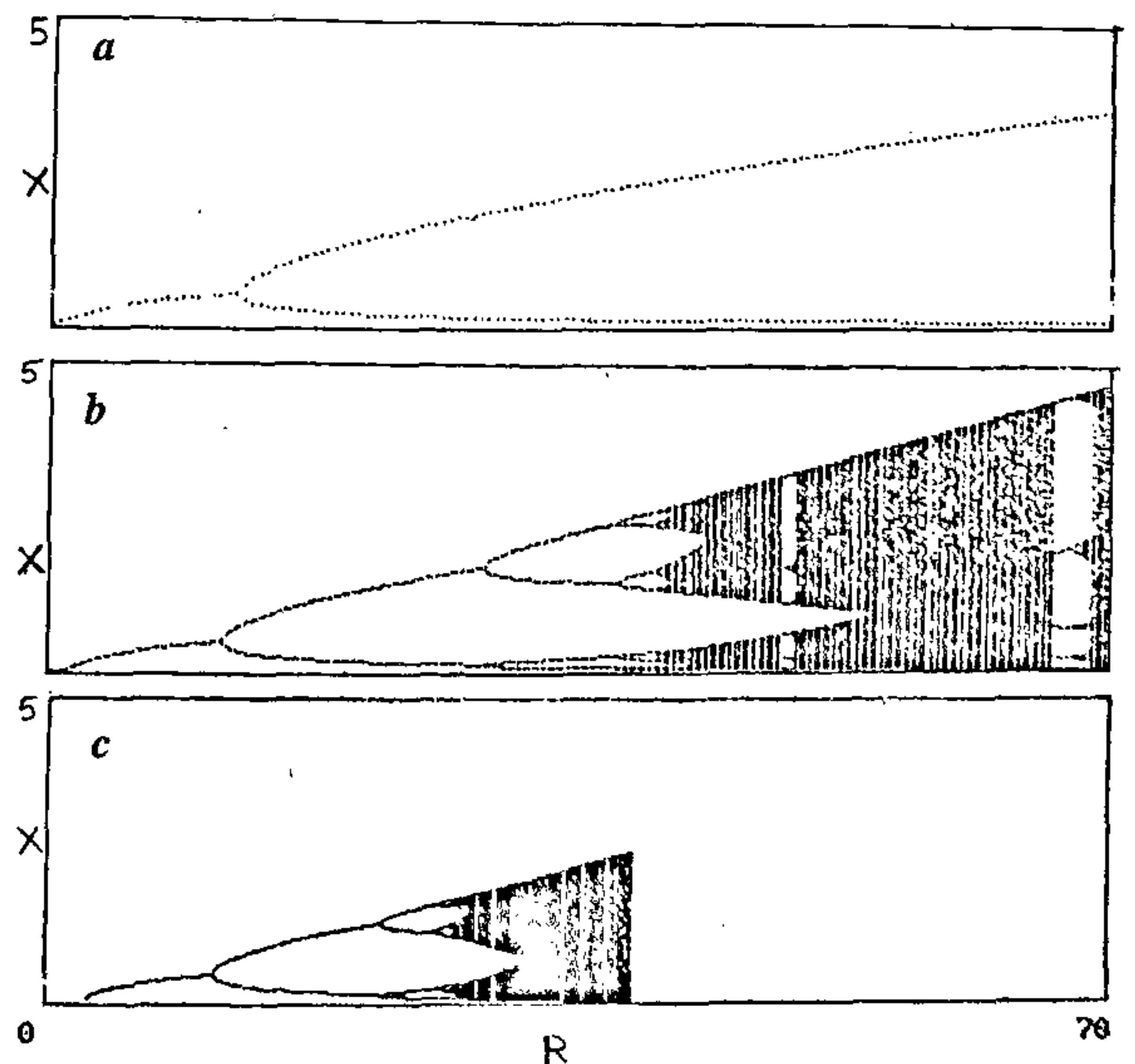


Figure 5. Dynamics of the model population ($b=6$) with increasing growth rate during (a) immigration $L=0.05$, (b) free growth, and (c) emigration $L=0.05$.

occurs at lower L as b is increased (for $b=2$ extinction occurs by $L=4.2$). The other interesting fact that is seen in the plots in Figure 8a is that for $b=3$ and 4 the dynamic complexity first increases and then decreases with increasing emigration, and extinction occurs during the stable dynamic mode. For $b=4$, a freely-growing population shows P-2 oscillation in its size. As emigration rate increases, its long-term dynamics goes through period-doubling oscillations (P-4, P-8, etc.) to chaos. But this trend is reversed as migration rate is increased further, and there is reversal from chaos to stability through period-halving bifurcations.

The bifurcation diagrams in Figures 8b and c exhibit the growth dynamics of the population ($R=20$) at a higher b ($b=5$) undergoing increasing levels of emigration and immigration respectively. Figure 8b shows an unusual survival-extinction behaviour of the population with increasing emigration. Here the model population survives for small and high emigration rates but shows extinction for intermediate range of emigration rates. Other than this, the population follows all the other features such as, increase and decrease of dynamic complexity, and extinction at lower emigration rate as seen in Figure 8a. Figure 8c shows the dynamics of population growth under immigration and it follows the general trend of increasing stability by suppression of oscillation as immigration rate increases. These results have the following important implications:

- Increasing b shows increased dynamic complexity as emigration increases up to a certain range, but then show period reversal and suppress instability to finally exhibit stable dynamics before extinction.
- For higher b or R there is an intermediate range of emigration rate at which the population go extinct,

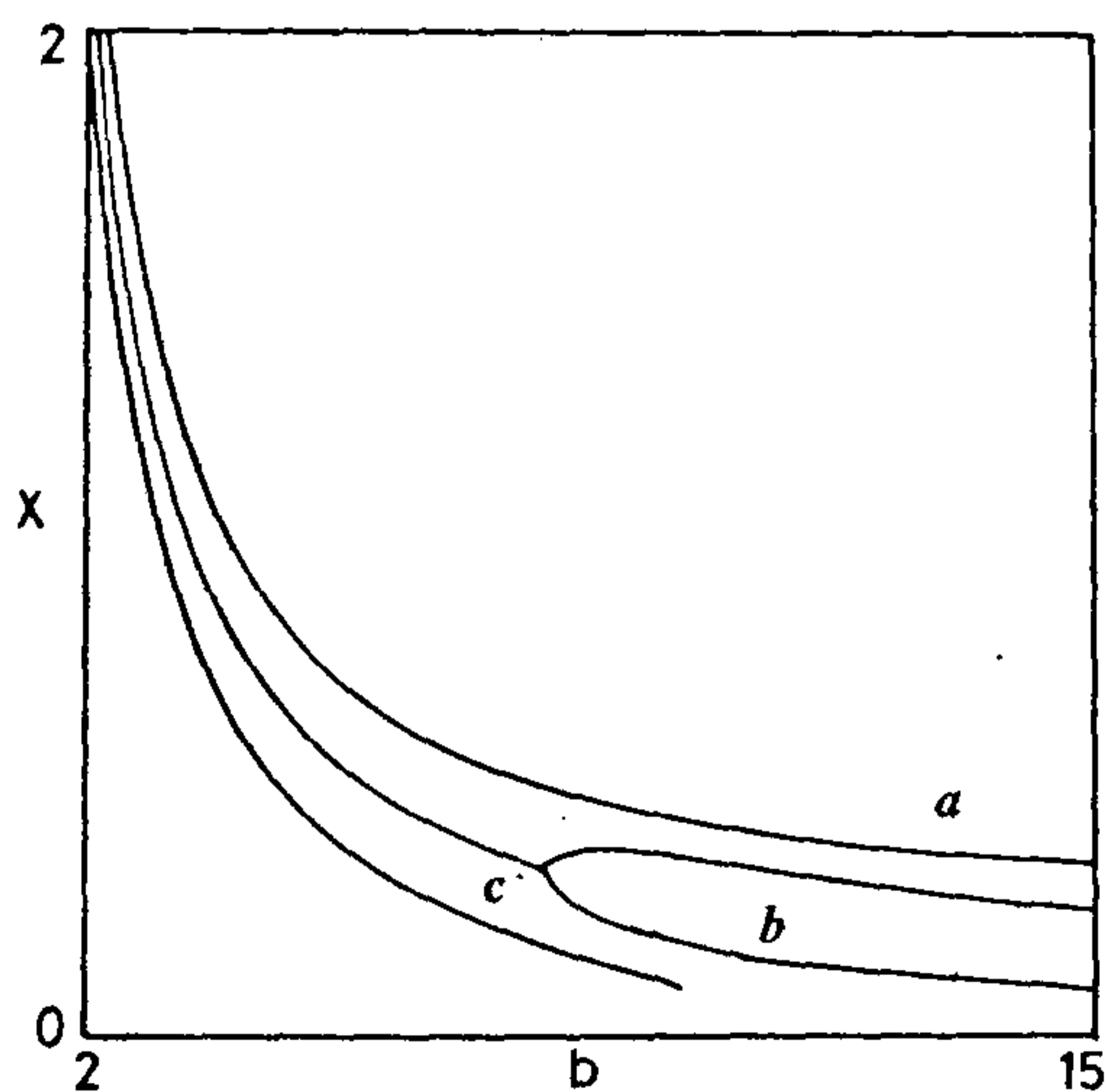


Figure 6. Dynamics of a slow-growing ($R=10$) model population with increasing b during (a) immigration $L=0.3$, (b) free growth, and (c) emigration $L=0.3$.

though it can survive at lower and higher emigration.
- Immigration induces stability.

Implications of the results

The two main arguments that are forwarded against the relevance of chaos in ecological systems have been based on: a) field data of a large number of insect populations, when fitted in a realistic discrete growth model, have population parameters corresponding to stable dynamics, and b) chaos increases the risk of extinction because of the violent oscillations associated with it. We have shown, through the study on the specific model used for fitting the insect data sets, that both these points can be argued against.

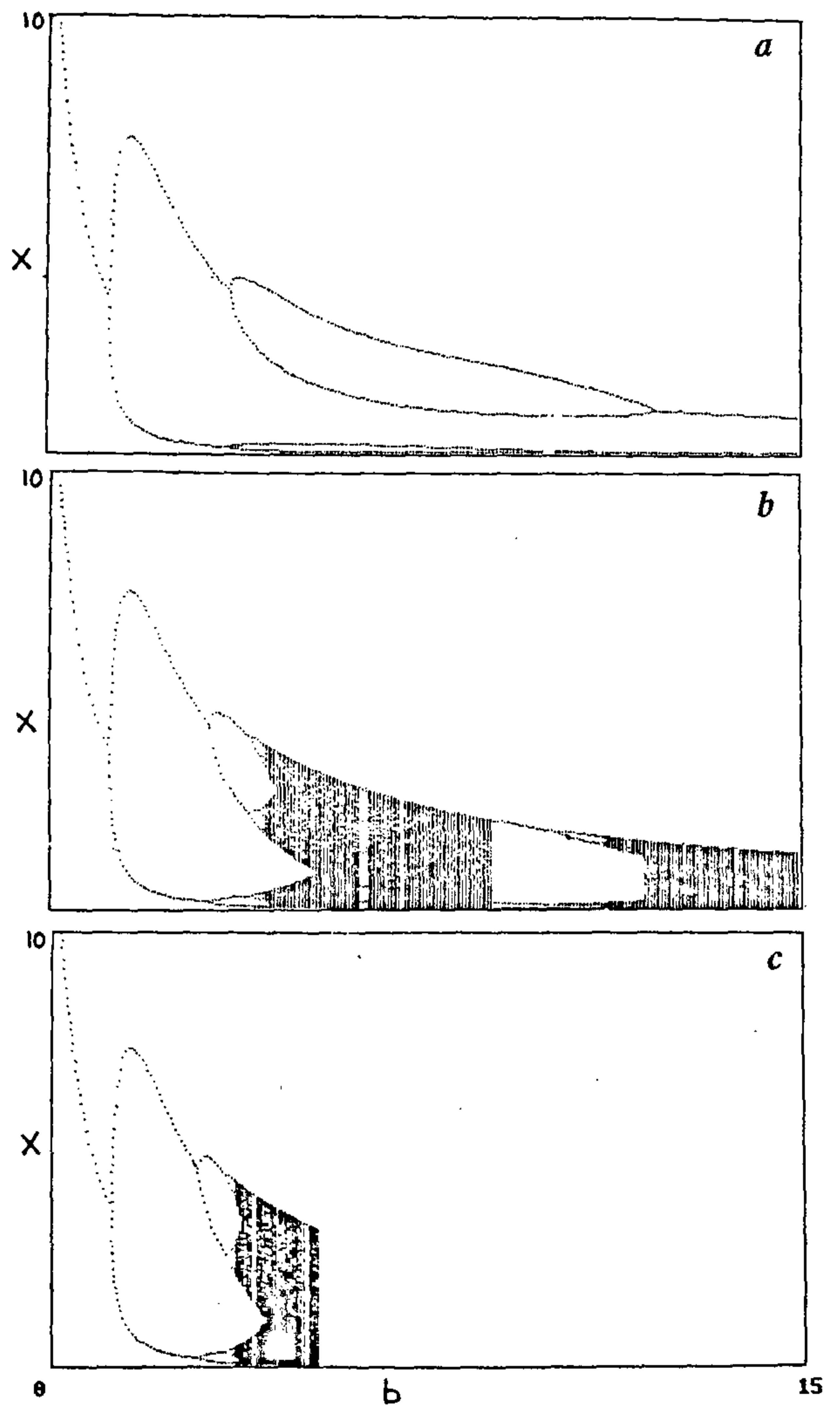


Figure 7. Dynamics of a fast-growing ($R=50$) model population with increasing b during (a) immigration $L=0.02$, (b) free growth, and (c) emigration $L=0.02$.

First, when dispersal, a common ecological process in nature, is considered in this model. It shows suppression of higher order oscillations and chaos even in populations having intrinsic growth rate which predict irregular (chaotic) growth dynamics. Thus the observed stable dynamics in natural insect populations does not necessarily mean that the population parameters have to be in the stable region in the model. They can have R or b in the unstable region, but could show stable dynamics by suppressing chaos due to migration. This justifies one of the reservations mentioned by the authors

of the study¹³ that their model 'does not take explicit account of migration and dispersal, and may give a misleading account of some natural populations'. The fact that single populations in the laboratory did show unstable dynamics under controlled conditions implies the existence of nonlinear interactions which contribute to complex dynamics in these systems. Here, in this realistic model for insect populations, we have shown that immigration always suppresses unstable dynamics, and even high emigration induces reversal to stability for populations having varied population parameters.

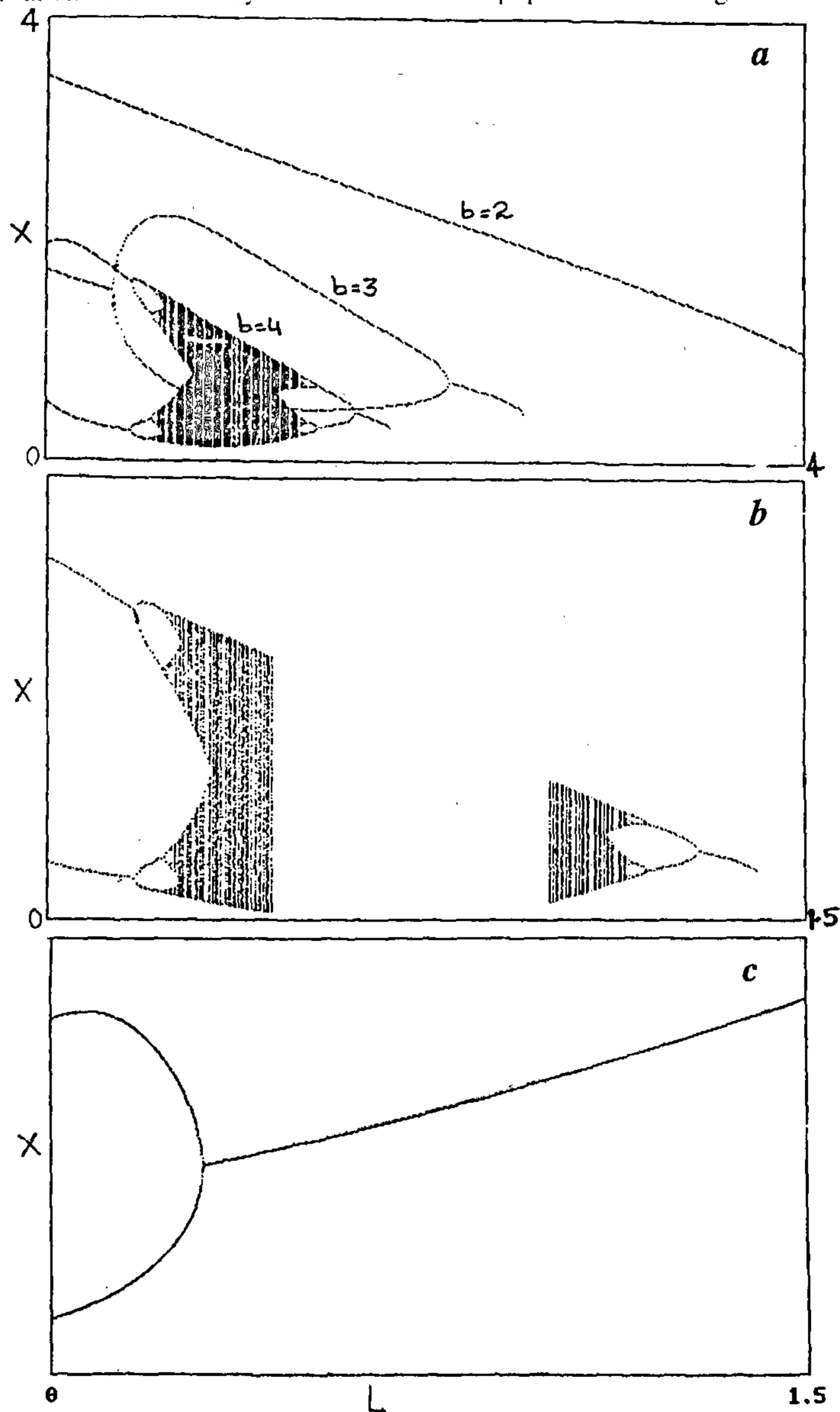


Figure 8. Dynamics of the model population ($R=20$) with increasing migration (L) for (a) during emigration for $b=2, 3, 4$; (b) during emigration for $b=5$; and (c) during immigration for $b=5$.

Thus the field population data¹⁸ need not argue against chaos in natural ecological systems.

Secondly, the evolutionary argument against chaos stems from the belief that chaotic oscillations involve large amplitude fluctuations in size ('boom and bust'), coupled with very low minimum value which increases the risk of extinction of population under small environmental perturbations. The point to remember in this regard is that it is not chaos which makes the population vulnerable, but the violent oscillations and low minimum size that are the culprits. This is clearly seen in Figure 8a and b. As long as the amplitude of fluctuations in population size remains small and the minimum size is not too low, populations can survive and exhibit chaotic dynamics under both low and high rate of emigration. On the other hand, large amplitude fluctuations with very small minimum lead to extinction under small emigration rate as shown in Figure 8b. There have been studies^{16,26,27} which have correlated large coefficient of variation in size and small population size with high risk of extinction. Thus there seems to be no reason for chaotic dynamics *per se* to be selected against during evolution and the erratic fluctuations observed in time series data (of the kind shown in Figure 1) can as well exhibit intrinsic chaotic dynamics.

Some of the results of this model have been shown to occur in other simpler single population models²⁸⁻³⁴, indicating its generality in ecology. Therefore, the fluctuations in population size observed in nature can represent inherent chaotic dynamics, and the 'stable dynamics' found in field populations may be a case of suppression of chaos due to simple ecological processes. This, of course, does not imply that there is no role of 'environmental noise'. It is possible to get similar fluctuations in data (as in Figure 1) when 'noise' is superimposed on stable or limit cycle dynamics. In fact the variability observed in nature most likely is a combination of environmental stochasticity and from the nonlinear interactions inherent in ecological systems^{12,35}.

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