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EXIT PROBABILITIES FOR STOCHASTIC POPULATION MODELS: INITIAL TENDENCIES FOR EXTINCTION, EXPLOSION, OR PERMANENCE

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ABSTRACT. Let $X(t) = X(t, \omega)$ be a stochastic process which represents the (ω-th sample) population density at time t, $t \geq 0$ ($\omega \in \Omega$, a sample space), and let P be the underlying probability measure (defined on Ω). Let $L < U$ be positive constants, and fix an initial population distribution $X(0)$ satisfying $P(L < X(0) < U) = 1$; the population density levels L and U may correspond to effective extinction and explosion respectively, for the population, for example. Denote by $\tau = \tau(\omega)$ the first exit time of X from the interval $(L, U) : \tau = \inf\{t : X(t) \notin (L, U)\}$. The probabilities $P(\tau = +\infty)$, $P(\tau < +\infty, X(\tau) \geq U)$, and $P(\tau < +\infty, X(\tau) \leq L)$ represent the permanence probability, and the initial tendencies of the population toward explosion and extinction respectively relative to the interval $[L, U]$. These probabilities are calculated for some diffusion process models. A result is given which shows that initial tendencies not to explode or go extinct for diffusion process models follow from dissipativeness or persistence for associated deterministic models respectively.

1. Introduction. The exponential population growth model corresponding to the assumption of constant per capita net growth rate is generally rejected since it predicts that population densities become unbounded. Indeed, boundedness of solutions, as a crudest form of stability, is usually expected of dynamical system models of population evolution, since this type of behavior is observed in real populations. Thus, checking that solutions are bounded constitutes an important step in validating a specific model. Once the boundedness question is answered, qualitative considerations such as persistence can be addressed: Does the model predict that the population(s) will survive indefinitely? When environmental or demographic variability are accounted for via stochastic models, a number of interpretations of boundedness and persistence are possible. Exactly how such variability as expressed by stochastic models effects qualitative behavior is as yet unsettled (Chesson [1, 2, and 3], Murdoch [14], for example). Tractable

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mathematical descriptions of qualitative behavior of stochastic models provide necessary tools to address such problems. Qualitative properties of stochastic models are indicated by trends in (time-varying) statistics and the existence of invariant distributions, generally. But transient information about stochastic models, given by certain first exit probabilities, can be important also, for example when they correspond to the degree of certainty of the model's attaining threshold levels. Specifically let $X(t) = X(t,\omega)$ represent the ω-th sample population density at time t, $t \geq 0$, and $\omega \in \Omega$, a sample space equipped with a probability measure P. For an interval $[L,U] \subseteq \mathbf{R}_+ = (0,\infty)$, and assuming $X(0)$ in (L,U) with probability one, define the first exit time of X from (L,U) by

$$\tau = \tau(\omega) = \inf\{t : X(t,\omega) \notin (L,U)\}.$$

The complementary probabilities $P(\tau < +\infty, X(\tau) \geq U)$, $P(\tau < +\infty, X(\tau) \leq L)$, and $P(\tau = +\infty)$ indicate the transient behavior of X relative to $[L,U]$ and can represent, for appropriate choices of L and U, relative certainties of significant ecological events, such as effective explosion, extinction, or permanence; these first exit probabilities can be regarded as describing initial tendencies of the population toward boundedness or persistence.

In this paper the above probabilities are calculated for continuous Markov diffusion process models of population dynamics. Diffusion processes form a class of stochastic models which arise when random environmental effects are modelled by additive white noise (Ludwig [12, 13], Hoppensteadt [10], Ricciardi [16], Turelli [18, 19], Gard [6]). Multispecies diffusion process models are considered: the main result estimates first exit probabilities for such models via Lyapunov functions. As a consequence it is shown that criteria for dissipativeness and persistence for deterministic models correspond to conditions for first exit bias toward boundedness and persistence for related stochastic models. Also an example is given which illustrates that inward first exit (boundedness) bias is possible even when the deterministic models corresponding to the drift terms are not dissipative. To begin, the calculation of first exit probabilities for scalar diffusion processes is reviewed and applied to a stochastic version of the logistic equation recently derived by Tuckwell and Koziol [17].

2. Stochastic population models. This paper is concerned with continuous Markov diffusion process models, an important class of stochastic models arising in population ecology. The probability law for such a process is characterized by drift f and diffusion g^2 coefficient functions determining the infinitesimal mean and variance of the process:

$$\begin{aligned} &\operatorname*{limit}_{h\to 0^+} \frac{1}{h}\mathrm{E}\left(X(t+h)-X(t) \mid X(t)=x\right)=f(x) \\ &\operatorname*{limit}_{h\to 0^+} \frac{1}{h}\mathrm{E}\left([X(t+h)-X(t)]^2 \mid X(t)=x\right)=g^2(x), \end{aligned} \tag{2.1}$$

where $\mathrm{E}(\cdot \mid X(t) = x)$ denotes the conditional expectation given $X(t) = x$. An alternate characterization views the diffusion process X as a solution of the (Ito-interpreted) stochastic differential equation

$$dX = f(X)\,dt + g(X)\,dW. \tag{2.2}$$

(Diffusion process analogues of the logistic (Verhulst) equation originally suggested by Robert May, for example, are obtained by taking $f(x) = rx(1 - x/K)$ and various choices for $g(x)$; see Feldman and Roughgarden [4], Turelli [18], Polansky [15], and Tuckwell and Koziol [17].) In these models $g(x)$ represents the effective fluctuation intensity of the random environment. Generally there is no reason why g should vanish at an arbitrary population level x. A mathematical consequence (see Friedman [5; Chapter 6], for example) of $g \neq 0$ on $[L, U]$ is that permanence relative to $[L, U]$ is impossible. Since sample paths are continuous, $X(\tau) = L$ or $X(\tau) = U$, and the probabilities of these events indicate the initial tendency of the population to go extinct or explode relative to $[L, U]$. For this type of model the probability

$$p(x_0) = P(X(\tau) = U \mid X(0) = x_0)$$

can be calculated directly:

$$p(x_0) = \int_L^{x_0} \phi(u)\,du \Big/ \int_L^U \phi(u)\,du, \tag{2.3}$$

where

$$\phi(u) = \exp\left\{-\int_{x_1}^{u} \frac{2f(v)}{g^2(v)}\,dv\right\}$$

and x_1 is an arbitrary positive number (see Gihman and Skorohod [8; pp. 108, 109], for example); $x_0 = (L+U)/2$ is of particular interest here. As a specific example, consider the equation

$$dX = rX(1 - X/K)\,dt + \sqrt{rX(1-X/K)}\,dW. \tag{2.4}$$

Equation (2.6) is the death rate $= 0$ case of the stochastic logistic model derived by Tuckwell and Koziol [17] as a diffusion approximation of a more intractable stochastic population model. In (2.4), $f = g^2$, which implies that $\phi(u) = (\text{const.})\, e^{-2u}$, and so, from (2.3),

$$p \equiv p\left(\frac{L+U}{2}\right) = [e^{L-U} + 1]^{-1} > \frac{1}{2} \tag{2.5}$$

for any interval $[L, U] \subseteq (0, K)$. The population density always exhibits a bias to exit $[L, U]$ through the boundary point U. In this case, an initial tendency toward the carrying capacity K (rather than explosion) is the interpretation. Actually, for any $x_0 \in [L, U]$ in this case, (2.3) becomes

$$p(x_0) = (1 - e^{2(L-x_0)})/(1 - e^{2(L-U)}). \tag{2.6}$$

Letting $L \to 0$ and $U \to K$ in (2.6) obtains the quantity

$$\tilde{p}(x_0) = (1 - e^{-2x_0})/(1 - e^{-2K}), \tag{2.7}$$

which can be interpreted as the survival probability of a population at level x_0 at some time $t = 0$. The complementary probability

$$1 - \tilde{p}(x_0) = (e^{-2x_0} - e^{-2K})/(1 - e^{-2K}) \tag{2.8}$$

corresponds to the extinction probability of the population. Tuckwell and Koziol point out that the boundaries $X = 0$ and $X = K$ for the diffusion process on $(0, K)$ defined by (2.4) are of exit type in the Feller boundary classification scheme. For this transient process, the first exit probabilities for small L and large (near K) U give, therefore, not only the initial tendencies but also the entire qualitative picture. The variability introduced by (2.4) allows for the possibility of extinction, in contrast to the deterministic and other stochastic logistic models. Also, one can see immediately, from (2.7) and (2.8), the impact of any environmental deterioration (decreased K), for example, on the survival/extinction question.

Generally

$$p < \frac{1}{2}, \tag{2.9}$$

for L sufficiently large, would represent an initial tendency toward boundedness. If, after a transformation such as $Y = -\ln X$, (2.9) holds for L sufficiently large, a first tendency toward persistence would be indicated. The main result of this paper given in the next section establishes (2.9) for multispecies models under certain conditions involving Lyapunov type functions.

3. Multispecies population models. Explicit formulas like (2.3) are not available generally in the multidimensional case (because the boundary value problem characterizing the exit point distribution does not admit a closed form solution generally). To deal with this situation Lyapunov type functions are introduced in this section so that estimates, at least, for the appropriate probabilities can be obtained. The multispecies population density configuration is represented by a multidimensional continuous Markov diffusion process $X(t) = \{X_i(t)\}$ characterized by a (vector-valued) drift function f and a (matrix-valued) diffusion function GG^T (superscript T denoting transpose) which, as in the scalar case (2.3), determine the infinitesimal statistics of the process:

$$\begin{aligned} &\operatorname*{limit}_{h\to 0^+} \frac{1}{h}\mathrm{E}\left(X(t+h) - X(t) \mid X(t) = x\right) = f(x) \\ &\operatorname*{limit}_{h\to 0^+} \frac{1}{h}\mathrm{E}\left([X(t+h) - X(t)][X(t+h) - X(t)]^T \mid X(t) = x\right) \\ &\qquad = G(x)G^T(x). \end{aligned} \tag{3.1}$$

More specifically, suppose X represents an n-species population density configuration. Let $\mathbf{R}^n, \mathbf{R}^{n\times m}$, and $\mathbf{R}^n_+$ denote the usual Euclidean n-space, the space of $n \times m$ real matrices, and the positive cone $\{x = \{x_i\} \in \mathbf{R}^n : x_i > 0,\ \text{all } i\}$ in $\mathbf{R}^n$, respectively. If the functions $f : \mathbf{R}^n_+ \to \mathbf{R}^n$ and $G : \mathbf{R}^n_+ \to \mathbf{R}^{n\times m}$ are sufficiently smooth (continuously differentiable suffices) and if $x_0 \in \mathbf{R}_+^n$, the unique solution $X(t)$ of the vector Ito stochastic differential equation

$$dX = f(X)\,dt + G(X)\,dW, \tag{3.2}$$

with initial value $X(0) = x_0$, is a diffusion process satisfying (3.1); in (3.2), $W = \{W_j\}$ represents a standard m-dimensional Wiener process—the components W_j are independent standard scalar Wiener processes—the prototype continuous Markov diffusion process. In component form (3.2) is written as

$$dX_i = f_i(X)\,dt + \sum_{j=1}^{m} g_{ij}(X)\,dW_j, \quad i = 1, \ldots, n, \tag{3.3}$$

where $f = \{f_i\}$ and $G = \{g_{ij}\}$. Further, it is assumed that there exist continuous functions $\{\tilde{f}_i\}$ and $\{\tilde{g}_{ij}\}$ on $\overline{\mathbf{R}}_+^n = \{x \in \mathbf{R}^n : x_i \geq 0, \quad i = 1, \ldots, n\}$ such that

$$f_i(x) = x_i \tilde{f}_i(x) \quad \text{and} \quad g_{ij}(x) = x_i \tilde{g}_{ij}(x), \tag{3.4}$$

which makes the specific form of (3.3) under consideration here

$$dX_i = X_i \left[\tilde{f}_i(X)\,dt + \sum_{j=1}^{m} \tilde{g}_{ij}(X)\,dW_j \right]; \tag{3.5}$$

the expression in the square brackets in (3.5) represents the stochastic per capita net growth differential for the i-th component species. (For example, taking

$$\tilde{f}_i(x) = a_i + \sum_{j=1}^{n} b_{ij} x_j \tag{3.6}$$

with a_i and b_{ij} constants in (3.5) produces a stochastic analogue of the classical Lotka-Volterra model for multispecies population dynamics.) Basic properties of (3.5) are analogous to those of the corresponding deterministic (Kolmogorov) model

$$\frac{dx_i}{dt} = x_i \tilde{f}_i(x); \tag{3.7}$$

in particular, for each $x_0 \in \mathbf{R}_+^n$, the solution $X(t)$ of (3.5) with $X(0) = x_0$ does not hit the boundary of $\mathbf{R}_+^n$ in finite time.

The main result given below involves Lyapunov type functions $V(x)$, and is similar to various well-known theorems for deterministic and stochastic dynamical systems. The general idea behind the use of Lyapunov functions, of course, is to affect a transformation of the system to one or more inequalities with known qualitative properties; the structure of the Lyapunov function indicates what these properties say about the original system. Crucial in application of such results is the construction of appropriate Lyapunov functions for specific models. The assumptions required on the Lyapunov functions $V(x)$ here are as follows:

$$\begin{aligned}&V(x) \geq 0, \text{ and has continuous}\\ &\text{second partial derivatives } \partial^2 V/\partial x_i \partial x_j\\ &\text{for } x \in \mathbf{R}_+^n;\end{aligned} \tag{3.8}$$

$$\begin{gathered}V(x) \text{ is radially unbounded, i.e.,}\\ \operatorname*{limit}_{||x|| \to \infty} V(x) = \infty;\end{gathered} \tag{3.9}$$

and there are positive numbers C and L such that
(3.10)

$$\mathcal{L}\, V(x) = \left[\sum_{i=1}^{n} f_i \frac{\partial V}{\partial x_i} + \frac{1}{2} \sum_{i,j=1}^{n} \left(\sum_{k=1}^{m} g_{ik} g_{jk} \right) \frac{\partial^2 V}{\partial x_i \partial x_j} \right] (x) \leq -C$$

for all $x \in \{x \in \mathbf{R}_+^n : V(x) > L\}$.

THEOREM. *Let U and L be positive numbers with $U > L$, and suppose there exists a function $V(x)$ satisfying* (3.8)–(3.10), *with* (3.4) *holding. Suppose $X(t)$ is a solution of* (3.5) *with $X(0) = x_0$ and $V(x_0) = (L + U)/2$. Let τ be the first exit time of $X(t)$ from the set $Q = \{x \in \mathbf{R}_+^n : L < V(x) < U\}$. Then*

$$P(V(X[\tau]) = U) \leq \frac{1}{2} - C \mathrm{E}\, \tau/(U - L). \tag{3.11}$$

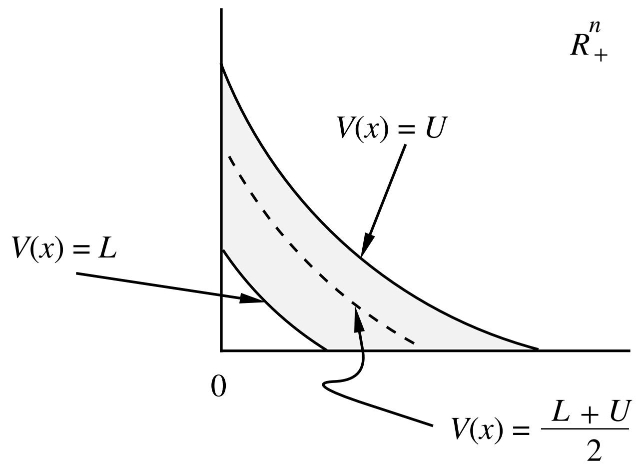

FIGURE. Typical region Q.

Conditions (3.8)–(3.10) suffice to give the existence of a (possibly degenerate) stationary distribution for (3.5) in $\overline{\mathbf{R}}^n_+$ (Has'minskii [9; Theorem 5.1, pp. 90, 91], applied to the invariant set $\mathbf{R}^n_+$). The conclusion (3.11) of this theorem gives more specific information which may be useful for particular x models of interest.

The proof of this theorem is given in the next section. The first part of the proof verifies that the exit time from Q is finite with probability one. Since the boundary of $\mathbf{R}^n_+$ is unattainable from the interior in finite time, exit from Q must be through the lower $\{x \in \mathbf{R}^n_+ : V(x) = L\}$ or upper $\{x \in \mathbf{R}^n_+ : V(x) = U\}$ boundaries. (See figure above.) Continuity of the sample paths of X and of the function V imply that the exit time is positive with probability one. The conclusion of the theorem indicates a tendency to exit through the lower boundary which is enhanced by the mean elapsed time to exit. At least numerical approximations of the mean exit time $\mathrm{E}\,\tau$ can be obtained from its representation (as a function of x_0) as the solution of the Dirichlet problem

$$\begin{aligned} \mathcal{L}\,u &= -1 \quad \text{in} \quad Q \\ u &= 0 \quad \text{on} \quad \partial Q \quad \text{(boundary of } Q) \end{aligned}$$

(See Friedman [5; Chapter 6], for example). Also, Ludwig [13] has pointed out that $\mathrm{E}\,\tau$ can be characterized as the reciprocal of the smallest eigenvalue of a similar Dirichlet problem involving the adjoint operator $\mathcal{L}^*$ of $\mathcal{L}$ and suggested some computational methods especially for the small noise perturbation case.

The example below indicates that (3.11) is "generic" in the sense that this property holds whenever the corresponding deterministic system (3.7) exhibits ultimate uniform boundedness of solutions verifiable by a linear Lyapunov function.

EXAMPLE (Kolmogorov model). Consider (3.5) and suppose there exist positive constants $\alpha_1, \ldots, \alpha_n$, C, and L such that

$$\sum_{i=1}^{n} \alpha_i x_i \tilde{f}_i(x) \leq -C \tag{3.12}$$

for all $x \in \{x \in \mathbf{R}_+^n : \sum \alpha_i x_i > L\}$. The function $V(x) = \sum_{i=1}^n \alpha_i x_i$ satisfies the assumptions of the theorem for any $U > L$, and so (3.11) obtains in this case. Note that the required condition (3.12), which is independent of the (per capita) random noise intensities $\{\tilde{g}_{ij}\}$, suffices to give (3.10) since the second partial derivatives of V occurring in (3.10) multiplying the noise intensities all vanish, i.e.,

$$\mathcal{L}\,V(x) = \sum_{i=1}^{n} f_i(x) \frac{\partial V}{\partial x_i} = \sum_{i=1}^{n} \alpha_i x_i \tilde{f}_i(x).$$

Condition (3.12) guarantees that the corresponding deterministic model (3.7) is dissipative: all solutions tend to the set $\{V(x) \leq L\}$ asymptotically. This condition is satisfied generally by simple food chain and competition models including the classical Lotka-Volterra type models (see Gard [7] and included references, for example).

Initial trends toward persistence may also be ascertained via application of the theorem—upon an appropriate change of variables in the model equations. For example, consider the transformation of the above Kolmogorov model by $Y_i = -\ln X_i$ (and write $X = e^{-Y}$): invoking Ito's formula, (3.5) becomes

$$dY_i = \left[-\tilde{f}_i(e^{-Y}) + \frac{1}{2}\sum_{j=1}^{m} \tilde{g}_{ij}^2(e^{-Y}) \right] dt - \sum_{j=1}^{m} \tilde{g}_{ij}(e^{-Y})\, dW_j. \tag{3.5$'$}$$

Note that Y_i failing to explode beyond a positive level U_i implies persistence of X_i; we apply the theorem with $V = \sum_{i=1}^{n} \beta_i y_i$. The conclusion (3.11) interprets in this case as an initial tendency toward persistence. Similar to the boundedness case above, the required condition is that there exist positive constants $\beta_1, \ldots, \beta_n$, C, and L such that

$$\sum_{i=1}^{n} \beta_i \left[-\tilde{f}_i + \frac{1}{2}\sum_{j=1}^{m} \tilde{g}_{ij}^2 \right] \leq -C \tag{3.13}$$

for all $y \in \{y \in \mathbf{R}_+^n : \sum \beta_i Y_i > L\}$; the hypothesis of the theorem is fulfilled for any $U > L$. Here, unlike the boundedness case, the required condition is dependent on the per capita effective noise intensities $\tilde{g}_{ij}$. However, if the $\tilde{g}_{ij}$ are sufficiently small, (3.13) will hold whenever

$$\sum \beta_i \tilde{f}_i \geq \mu \tag{3.14}$$

for some positive constant μ. It is known (Gard [1987]) that (3.14) implies persistence for the deterministic (Kolmogorov) model (3.7).

The above example illustrates that sufficient conditions for dissipativeness (and persistence) for deterministic models defined by the drift coefficients imply analogous initial tendencies for diffusion models. To conclude the paper, an example is given below which shows that such conditions are not necessary; however, a first exit bias toward boundedness may occur even when the deterministic model given by the drift coefficients is not dissipative.

EXAMPLE (Mutualist pair model). Consider the stochastic system

$$
\begin{aligned}
dX_1 &= X_1 \left[(a - bX_1 + cX_2)\,dt + \sum_{j=1}^{2} \tilde{g}_{ij}(X)\,dW_j \right] \\
dX_2 &= X_2 \left[(d + eX_1 - fX_2)\,dt + \sum_{j=1}^{2} \tilde{g}_{2j}(X)\,dW_j \right],
\end{aligned}
\tag{3.15}
$$

where $a, b, c, d, e,$ and f are positive constants, the functions $\tilde{g}_{ij}$ are continuous, and W_1 and W_2 are independent scalar Wiener processes. Kesten and Ogura [11] have discussed (3.15) (as well as the corresponding prey-predator and competition models) in case the $\tilde{g}_{ij}$ are constant with

$$
\det\{\tilde{g}_{ij}\} \neq 0.
$$

In particular they established that the solution $X = (X_1, X_2)$ was positive recurrent (and consequently a stable invariant distribution exists) if

$$
bf > ec, \tag{3.16}
$$

and X is transient otherwise. It is well known that condition (3.16) is necessary and sufficient for boundedness of solutions of the corresponding deterministic model

$$
\begin{aligned}
\frac{dx_1}{dt} &= x_1(a - bx_1 + cx_2) \\
\frac{dx_2}{dt} &= x_2(d + ex_1 - fx_2).
\end{aligned}
\tag{3.17}
$$

The next proposition indicates that inward first exit bias as characterized by (3.11) may hold for solutions of (3.15) even when (3.16) fails, if the noise intensity is of sufficient strength.

PROPOSITION. *Suppose there are constants $K_1 > 2c$, $K_2 > 2e$, and $K > 0$ such that, for $|x| = |(x_1, x_2)| \geq K$,*

$$
\sum_{j=1}^{2} \tilde{g}_{1j}^2(x_1, x_2) \geq K_1 x_2 \quad \textit{and} \quad \sum_{j=1}^{2} \tilde{g}_{2j}^2(x_1, x_2) \geq K_2 x_1. \tag{3.18}
$$

Then (3.11) *holds for solutions of* (3.15) *if* L *is sufficiently large.*

PROOF. Let $\alpha = 1 - (2c)/K_1$, $\beta = 1 - (2e)/K_2$ and $0 < \lambda < 1$. For the choice

$$\begin{aligned} V(x_1, x_2) &= V_1(x_1) + V_2(x_2) \\ &= \lambda x_1^\alpha + (1-\lambda) x_2^\beta, \end{aligned} \tag{3.19}$$

one obtains

$$\begin{aligned} \mathcal{L}V(x_1, x_2) =& a\alpha\lambda x_1^\alpha + d\beta(1-\lambda)x_2^\beta - (b\alpha\lambda x_1^{\alpha+1} + f\beta(1-\lambda)x_2^{\beta+1}) \\ &+ \alpha\lambda x_1^\alpha \left[cx_1 + \frac{1}{2}(\alpha - 1)\sum_{j=1}^{2} \tilde{g}_{1j}^2 \right] \\ &+ \beta(1-\lambda)x_2^\beta \left[ex_1 + \frac{1}{2}(\beta - 1)\sum_{j=1}^{2} \tilde{g}_{2j}^2 \right]. \end{aligned} \tag{3.20}$$

Now the assumption (3.18), together with the choices of α and β, imply that the last two terms in (3.20) are nonpositive for $|(x_1, x_2)| \geq K$. Also, if $\gamma = \min\{\alpha^{-1}, \beta^{-1}\}$, by convexity,

$$\begin{aligned} \lambda x_1^{\alpha+1} + (1-\lambda)x_2^{\beta+1} &\geq \lambda(x_1^\alpha)^{1+\gamma} + (1-\lambda)(x_2^\beta)^{1+\gamma} \\ &\geq [\lambda x_1^\alpha + (1-\lambda)x_2^\beta]^{1+\gamma}. \end{aligned}$$

Setting $A = \max\{a\alpha, d\beta\}$ and $B = \min\{b\alpha, f\beta\}$, one has, then, from (3.20),

$$\mathcal{L}V \leq AV - BV^{1+\gamma}, \quad \text{for} \quad |(x_1, x_2)| \geq K. \tag{3.21}$$

So

$$\begin{aligned} &\mathcal{L}V(x_1, x_2) \leq -C \\ &\text{if} \quad V(x_1, x_2) > L = \max\left\{ \left(\frac{A+1}{B}\right)^{1/\gamma}, C \right\}, \end{aligned} \tag{3.22}$$

verifying (3.10), and so the Proposition follows from the Theorem. □

Note from (3.22) that the decay rate C for the probability of exit through the upper boundary increases as $L \to \infty$; the bias toward exit through the lower boundary strengthens as $|X|$ increases, for solutions with the same exit time. As a final remark, it may be observed that the deterministic part of the Stratonovich version of (3.15) is

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(a - bx_1 + (c - K_1/2)x_2) \\ \frac{dx_2}{dt} &= x_2(d + (e - K_2/2)x_1 - fx_2) \end{aligned} \tag{3.23}$$

for the (simplest) special case

$$\tilde{g}_{11} = \sqrt{K_1 x_2}, \quad \tilde{g}_{22} = \sqrt{K_2 x_1}, \quad \tilde{g}_{12} = \tilde{g}_{21} = 0.$$

The interesting point here is that the conditions on the K_i in the Proposition precisely make (3.23) a *competition* (rather than mutualist) model. As such, (3.23) is dissipative, even if (3.16) fails. This suggests sharper results may be obtainable by considering Stratonovich-interpreted stochastic models.

4. Proof of the Theorem. First consider the exit time τ itself. As mentioned earlier, continuity of the function V and the sample paths of X imply that

$$P(\tau > 0) = 1. \tag{4.1}$$

It is useful to establish

$$P(\tau < \infty) = 1 \tag{4.2}$$

as well. Toward obtaining (4.2), one can apply a special case of Dynkin's formula (see Has'minskii [9; p. 82], for example) to get

$$\mathrm{E}\, V(\mathrm{X}\,[\tau(t)]) - \mathrm{E}\, v(X(0)) = \mathrm{E} \int_0^{\tau(t)} \mathcal{L}\, V(X(s))\, ds, \tag{4.3}$$

where $\tau(t) = \min\{\tau, t\}$. Until time $\tau \geq \tau(t)$, X remains in Q, so

$$\mathrm{E}\, V(X[\tau(t)]) \geq L, \tag{4.4}$$

and, from (3.10),

$$\mathcal{L}\, v(X(s)) \leq -C. \tag{4.5}$$

Therefore, applying (4.4) and (4.5) to (4.3) and recalling that $V(X(0)) = (L+U)/2$, gives the estimate

$$L - \frac{L+U}{2} \leq -C\mathrm{E}\,\tau(t). \tag{4.6}$$

Letting $t \to \infty$ in (4.6) obtains a contradiction unless (4.2) holds. More precisely, (4.6) yields

$$\mathrm{E}\,\tau \leq (U-L)/2C. \tag{4.7}$$

Now the proof of this theorem verifies an estimate for the probability

$$p = P(V(X[\tau]) = U).$$

Since exit from Q occurs in finite time w.p.l and since the boundary of $\mathbf{R}^n_+$ is unattainable by $X(t)$ in finite time, exit must be effected through the lower or upper boundaries of Q. Thus

$$\mathrm{E}\,V(X[\tau]) = L(1-p) + Up. \tag{4.8}$$

Letting $t \to \infty$ in (4.3), noting that $V(X(0)) = (L+U)/2$ and using (4.5), obtains

$$\begin{aligned} \mathrm{E}\,V(X[\tau]) &= (L+U)/2 + \mathrm{E}\int_0^\tau \mathcal{L}\,V(X(s))\,ds \\ &\leq (L+U)/2 - C\mathrm{E}\,\tau. \end{aligned} \tag{4.9}$$

From (4.8) and (4.9) it follows that

$$L(1-p) + Up \leq (L+U)/2 - C\mathrm{E}\,\tau \tag{4.10}$$

or

$$p \leq \frac{1}{2} - C\mathrm{E}\,\tau/(U-L) \tag{4.11}$$

which completes the proof. □

As a final remark, it is noted that (4.11) indicates that $p < 1/2$ since $\mathrm{E}\,\tau > 0$, and, whenever $\mathrm{E}\,\tau$ achieves its maximum value (4.7), $p = 0$.

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