Z. Wahrscheinlichkeitstheorie verw. Gebiete
66, 97–107 (1984)

Zeitschrift für
Wahrscheinlichkeitstheorie
und verwandte Gebiete

Persistence of a Markovian Population in a Patchy Environment

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Summary. An infinite system of Markov chains is used to describe population development in an interconnected system of local populations. The model can also be viewed as an inhomogeneous Markov chain where the temporal inhomogeneity is a function of the mean of the process. Conditions for population persistence, in the sense of stochastic boundedness, are found.

1. Introduction

Markov processes have long been used to model the dynamics of animal populations (Bartlett 1973). However in the majority of cases the animals are assumed homogeneously distributed in space. In contrast, Andrewartha and Birch (1954) stressed that animal populations are not homogeneous in space, but are made up of a number of partially independent local populations, connected by migration. When this is recognized, a system of interacting Markov processes is necessary for the description of population dynamics. Such systems are not easy to analyze and consequently models in population ecology have involved restrictive assumptions to achieve analytical tractability (Caswell 1978; Chesson 1978, 1981). Typically such models consider a finite or infinite system of "patches" (areas of suitable habitat) where each patch supports a local population. For analytical tractability, the number of patches is usually infinite and migration is random, that is, any two patches are assumed equally accessible to migrating organisms from any other patch. Most restrictive, however, is the assumption that a two-state Markov chain is sufficient to describe local population dynamics. Essentially, one must assume that simply knowing whether a local population is extinct or not, is sufficient.

To overcome the last and perhaps most serious problem with these population models, Chesson (1978, 1981) introduced a model that retains the assump-

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tions of random migration and infinitely many patches, but allows local populations to be described by an essentially arbitrary Markov process on the nonnegative integers. The model can be thought of as a infinite set of interacting Markov chains. However because of the random migration assumption, the interaction between these chains is very simple and an alternative description is available: the population on any patch can be regarded as an inhomogeneous Markov chain where the inhomogeneity is a function of the expected value of process. Thus the transition probabilities are a functional of the marginal distribution.

For this model, we study the fundamental problem of population persistence. Our definition of persistence uses the notion of stochastic boundedness (Chesson 1978), which is a concept closely related to positive recurrence of the states of a Markov chain. Both necessary and sufficient conditions for persistence are found.

2. The Model

In the discussion below h is some fixed number ($0<h<1$), t is a non-negative integer while s is a member of $\{0, h, 1, 1+h, \dots\}$.

We deal with just the single species models in the class introduced by Chesson (1978, 1981). In this class migration and population growth are assumed separated in time. Migration occurs during the periods $(0, h]$, $(1, 1+h]$, $(2, 2+h]$. During $(h, 1]$, $(1+h, 2]$, $(2+h, 3], \dots$ local populations are isolated and local population growth occurs.

Let $Z_j(s)$ be a non-negative integer-valued random variable representing the local population size on patch j at time s and define $\bar{Z}(s)=EZ_j(s)$ (it will not depend on j). The population size $Z_j(t+h)$, following a migration period, is written $Z_j(t+h)=Z_j(t)+I_j(t+h)-E_j(t+h)$, where I_j and E_j respectively represent immigration to, and emigration from, patch j.

Define $\mathscr{H}_s$ to be the σ-field generated by

$$\{Z_j(u), u \leqq s;\ I_j(t+h), E_j(t+h), t+h \leqq s;\ j=1, 2, \dots\}.$$

The following assumptions are made.

1. $Z_1, Z_2, \dots$ are i.i.d. stochastic processes.

2. Conditional on $\mathscr{H}_t$, $\{I_j(t+h), E_j(t+h), j=1, 2, \dots\}$ is a collection of mutually independent random variables. $I_j(t+h)$ is conditionally Poisson with mean $\mu\bar{Z}(t)$ and $E_j(t+h)$ is conditionally binomial with parameters $Z_j(t)$ and μ. (Note that $EI_j(t+h)=EE_j(t+h)$ and so $\bar{Z}(t+h)=\bar{Z}(t)$).

3. $P(Z_j(t+1)=z \mid \mathscr{H}_{t+h})=\gamma(z, Z_j(t+h))$ where γ is some transition function.

Heuristically condition 2 can be described as follows: For each patch, each individual animal emigrates with probability μ, independently of the other individuals. The emigrants from all patches join a common pool of migrating individuals, which are redistributed at random to all patches to give the Poisson distribution of immigrants.

Condition 1 may seem a little odd since it appears that different patches, though connected by migration, do not affect each other. In fact the effect of all other patches on any given patch is deterministic, not stochastic. Any individual patch is affected by the average population density of all patches, viz

$$\lim_{n\to\infty} \frac{1}{n} \sum_{j=1}^{n} Z_j(s) = \bar{Z}(s). \qquad \text{a.s.,}$$

and is nonrandom by virtue of the law of large numbers. Chesson (1981) shows how the model described here can be obtained as a limit as $k\to\infty$ of a model with $k<\infty$ patches. In this latter model the $Z_j, j=1, \ldots, k$, are not independent.

An important quantity is the conditional mean

$$g(Z_j(t+h)) = E[Z_j(t+1)|\mathscr{H}_{t+h}] = \sum_z z\gamma(z, Z_j(t+h)).$$

It must satisfy the condition $g(0)=0$ i.e. a zero population has zero growth. This is of course equivalent to the condition $\gamma(z,0)=1_{\{0\}}(z)$. To avoid triviality it is also assumed that $\bar{Z}(0)>0$ and $\mu>0$.

3. Stochastic Boundedness

Stochastic boundedness (Chesson 1978) is closely related to tightness of a family of probability measures which is sometimes also given the name stochastic boundedness (e.g. Feller 1971).

Definition 1. The population on the jth patch is said to be stochastically bounded from above (sba) if for every $\varepsilon>0$ there is an $N<\infty$ such that $P(Z_j(s)>N)<\varepsilon$ for all s.

Definition 2. The population on the jth patch is said to be stochastically bounded from below (sbb) if the event $\{Z_j(s)>0\}$ occurs for infinitely many s, a.s., and there is a positive number ε such that $P(Z_j(s)>0)\geqq\varepsilon$ for all s.

In this paper the Z_j are identically distributed and so either all local populations are stochastically bounded or all local populations are not stochastically bounded. Hence we shall speak of stochastic boundedness of local populations rather than stochastic boundedness of the population on the jth patch. While the set of processes $Z_1, Z_2, \ldots$, serves to motivate the model, the mathematical structure of Z_j does not depend on the presence of other stochastic processes and it can be defined in isolation. Thus the subscript j will be suppressed in all that follows.

Stochastic boundedness from below is one way of defining population persistence and is the main subject of this article. Stochastic boundedness from above can be dealt with very simply, for it is not difficult to see that the population will be sba if and only if $\bar{Z}(t)\leqq M$, for all t, for some finite constant M. Moreover the following simple condition on g is easy to derive: the population will be sba if there are positive constants $\rho<1$, and $N<\infty$, such that $g(z)\leqq\rho z$ for all $z>N$.

3.1. Sufficient Conditions for Stochastic Boundedness from Below

For convenience, in this subsection we assume stochastic boundedness from above so that there is an $M<\infty$, with $\bar{Z}(t)\leqq M$, for all t. In the presence of this condition, sbb reduces to a simple condition on $\bar{Z}$:

Lemma 3.1.1. *Local populations are sbb if and only if there is an $\varepsilon>0$ such that $\bar{Z}(t)\geqq\varepsilon$ for all t.*

Proof. The "only if" part follows from the inequality $P(Z(t)>0)\leqq\bar{Z}(t)$. To prove the "if" part assume $\bar{Z}(t)\geqq\varepsilon>0$. Then $P(Z(t+h)>0)\geqq 1-e^{-\mu\varepsilon}$. Moreover

$$P(Z(t+h)=l)\geqq E\mu^{Z(t)}v_l,$$

where $v_l=\inf\{(\mu z)^l e^{-\mu z}/l!\,|\,\varepsilon\leqq z\leqq M\}$, and using Jensen's inequality it follows that $P(Z(t+h)=l)\geqq\mu^M v_l$. Defining $\rho_l=P(Z(t+1)>0\,|\,Z(t+h)=l)$ we have

$$P(Z(t+1)>0)\geqq\sum_{l=1}^{\infty}\mu^M v_l\rho_l.$$

The RHS above is positive because $v_l>0$ and ρ_l must be positive for some l, since $\bar{Z}(t)>0$ for all t. Thus we have proved that $P(Z(s)>0)$ is bounded away from 0.

To complete the proof we must show that $\{Z(s)>0\}$ occurs infinitely often, a.s., whenever $\bar{Z}(t)\geqq\varepsilon>0$ for all t. If $\bar{Z}(t)\geqq\varepsilon$ then $P(Z(t+h)>0\,|\,\mathscr{H}_{t-1+h})\geqq 1-e^{-\mu\varepsilon}$. It follows that

$$\sum_{t=1}^{\infty}P(Z(t+h)>0\,|\,\mathscr{H}_{t-1+h})=\infty$$

and hence, by the extended Borel-Cantelli lemma (Breiman 1968, p. 96) $Z(t+h)>0$ infinitely often, a.s.

We now come to general sufficient conditions for sbb. In order to define them we need to introduce another model.

Let Y be a Markov chain with index set $\{0,h,1,1+h,\ldots\}$ and state space $\{0,1,2,\ldots\}$ such that

$$P(Y(t+1)=j\,|\,Y(t+h))=\gamma(j,Y(t+h))$$

and, given $Y(t)$, $Y(t+h)$ is conditionally binomial with parameters $(Y(t),(1-\mu))$. The process Y behaves like the population process for an individual patch with immigration excluded, i.e. with $I(t+h)$ set equal to 0.

Define $f(t)=E[Y(t)\,|\,Y(h)=1]$.

Theorem 3.1.2. *If*

$$\sum_{t=1}^{\infty}f(t)\mu>1$$

then local populations are sbb.

In order to prove the theorem we need some lemmas. We shall assume that at least one $\rho_l=P(Z(t+1)>0\,|\,Z(t+h)=l)$ is positive, as must be so if any of the $f(t)$ are positive. Define $A(t,u)=\{Z(t)>0,\ldots,Z(t-u+1)>0,\ Z(t-u)=0,$

$Z(t-u+h)=1\}$, $u=1,2,\ldots$, $A(t,0)=\{Z(t)=0,\ \ Z(t+h)=1\}$, $B(t,u)=\{I(t+h)=\ldots=I(t-u+1+h)=0\}$ and $C(t-u)=\{Z(t-u+h)=1,\ Z(t-u)=0\}$.

Lemma 3.1.3.

$$E[Z(t+1)1_{A(t,u)}|\,C(t-u)]\geqq f(u+1)\exp\left\{-\mu\sum_{v=0}^{u-1}\bar{Z}(t-v)\right\}. \tag{1}$$

Proof. The conditional distribution of $Z(t+1)$ given $B(t,u)\cap C(t-u)$ is equal to the conditional distribution of $Y(u+1)$ given $Y(h)=1$. Hence

$$E[Z(t+1)|B(t,u)\cap C(t-u)]=f(u+1).$$

Note also that on $B(t,u)\cap C(t-u)$, $Z(t+1)=Z(t+1)1_{A(t,u)}$ because, in the absence of immigration, an extinct population remains extinct. Hence

$$E[Z(t+1)1_{A(t,u)}|B(t,u)\cap C(t-u)]=f(u+1) \tag{2}$$

and since $Z(t+1)\geqq 0$ we have

$$E[Z(t+1)1_{A(t,u)}|\,C(t-u)]\geqq f(u+1)P(B(t,u)|\,C(t-u)).$$

The lemma is now proved by the observation

$$P(B(t,u)|\,C(t-u))=\exp\left\{-\mu\sum_{v=0}^{u-1}\bar{Z}(t-v)\right\}.$$

Lemma 3.1.4. *Suppose that for some given value of* $t, 0<\varepsilon\leqq\bar{Z}(t)\leqq M$, *then there is a number* $\varepsilon'>0$, *independent of* t, *such that* $\bar{Z}(t+1)\geqq\varepsilon'$.

Proof. As in Lemma 3.1.1

$$P(Z(t+1)>0)\geqq\sum_{l=1}^{\infty}\mu^M v_l\rho_l\stackrel{\text{def}}{=}\varepsilon'>0;$$

and it is clear that $\bar{Z}(t+1)\geqq\varepsilon'$. As a corollary we can conclude that $\bar{Z}(t)\neq 0$ for any t when $\bar{Z}(0)\neq 0$.

Lemma 3.1.5. *If* $\underline{\lim}\,\bar{Z}(t)=0$ *then, for every* $\varepsilon>0$ *and every positive integer* N, *there is a* $t>0$ *such that* $\bar{Z}(t),\ldots,\bar{Z}(t-N+1)<\varepsilon$.

Proof. For ε and ε' as in Lemma 3.1.4 define $\sigma(\varepsilon)=\min(\varepsilon,\varepsilon')$. Let $\sigma^{(N)}$ be the Nth composition of σ with itself. If

$$\bar{Z}(t+1)<\sigma^{(N)}(\varepsilon) \tag{3}$$

then $\bar{Z}(t),\ldots,\bar{Z}(t-N+1)<\varepsilon$. Since σ is a positive function $\underline{\lim}\,\bar{Z}(t)=0$ implies that (3) is satisfied for infinitely many t and so the lemma is proved.

Proof of Theorem 3.1.2. Let N be a positive integer for which $\sum_{u=1}^{N} f(u)\mu>1$. Let $\varepsilon>0$ be such that

$$\sum_{u=1}^{N} f(u)\mu e^{-\mu u\varepsilon}(1-\varepsilon)\stackrel{\text{def}}{=}\rho>1. \tag{4}$$

By Lemma 3.15 either the population is sbb or there is a t such that $\bar{Z}(t-u)<\varepsilon$ for $u=0,\dots,N-1$. Assume the latter and define $\bar{Z}_{\min}(t,N)=\min\{\bar{Z}(t),\dots,\bar{Z}(t-N+1)\}$. The sets $A(t,u)$, $u=0,1,\dots$ are pairwise disjoint and so

$$\bar{Z}(t+1)\geqq\sum_{u=0}^{N-1} EZ(t+1)\,1_{A(t,u)}=\sum_{u=0}^{N-1} E[Z(t+1)\,1_{A(t,u)}\,|\,C(t-u)]\,P(C(t-u)). \quad (5)$$

Since $P(Z(t-u)=0)\geqq 1-\bar{Z}(t-u)$, $P(Z(t-u+h)=1\,|\,Z(t-u)=0)=\mu\bar{Z}(t-u)\exp\cdot(-\mu\bar{Z}(t-u))$ and $\bar{Z}(t-u)<\varepsilon$, we have $P(C(t-u))>\mu\bar{Z}(t-u)e^{-\mu\varepsilon}(1-\varepsilon)$. Combining this with (1), (4) and (5) we obtain

$$\begin{aligned}\bar{Z}(t+1)&\geqq\sum_{u=1}^{N} f(u)\mu e^{-\mu u\varepsilon}(1-\varepsilon)\bar{Z}(t-u+1)\\ &\geqq\rho\bar{Z}_{\min}(t,N).\end{aligned}$$

Clearly $\bar{Z}(t+1),\dots,\bar{Z}(t+N)\geqq\rho\bar{Z}_{\min}(t,N)$, provided none exceeds ε. Hence $\bar{Z}_{\min}(t+N,N)\geqq\rho\bar{Z}_{\min}(t,N)$. This means that $\bar{Z}_{\min}(t+rN,N)$ will increase as a function of r until $\sup\{\bar{Z}(t+v),\ v=1,\dots,rN\}$ exceeds ε. It is then possible that $\bar{Z}_{\min}(t+rN,N)$ may decrease but it must remain above $\varepsilon^*=\sigma^{(N)}(\varepsilon)$.

It is now clear that $\underline{\lim}\,\bar{Z}(t)\geqq\varepsilon^*>0$ and by Lemma 3.1.1 this proves the theorem.

Note that the asymptotic lower bound, ε^*, is independent of the distribution of $Z(0)$.

3.2. *Necessary Conditions for Stochastic Boundedness from Below*

Throughout this subsection we assume that there is an $M<\infty$ such that

$$E[Z(t+1)\,|\,Z(t+1)>0,\mathscr{H}_{t+h}]\leqq M. \quad (6)$$

Thus there is an upper bound on the conditional mean population size of positive populations. From (6) it follows that $E[Z(t+1)\,|\,\mathscr{H}_{t+h}]\leqq M$, $\bar{Z}(t)\leqq M$ for all $t\geqq 1$, and hence that local populations are sba. We have the following:

Theorem 3.2.1. *If*

$$\sum_{t=1}^{\infty} f(t)\mu<1$$

then there is an $\varepsilon>0$ *such that* $\lim_{t\to\infty}\bar{Z}(t)=0$ *whenever* $\bar{Z}(0)<\varepsilon$. *Hence local populations are not sbb for such values of* $\bar{Z}(0)$.

To prove the theorem we need several lemmas.

Lemma 3.2.2.

$$E[Z(t+1)\,1_{A(t,u)}\,|\,C(t-u)]\leqq f(u+1)+\mu M\sum_{v=0}^{u-1}\bar{Z}(t-v). \quad (7)$$

Proof. Using Z, A, B, C respectively for $Z(t+1)$, $A(t, u)$, $B(t, u)$ and $C(t-u)$ we have

$$\begin{aligned} E[Z1_A|C] &= E[Z1_{A\cap B}|C] + E[Z1_{A\cap B^c}|C] \\ &\leqq E[Z1_A|B\cap C] + E[Z|B^c\cap C]\,P(B^c|C). \end{aligned}$$

By (2) $E[Z1_A|B\cap C]=f(u+1)$. Moreover $E[Z|\mathscr{H}_{t+h}]\leqq M$ and since $B^c\cap C\in\mathscr{H}_{t+h}$ it follows that $E[Z|B^c\cap C]\leqq M$. Finally

$$P(B^c|C)=1-\exp\left\{-\mu\sum_{v=0}^{u-1}\bar{Z}(t-v)\right\}\leqq\mu\sum_{v=0}^{u-1}\bar{Z}(t-v).$$

Putting this together we get the stated result.

For the next result we need to define the event

$$D(t, N)=\{Z(u)>0, u=t-N+1, \dots, t\}.$$

Lemma 3.2.3. *There is a number $\chi<1$ such that*

$$P(D(t, N))\leqq\chi^N$$

for all $N\leqq t$.

Proof.

$$\begin{aligned} P(Z(t+1)=0|\mathscr{H}_t) &\geqq P(Z(t+h)=0|\mathscr{H}_t) \\ &\geqq \mu^{Z(t)}e^{-\mu\bar{Z}(t)} \\ &\geqq \mu^{Z(t)}e^{-\mu M} \end{aligned}$$

Thus

$$P(Z(t+1)>0|\mathscr{H}_t)\leqq 1-e^{-\mu M}\mu^{Z(t)}\overset{\text{def}}{=}p(Z(t)). \tag{8}$$

Now

$$\begin{aligned} P(D(t, N)) &= \prod_{u=0}^{N-1} P(Z(t-u)>0|D(t-u-1, N-u-1)) \\ &\leqq \prod_{u=0}^{N-1} E[p(Z(t-u-1))|D(t-u-1, N-u-1)] \\ &\leqq \prod_{u=0}^{N-1} p(E[Z(t-u-1)|D(t-u-1, N-u-1)]). \end{aligned}$$

(The last inequality is Jensen's.) Using (6) we see that the conditional expectation is $\leqq M$ and so $P(D(t, N))\leqq p(M)^N\overset{\text{def}}{=}\chi^N$ with $\chi<1$.

Lemma 3.2.4. For $u\geqq 0$

$$EZ(t+1)1_{\{Z(t-u=0, Z(t-u+h)>1\}}\leqq M[\mu\bar{Z}(t-u)]^2. \tag{9}$$

Proof. The LHS of (9) equals

$$\begin{aligned} &E\{E[Z(t+1)|\mathscr{H}_{t+h}]|Z(t-u)=0, Z(t-u+h)>1\}\,P(Z(t-u)=0, Z(t-u+h)>1) \\ &\quad\leqq MP(Z(t-u+h)>1|Z(t-u)=0) \\ &\quad= M\{1-[1+\mu\bar{Z}(t-u)]\exp[-\mu\bar{Z}(t-u)]\} \end{aligned}$$

and the desired result follows from the inequality $e^x-1-x \leqq x^2 e^x$ for all positive x.

Lemma 3.2.5. *Let $\{z_t\}$ and $\{\phi_t\}$ be sequences of non negative numbers such that*

$$\sum_{t=1}^{\infty} \phi_t < 1, \tag{10}$$

and for all $N \leqq t$

$$z_{t+1} \leqq \sum_{u=1}^{N} \left[\phi_u + a \sum_{v=0}^{u-1} z_{t-v}\right] z_{t-u+1} + M\chi^N, \tag{11}$$

where a, M, χ are positive constants with $\chi<1$. Then there is an $\varepsilon>0$ and an $N<\infty$ such that

$$z_1, \ldots, z_N < \varepsilon \quad \textit{implies } z_t \to 0 \textit{ as } t \to \infty.$$

Proof. Define $z(t, N)=\max\{z(t), \ldots, z(t-N+1)\}$, $\rho=\sum_{t=1}^{\infty} \phi_t$ and assume that for some fixed t and N, $z(t, N) \leqq N^{-3}$. From (11) we obtain

$$z_{t+1} \leqq \rho z(t, N) + aN^{-4} + M\chi^N. \tag{12}$$

If

$$aN^{-4} + M\chi^N < \tfrac{1}{8}(1-\rho)N^{-3} \tag{13}$$

then $z_{t+1} \leqq N^{-3}$ which means $z(t+1, N) \leqq N^{-3}$, indeed $z(t+r, N) \leqq N^{-3}$ for all $r \geqq 0$. As a consequence (12) holds for all t greater than or equal to the given t. Since $\overline{\lim}\, z_t = \overline{\lim}\, z(t, N)$ it follows that

$$\overline{\lim}\, z_t \leqq \rho\, \overline{\lim}\, z_t + aN^{-4} + M\chi^N.$$

Hence

$$\overline{\lim}\, z_t \leqq \frac{aN^{-4}+M\chi^N}{1-\rho} < 1/8N^{-3}. \tag{14}$$

Now choose N_0 so that (13) holds for $N \geqq N_0$ and let $\varepsilon = N_0^{-3}$. If $z_1, \ldots, z_{N_0} < \varepsilon$ then $\overline{\lim}\, z_t < 1/8 N_0^{-3}$. Define $N_n = 2^n N_0$. If t_n is given and $z_t \leqq N_n^{-3}$ for $t \geqq t_n$ then it follows from (14) that there is a t_{n+1} such that $z_t \leqq N_{n+1}^{-3}$ for $t \geqq t_{n+1}$. Choosing $t_0=1$ it now follows inductively that $\overline{\lim}\, z_t \leqq N_n^{-3}$ for every n, which proves the lemma.

Proof of Theorem 3.2.1. First of all

$$\begin{aligned} \bar{Z}(t+1) = & \sum_{u=0}^{N-1} EZ(t+1)1_{A(t,u)} \\ & + EZ(t+1)1_{D(t,N)} \\ & + \sum_{u=0}^{N-1} EZ(t+1)1_{D(t,u) \cap \{Z(t-u)=0,\, Z(t-u-h)>1\}}. \end{aligned} \tag{15}$$

We have $EZ(t+1)1_{A(t,u)} = E[Z(t+1)1_{A(t,u)} \mid C(t,u)]\, P(C(t,u))$, $P(C(t,u)) \leqq \mu \bar{Z}(t$

$-u)$ and using Lemma 3.2.2 we obtain

$$EZ(t+1)1_{A(t,u)} \leqq \left[f(u+1)+\mu M \sum_{v=0}^{u-1} \bar{Z}(t-v)\right] \mu \bar{Z}(t-u). \tag{16}$$

Also $EZ(t+1)1_{D(t,N)} = EE[Z(t+1)|\mathscr{H}_{t+h}]1_{D(t,N)}$.

Using Lemma 3.2.3 it follows that

$$EZ(t+1)1_{D(t,N)} \leqq M\chi^N. \tag{17}$$

Finally, using Lemma 3.2.4, we have

$$\begin{aligned} EZ(t+1)\,1_{D(t,u)\cap\{Z(t-u)=0,\, Z(t-u+h)>1\}} &\leqq EZ(t+1)1_{\{Z(t-u)=0, Z(t-u+h)>1\}} \\ &\leqq M[\mu\bar{Z}(t-u)]^2. \end{aligned} \tag{18}$$

Combining (15)–(18) we obtain

$$\bar{Z}(t+1) \leqq \sum_{u=1}^{N} \left[f(u)+\mu M \sum_{v=0}^{u-1} \bar{Z}(t-v)\right] \mu \bar{Z}(t-u+1) + M\chi^N. \tag{19}$$

Using Lemma 3.2.5 we now deduce that there is an $\varepsilon' > 0$ and an $N < \infty$ *such that* $\bar{Z}(0), \ldots, \bar{Z}(N-1) < \varepsilon'$ implies that $\bar{Z}(t) \to 0$. Given such N and ε' choose $\varepsilon = \varepsilon'/M^N$. Then $\bar{Z}(0) < \varepsilon$ implies $\bar{Z}(0), \ldots, \bar{Z}(N-1) < \varepsilon'$ because

$$\begin{aligned} \bar{Z}(t+1) &= EE[Z(t+1)/Z(t+h)|\mathscr{H}_{t+h}]Z(t+h) \\ &\leqq EE[Z(t+1)|\mathscr{H}_{t+h}]Z(t+h) \\ &\leqq MEZ(t+h) \\ &= M\bar{Z}(t). \end{aligned}$$

Hence $\bar{Z}(0) < \varepsilon$ implies $\bar{Z}(t) \to 0$.

4. Interpretation and Application

The condition for sbb given in the previous section has a natural interpretation in terms of the expected number of emigrants from a patch that is begun with one individual, and to which subsequent immigration is excluded. The expected number of emigrants from such a patch during $(t, t+h]$ is $E[Y(t)|Y(h)=1]\mu = f(t)\mu$. It follows that $\sum_{t=1}^{\infty} f(t)\mu$ is the expected total number of emigrants from a patch treated in this way. We have shown that stochastic boundedness from below depends on whether this quantity is greater than 1 or less than 1. The intuitive strength of these results suggests that they are likely to hold in a much broader class of models than is considered here.

I now give a simple example of the application of the results in Sect. 3 to a particular model.

Example. Suppose

$$\gamma(z,\xi)=\begin{cases}1_{\{0\}}(z), & \xi=0\\ \gamma_1(z), & \xi>0.\end{cases}$$

Then

$$E[Y(t+1)\,|\,Y(t+h)>0]=\sum_{z=0}^{\infty} z\gamma_1(z)\overset{\text{def}}{=}\zeta$$

$$P(Y(t+h)>0\,|\,Y(t+h-1)>0)=\sum_{z=0}^{\infty}\gamma_1(z)(1-\mu^z)$$
$$=1-\phi(\mu)$$

where ϕ is the probability generating function of γ_1. It follows that $P(Y(t+h)>0\,|\,Y(h)=1)=[1-\phi(\mu)]^t$ and $E[Y(t+1)\,|\,Y(h)=1]=\zeta[1-\phi(\mu)]^t$ and so $\sum_{t=1}^{\infty} f(t)\mu=\mu\zeta/\phi(\mu)$. Thus local populations will be sbb for all possible $\bar{Z}(0)>0$ if $\mu\zeta/\phi(\mu)>1$. If γ_1 is Poisson with parameter λ this criterion reduces to

$$\lambda\mu>e^{\lambda(\mu-1)}.$$

Despite the ease of interpretation of the condition for sbb, in situations more complex than the example above the $f(t)$ are not readily calculated except for small t. Clearly sufficient conditions can be found by considering partial sums of the $f(t)$. In addition the example above can be used to find both necessary and sufficient conditions for any particular example. For an arbitrary transition function γ, γ_1 can be defined generally by the equation

$$\gamma_1(z)=\inf_{\xi>0}\gamma(z,\xi)$$

for $z>0$, and $\gamma_1(0)=1-\sum_{z=1}^{\infty}\gamma_1(z)$. ζ and ϕ are defined in terms of γ_1 as above. Clearly $E[Y(t+1)\,|\,Y(t+h)>0]\geqq\zeta$ and $P(Y(t+h)>0\,|\,Y(t+h-1))>0\geqq 1-\phi(\mu)$. It is now easily seen that

$$\sum_{t=1}^{\infty} f(t)\mu\geqq\mu\zeta/\phi(\mu)$$

and that $\mu\zeta/\phi(\mu)>1$ is a sufficient condition for sbb for any $\bar{Z}(0)>0$.

Now define $\Gamma_2(z)=\inf_{\xi}\sum_{z_1\leqq z}\gamma(z_1,\xi)$. If Γ_2 is a proper distribution function then define $\gamma_2(z)=\Gamma_2(z)-\Gamma_2(z-1)$. With ζ^+ and ϕ^+ defined in terms of γ_2 in the same way that ζ and ϕ are defined in terms of γ_1, we can say that local populations will not be sbb for all possible $\bar{Z}(0)>0$ if

$$\mu\zeta^+/\phi^+(\mu)<1.$$

Acknowledgements. I am grateful for the suggestions of several anonymous reviewers, who have removed some errors and greatly improved the paper. This work was supported by NSF grant DEB 77-14470.

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Received October 7, 1982; in final form October 20, 1983