The Annals of Applied Probability
2001, Vol. 11, No. 3, 952–963

LONG TERM BEHAVIOR OF SOLUTIONS OF THE LOTKA–VOLTERRA SYSTEM UNDER SMALL RANDOM PERTURBATIONS

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A stochastic analogue of the Lotka–Volterra model for predator–prey relationship is obtained when the birth rate of the prey and the death rate of the predator are perturbed by independent white noises with intensities of order ε^2, where $\varepsilon > 0$ is a small parameter. The evolution of this system is studied on large time intervals of $O(1/\varepsilon^2)$. It is shown that for small initial population sizes the stochastic model is adequate, whereas for large initial population sizes it is not as suitable, because it leads to ever-increasing fluctuations in population sizes, although it still precludes extinction. New results for the classical deterministic Lotka–Volterra model are obtained by a probabilistic method; we show in particular that large population sizes of predator and prey coexist only for a very short time, and most of the time one of the populations is exponentially small.

1. Introduction. The Lotka–Volterra system of ordinary differential equations, proposed originally by Lotka (1925) and Volterra (1926) is one of the simplest models of interacting populations. It describes the behavior of a predator–prey system by the following dynamics:

$$\dot{x} = \frac{dx}{dt} = x(a - by), \quad \dot{y} = \frac{dy}{dt} = y(-c + fx) \quad (x_0, y_0, a, b, c, f > 0), \tag{1.1}$$

where $x = x(t)$ the density of prey and $y = y(t)$ that of the predator and the coefficients a, b, c and f are positive constants. This model reflects the assumption that the growth rate of the prey population, in absence of predators, is $a > 0$, but decreases linearly with presence of predators, and in the absence of prey, the predators die at a constant rate $c > 0$, but increase linearly with with the density of prey [see, e.g., May (1976)]. The system starts at some point of the positive quadrant $(x(0), y(0))$.

It is well known (and easy to check) that the trajectories of the system (1.1) in the phase space x, y are closed curves described by the first integral,

$$\begin{aligned} r(x, y) &= fx - c - c\ln\bigl(1 + (fx - c)/c\bigr) + by - a - a\ln\bigl(1 + (by - a)/a\bigr) \\ &= \text{constant} = r, \end{aligned} \tag{1.2}$$

that is, for any $t \geq 0$, $r(x(t), y(t)) = r(x(0), y(0))$. We have chosen to write the first integral in such a form that for all x, y, $r(x, y) \geq 0$; moreover, $r(x, y) = 0$ if and only if $x^* = c/f$ and $y^* = a/b$.

Received May 1999; revised October 2000.
[1]Supported in part by NSF Grant DMS 99-71608 and the Australian Research Council.
[2]Supported in part by the Australian Research Council.
AMS 2000 *subject classifications*. 2000 MSC, 34F05, 34E10, 60H10, 92D25.
Key words and phrases. Stochastic differential equations, predator–prey coexistence.

It is also known that solutions are periodic; we denote the period corresponding to the value r of the first integral by $T = T(x(0), y(0)) = T(r)$.

System (1.1) has two fixed points, $(0, 0)$ and $(x^*, y^*) = (c/f, a/b)$, with the latter being the only equilibrium state in the positive quadrant.

Random perturbations to the Lotka–Volterra model were considered in the literature; see, for example Goel, Maitra and Montroll (1971) and Arnold, Horsthemke and Stucki (1979). It was shown in Arnold, Horsthemke and Stucki (1979) in particular, that when the coefficient a is randomly perturbed by white Gaussian noise in the Itô sense then the resulting system cannot have a stationary distribution; see also our remark in Section 2. Here we consider a more natural type of random perturbations (in the sense of Stratonovich) of both coefficients a and c. Arguments of Arnold, Horsthemke and Stucki (1979) do not work in this situation. However, under natural assumption of smallness of perturbations we obtain results by the stochastic method of averaging.

The paper is organized as follows. In Section 2 we introduce a stochastic Lotka–Volterra system, obtained by small random perturbations of the deterministic model, and give a limit theorem. The diffusion occurring as a limit involves unknown quantities of the deterministic system, which are found in Section 3. Analysis carried out in that section shows that the Lotka–Volterra model is a good model for small initial population sizes, but not for the large ones, since a noisy system leads to ever-increasing fluctuations in population sizes, which is not what is observed in nature. The stochastic model, however, precludes extinction, which may seem surprising at first look, as the population sizes become exponentially small. In Section 4 we give a new result on the coexistence of predator and prey as well as bounds on the population sizes for the deterministic Lotka–Volterra system, which is obtained by a probabilistic method.

2. Stochastic Lotka–Volterra system. We consider small random perturbations in the birth rate of the prey a and the death rate of the predator c by independent Gaussian white noises with intensities $\varepsilon^2\sigma_1^2$ and $\varepsilon^2\sigma_2^2$, where $\varepsilon > 0$ is a small parameter. Then from (1.1) we have

$$\begin{aligned} \dot{X}^\varepsilon &= X^\varepsilon(a + \varepsilon\sigma_1\dot{W}_1 - bY^\varepsilon), \\ \dot{Y}^\varepsilon &= Y^\varepsilon(-c + \varepsilon\sigma_2\dot{W}_2 + fX^\varepsilon) \quad (x_0, y_0, a, b, c, f > 0). \end{aligned} \tag{2.1}$$

In applications, Gaussian white noise is usually used as an approximation to a real noise with a short correlation interval (short memory). It is well known [see, e.g., Hasminskii (1980), paragraph 5 of Chapter 5] that when the limit is taken when the correlation function tends to Dirac's δ-function, a system of stochastic differential equations (SDE) in the Stratonovich form results:

$$\begin{aligned} dX^\varepsilon(t) &= X^\varepsilon(t)\big(a - bY^\varepsilon(t)\big)\,dt + \varepsilon\sigma_1 X^\varepsilon(t) \circ dW_1(t), \\ dY^\varepsilon(t) &= Y^\varepsilon(t)\big(-c + fX^\varepsilon(t)\big)\,dt + \varepsilon\sigma_2 Y^\varepsilon(t) \circ dW_2(t), \end{aligned}$$

where $W_i(t)$ are independent standard Brownian motions.

REMARK. Note here that if the noise in (2.1) is treated in the Itô sense, then it is easy to see by Itô's formula that

$$dR^\varepsilon(t) = dr\big(X^\varepsilon(t), Y^\varepsilon(t)\big) = \varepsilon\sigma_1\big(fX^\varepsilon(t) - c\big)\,dW_1(t) \\ + \varepsilon\sigma_2\big(bY^\varepsilon(t) - a\big)\,dW_2(t) + 1/2\varepsilon^2\big(c\sigma_1^2 + a\sigma_2^2\big)\,dt.$$

Therefore,

$$Er\big(X^\varepsilon(t), Y^\varepsilon(t)\big) = Er(x_0, y_0) + 1/2\varepsilon^2\big(c\sigma_1^2 + a\sigma_2^2\big)t,$$

so that the expectation grows linearly and there is no stationary distribution for the system [analogous arguments were used in Arnold, Horsthemke and Stucki (1979)]. Here we consider a more natural type of random perturbations in the sense of Stratonovich of both coefficients a and c. Arguments of Arnold, Horsthemke and Stucki do not work in this situation, however, under the assumption that perturbations are small we can use the averaging to obtain a result. It turns out that the resulting limiting diffusion is the same for both Itô and Stratonovich types of noise [see Theorem 1 and (3.3)].

It follows from the properties of the Stratonovich integral [see, e.g., Protter (1992) or Klebaner (1998)] that (2) is equivalent to the following system of Itô stochastic equations:

$$dX^\varepsilon(t) = X^\varepsilon(t)\big(a + \varepsilon^2\sigma_1^2/2 - bY^\varepsilon(t)\big)\,dt + \varepsilon\sigma_1 X^\varepsilon(t)\,dW_1(t),$$
$$dY^\varepsilon(t) = Y^\varepsilon(t)\big(-c + \varepsilon^2\sigma_2^2/2 + fX^\varepsilon(t)\big)\,dt + \varepsilon\sigma_2 Y^\varepsilon(t)\,dW_2(t).$$

The process $R^\varepsilon(t) = r(X^\varepsilon(t), Y^\varepsilon(t))$ is a slowly changing component for (2), and Itô's formula gives

$$dR^\varepsilon(t) = \frac{\varepsilon^2}{2}\Big(f\sigma_1^2 X^\varepsilon(t) + b\sigma_2^2 Y^\varepsilon(t)\Big)\,dt \\ + \varepsilon\Big(\sigma_1\big(fX^\varepsilon(t) - c\big)\,dW_1(t) + \sigma_2\big(bY^\varepsilon(t) - a\big)\,dW_2(t)\Big), \tag{2.2}$$

So we can consider the system (2) as a system with two time scales: a slow coordinate $R^\varepsilon(t)$, and a fast coordinate [for which we can take, for instance, one of the equations in (2)]. For SDEs with two time scales a result of Khasminskii (1968) can be applied. According to this result, the evolution of the slow coordinate $R^\varepsilon(t)$ on time intervals of $O(1/\varepsilon^2)$ can be approximated by a diffusion with coefficients given by the averages along the trajectories of the corresponding deterministic process. More precisely we have the following theorem.

THEOREM 1. *Let $T_0 > 0$ be fixed, and let the process $(X^\varepsilon, Y^\varepsilon)$ start from (x_0, y_0). Then on the interval $0 \le t < T_0$, the process $R^\varepsilon(t/\varepsilon^2)$ converges weakly as $\varepsilon \to 0$ to the diffusion process $R(t)$ which solves the following stochastic differential equation*:

$$dR(t) = \mu\big(R(t)\big)\,dt + \sigma\big(R(t)\big)\,dW(t), \tag{2.3}$$

where W is a standard Brownian motion; for a solution of the deterministic system (1.1) *$x(t)$, $y(t)$ starting at $(x(0), y(0))$, r denotes the value of its first integral in* (1.2) *$r(x(0), y(0)) = r$, $T = T(r)$ is its period, and for a function ϕ, $\overline{\phi(x, y)}(r)$ denotes the average*

$$\overline{\phi(x, y)}(r) = \frac{1}{T}\int_0^T \phi\big(x(t), y(t)\big)\, dt,$$
$$\mu(r) = \frac{1}{2}\Big(f\sigma_1^2 \bar{x}(r) + b\sigma_2^2 \bar{y}(r)\Big) \tag{2.4}$$

and

$$\sigma^2(r) = \sigma_1^2\overline{(fx - c)^2}(r) + \sigma_2^2\overline{(by - a)^2}(r). \tag{2.5}$$

Thus the description of the approximating diffusion R has reduced to the purely deterministic problem of finding first and second power averages of the deterministic solution, namely the quantities in the coefficients (2.4) and (2.5).

3. Behavior of averages of the deterministic Lotka–Volterra system and the limiting diffusion. In what follows, $T = T(r)$ denotes the period of a periodic solution $x(t)$, $y(t)$ corresponding to the value r of the first integral.

By separating variables and integration it is easy to see from (1.1) that

$$\ln\big(x(T)\big) - \ln\big(x(0)\big) = \int_0^T \big(a - by(t)\big)\, dt. \tag{3.1}$$

Since $x(t)$ is periodic, it follows that

$$\bar{y} = a/b. \tag{3.2}$$

Similarly $\bar{x} = c/f$.

Therefore from (2.4) we obtain that the drift coefficient

$$\mu(r) = \tfrac{1}{2}(c\sigma_1^2 + a\sigma_2^2) \tag{3.3}$$

is a constant independent of r.

The expression for the average of the squares of solutions is more complicated, and it seems that it is not available in the closed form. However, to determine the long term properties, such as recurrence or transient property of the limiting diffusion (2.3) we need only the behavior at zero and infinity of $\sigma(r)$, which is done next.

It is convenient to introduce $\xi = fx - c$ and $\eta = by - a$, since the diffusion coefficient $\sigma^2(r)$ involves only $\overline{\xi^2}$ and $\overline{\eta^2}$.

In the new coordinates, the system (1.1) becomes

$$\frac{d\xi}{dt} = -\eta(\xi + c), \qquad \frac{d\eta}{dt} = \xi(\eta + a), \tag{3.4}$$

and from (1.2) its first integral is given by

$$r(\xi, \eta) = \xi - c\,\ln(1 + \xi/c) + \eta - a\,\ln(1 + \eta/a) = r = \text{ const.} \tag{3.5}$$

Note that $r(\xi, \eta) \geq 0$ for all $\xi \geq -c$, $\eta \geq -a$, and it achieves its minimum 0 at $(0, 0)$.

It is immediate from (3.2) that

$$\bar{\xi} = 0 \quad \text{and} \quad \bar{\eta} = 0. \tag{3.6}$$

Integrating (3.4) directly, and taking into account $\bar{\xi} = 0$ and $\bar{\eta} = 0$, we obtain that

$$\overline{\xi\eta} = 0. \tag{3.7}$$

Multiply now the first equation in (3.4) by ξ to obtain that

$$\tfrac{1}{2} d\xi^2 = -\eta\xi^2 - c\eta\xi.$$

Integrating from 0 to T, it follows that

$$\overline{\xi^2\eta} = 0. \tag{3.8}$$

Similarly, multiplying the second equation in (3.4) by η and integrating from 0 to T we obtain that

$$\overline{\xi\eta^2} = 0. \tag{3.9}$$

Multiply now the equations in (3.4) by η and ξ respectively to obtain that

$$d(\xi\eta) = -\eta^2\xi - c\eta^2 + \xi^2\eta + a\xi^2,$$

from which it follows that

$$c\overline{\eta^2} = a\overline{\xi^2} := g^2(r), \tag{3.10}$$

where the last equality is the definition of the function $g^2(r)$. In what follows, solutions to (3.4) corresponding to the value r of the first integral $r(\xi, \eta)$ in (3.5) as well as related quantities will be indexed by r, for example $\xi(t, r)$ and $\overline{\xi^2}(r)$, although sometimes it will not be stated explicitly, for example, when we write $\xi(t)$ instead of $\xi(t, r)$.

We analyze the behavior of $g^2(r)$ and hence that of $\sigma^2(r)$ for $r \to 0$ in the next section and then consider the case $r \to \infty$.

3.1. *Behavior of the system for $r \to 0$.*

THEOREM 2. *The generator L of the limiting diffusion R on $[0, \infty)$ has the form for $r \to 0$,*

$$L = \frac{1}{2}\left(c\sigma_1^2 + a\sigma_2^2\right)\left(\frac{d}{dr} + r\left(1 + o(1)\right)\frac{d^2}{dr^2}\right). \tag{3.11}$$

The left boundary point 0 is unattainable and is an entrance boundary. Therefore it cannot be reached from any positive state r; moreover, $P(R(t) \to 0$ as $t \to \infty) = 0$.

It follows from the result that the noisy system can never reach the deterministic equilibrium (x^*, y^*) (which corresponds to $r = 0$) but it can be started there, in which case it will quickly leave equilibrium never to return.

PROOF. Once we show that L has the form (3.11), it is easy to check that the left boundary point 0 is unattainable and is an entrance boundary using Feller's conditions for classification of boundaries [see, e.g., Karlin and Taylor (1981)]. The form of L (3.11) follows from the next result by (3.3) and (3.14). □

THEOREM 3. *As $r \to 0$, the following hold*:

$$\overline{\xi^2}(r) = cr + o(r), \qquad \overline{\eta^2}(r) = ar + o(r), \tag{3.12}$$

$$g^2(r) = acr + o(r), \tag{3.13}$$

$$\sigma^2(r) = \bigl(\sigma_1^2 c + \sigma_2^2 a\bigr) r + o(r). \tag{3.14}$$

PROOF. Let $\xi(t), \eta(t)$ be a solution with the value of the first integral equal to r; then it follows from (3.5) and the elementary inequality $x - a\ln(1 + x/a) \geq 0$ for all $x \geq -a$ that for all $t \geq 0$,

$$0 \leq \xi(t) - c\ln\bigl(1 + \xi(t)/c\bigr) \leq r \quad \text{and} \quad 0 \leq \eta(t) - a\ln\bigl(1 + \eta(t)/a\bigr) \leq r. \tag{3.15}$$

It follows from (3.15) that when r is small, ξ and η also must be small, and that

$$|\xi| < \sqrt{2cr} + o(\sqrt{r}), \qquad |\eta| < \sqrt{2ar} + o(\sqrt{r}), \tag{3.16}$$

and we have from (3.5)

$$\frac{\xi^2}{2c} + \frac{\eta^2}{2a} = r + o(r), \qquad r \to 0. \tag{3.17}$$

Equation (3.17) shows that for small r the trajectories of the system (3.4) are approximately ellipses. This conclusion is known [see, e.g., Goel, Maitra and Montroll (1971)]. Averaging (3.17) we obtain

$$\frac{\overline{\xi^2}}{2c} + \frac{\overline{\eta^2}}{2a} = r + o(r), \qquad r \to 0, \tag{3.18}$$

and taking into account (3.10), we have (3.12), and consequently by (3.10) we have (3.13). (3.14) now follows from (2.5). □

3.2. *Behavior of the system for $r \to \infty$.*

THEOREM 4. *The generator L, the limiting diffusion $R(t)$, has the following form for $r \to \infty$*:

$$L = \frac{1}{2}(c\sigma_1^2 + a\sigma_2^2)\left(\frac{d}{dr} + \frac{r}{2}\bigl(1 + o(1)\bigr)\frac{d^2}{dr^2}\right). \tag{3.19}$$

Therefore the limiting diffusion $R(t)$ is transient; moreover, it converges to $+\infty$ almost surely, $P(R(t)\to\infty \text{ as } t\to\infty)=1$.

For the proof, once the form (3.19) is established, the result follows by Feller's test for recurrence [see, e.g., Gihman and Skorohod (1972), Klebaner (1998)]. Equation (3.19) follows from the next result by (3.3) and (2.5).

REMARK. It is known that the period $T(r)$ is an increasing function of r [see Waldvogel (1985) or Rothe (1985)]. Transient property implies that the trajectories of the stochastic system will expand to higher and higher values of the first integral r and the periods grow with time. Since it is not observed in nature, the Lotka–Volterra model is not good enough for the large size of initial populations [more precisely, when $fx(0)+c\ln(1/x(0))+by(0)+a\ln(1/y(0)\gg 1)$ if random perturbations of coefficients take place.

The next theorem is the main result of this section.

THEOREM 5. *The function $g^2(r)=a\overline{\xi^2}(r)=c\overline{\eta^2}(r)$ has the following asymptotics for $r\to\infty$:*

$$g^2(r)=\frac{ac}{2}r+O(r^{2/3}\ln^2 r). \tag{3.20}$$

The proof of this theorem relies on auxiliary propositions.

LEMMA 1.

$$\overline{\xi^2}=c\overline{\xi\ln(1+\xi/c)},\qquad \overline{\eta^2}=a\overline{\eta\ln(1+\eta/a)}. \tag{3.21}$$

PROOF. Multiplying (3.5) by ξ and averaging on the trajectory, we have

$$\overline{\xi^2}-c\overline{\xi\ln(1+\xi/c)}+\overline{\xi\eta}-a\overline{\xi\ln(1+\eta/a)}=\overline{r\xi}.$$

Since $\overline{\xi\eta}=r\bar\xi=0$, it is enough to prove that

$$\overline{\xi\ln(1+\eta/a)}=0. \tag{3.22}$$

We can write from the second equation of (3.4),

$$\int_0^t\xi(s)\,ds=-\int_0^t\frac{d\eta(s)}{\eta(s)+a}=\ln\bigl(1+\eta(0)/a\bigr)-\ln\bigl(1+\eta(t)/a\bigr).$$

Now, multiplying by $\xi(t)$ and integrating we have

$$\int_0^T\xi(t)\int_0^t\xi(s)\,ds\,dt=\ln\bigl(1+\eta(0)/a\bigr)\int_0^T\xi(t)\,dt-\int_0^T\xi(t)\ln\bigl(1+\eta(t)/a\bigr)\,dt.$$

However,

$$\int_0^T\xi(t)\int_0^t\xi(s)\,ds\,dt=\tfrac12\biggl(\int_0^T\xi(t)\,dt\biggr)^2=0,$$

and the lemma follows. □

The next lemma establishes two useful inequalities.

LEMMA 2. *Suppose that*

$$x - \ln(1+x) \le r. \tag{3.23}$$

Then for any $r > 3$,

$$-1 + e^{-1}e^{-r} < x \le r + 2\ln r. \tag{3.24}$$

Moreover, *for* $r > 7$,

$$0 < x\ln(1+x) < 2r\ln r. \tag{3.25}$$

PROOF. Denote by $h_1(x) = x - \ln(x+1)$ defined for $x > -1$. Then h_1 is strictly increasing for $x \ge 0$ and is strictly decreasing for $-1 < x \le 0$. It is easy to check that $h_1(r+2\ln r) > r$ for any $r > 3$. This gives the upper bound on x. Verifying that $h_1(-1+e^{-1}e^{-r}) > r$ for all r, gives the lower bound on x in (3.24). The function $h_2(x) = x\ln(1+x)$ is increasing for $x > 0$, and for $r > 7$ the following is true:

$$(r+2\ln r)\ln(1+r+2\ln r) < 2r\ln r, \tag{3.26}$$

Therefore it follows from the upper bound in (3.24) that if $x > 0$, then

$$0 < x\ln(1+x) < 2r\ln r. \tag{3.27}$$

The function $h_2(x)$ is decreasing on $-1 < x \le 0$, and it follows from the lower bound in (3.24) that if $x < 0$, then

$$0 < x\ln(1+x) < r + 1 < 2r\ln r. \tag{3.28}$$

□

COROLLARY 1. *There is a constant C such that for any $r > C$ solutions of* (3.4) *corresponding to the value r of the first integral satisfy*

$$-c + e^{-1}e^{-r/c} < \xi(t) \le r + 2\ln r, \ -a + e^{-1}e^{-r/a} < \eta(t) \le r + 2\ln r. \tag{3.29}$$

Moreover,

$$\begin{aligned} &0 < \xi(t)\ln\bigl(1+\xi(t)/c\bigr) < (2/c)r\ln r,\\ &0 < \eta(t)\ln\bigl(1+\eta(t)/a\bigr) < (2/a)r\ln r. \end{aligned} \tag{3.30}$$

PROOF. Recall that if $\xi(t), \eta(t)$ is such a solution, then for all $t \ge 0$ it satisfies (3.15),

$$\begin{aligned} &0 \le \xi(t) - c\ln\bigl(1+\xi(t)/c\bigr) \le r \quad \text{and}\\ &0 \le \eta(t) - a\ln\bigl(1+\eta(t)/a\bigr) \le r. \end{aligned} \tag{3.31}$$

The result now follows from the previous lemma by replacing $\xi(t)/c$ by x. □

LEMMA 3. *There is a constant C such that for any $r > C$ solutions of* (3.4) *corresponding to the value r of the first integral satisfy*

$$\overline{\xi^2}(r) \leq (2c) r \ln r, \qquad \overline{\eta^2}(r) \leq (2a) r \ln r. \tag{3.32}$$

PROOF. By Lemma 1, $\overline{\xi^2}(r) = c\overline{\xi \ln(1+\xi/c)}(r)$. The statement follows from inequality (3.30). □

Consider now the function

$$\gamma(t, r) = -c \ln\bigl(1 + \xi(t)/c\bigr) - a \ln\bigl(1 + \eta(t)/a\bigr), \tag{3.33}$$

where dependence on r is understood in the following way: $\xi(t)$, and $\eta(t)$ correspond to the value of r of the first integral (3.5).

We can see from (3.5) that

$$\gamma(t, r) = r - \xi(t) - \eta(t), \tag{3.34}$$

and taking averages,

$$\overline{\gamma(t, r)} = r. \tag{3.35}$$

For fixed r consider a probability measure on $[0, T(r)]$ defined by $P^r(dt) = dt/T(r)$. Then the solution of (3.4) with the value r in (3.5) and any measurable function of it are the random variables on this space.

It is clear that the expectation with respect to P^r is given by

$$E^r(\phi) = \bar{\phi},$$

and the variance

$$\mathrm{Var}^r(\phi) = \overline{(\phi - \bar{\phi})^2}.$$

The functions ξ, η have zero mean by (3.6), and Lemma 3 yields the following corollary.

COROLLARY 2. *There is a constant C such that for all r large enough*,

$$\mathrm{Var}^r\bigl(\xi(r)\bigr) \leq C r \ln r, \qquad \mathrm{Var}^r\bigl(\eta(r)\bigr) \leq C r \ln r. \tag{3.36}$$

The following lemma is Chebyshev's inequality coupled with the bound (3.36).

LEMMA 4. *For any $\varepsilon > 0$ there is a constant C, such that*

$$P^r(|\xi| > r^{1/2+\varepsilon}) \leq C r^{-2\varepsilon} \ln r. \tag{3.37}$$

Of course, a similar inequality holds for η.

We now prove the main Theorem 5.

PROOF OF THEOREM 5. Due to (3.10) and Lemma 1,

$$
\begin{aligned}
g^2(r) &= \frac{1}{2}\big(a\overline{\xi^2(r)} + c\overline{\eta^2(r)}\big) \\
&= \frac{ac}{2}\big(\overline{\xi \ln(1+\xi/c) + \eta \ln(1+\eta/a)}\big) \\
&= -\frac{ac}{2}\Big(c\ \overline{\ln(1+\xi/c) + a\ \ln(1+\eta/a)}\Big) \\
&\quad + \frac{ac}{2}\Big(\overline{(\xi+c)\ln(1+\xi/c) + (\eta+a)\ln(1+\eta/a)}\Big) \\
&= \frac{ac}{2}\bar{\gamma}(r) + \frac{ac}{2}\Big(\overline{(\xi+c)\ln(1+\xi/c) + (\eta+a)\ln(1+\eta/a)}\Big) \\
&= \frac{ac}{2}r + \frac{ac^2}{2}I_1 + \frac{a^2c}{2}I_2,
\end{aligned}
\tag{3.38}
$$

where $I_1 = \overline{(1+\xi/c)\ln(1+\xi/c)}$ and $I_2 = \overline{(1+\eta/a)\ln(1+\eta/a)}$.

To bound I_1 we write

$$
\begin{aligned}
|I_1| \le \frac{1}{T}\bigg(&\int_A \big|\big(1+\xi(t)/c\big)\ln\big(1+\xi(t)/c\big)\big|\,dt \\
&+ \int_{A^c} \big|\big(1+\xi(t)/c\big)\ln\big(1+\xi(t)/c\big)\big|\,dt\bigg),
\end{aligned}
\tag{3.39}
$$

with

$$
A = \{t\colon |\xi(t)| > r^{1/2+\varepsilon}\},
$$

and A^c its complement.

The first integral is bounded by using the global bound in (3.30) and Chebyshev's inequality above:

$$
\frac{1}{T}\int_A \big|\big(1+\xi(t)/c\big)\ln\big(1+\xi(t)/c\big)\big|\,dt \le Cr^{1-2\varepsilon}\ln^2 r. \tag{3.40}
$$

To bound the second integral in (3.39) notice that the function $(x+1)\ln(x+1)$ is bounded on $-1 \le x \le 0$, and monotone increasing for $x > 0$. This allows replacing $\xi(t)$ by its upper bound on A^c, which is $r^{1/2+\varepsilon}$, to obtain the bound

$$
\frac{1}{T}\int_{A^c} \big|\big(1+\xi(t)/c\big)\ln\big(1+\xi(t)/c\big)\big|dt \le Cr^{1/2+\varepsilon}\ln r. \tag{3.41}
$$

The bound for I_2 is similar. Choosing $\varepsilon = 1/6$ completes the proof. □

4. The most visited region of the deterministic system. Note that $P^r(\phi(t) \in A)$ gives the proportion of time a function $\phi(t)$ on $[0, T(r)]$ spends in a set A,

$$
P^r\big(\phi(t) \in A\big) = \frac{1}{T(r)}\int_{\{t:\phi(t)\in A\}} dt. \tag{4.1}
$$

THEOREM 6. *There exists a constant $C > 0$, such that for large values of r and any $\varepsilon > 0$ solutions of* (1.1) *satisfy*

$$P^r\Big(x(t) < e^{-r/(2c)+r^{\varepsilon+1/2}/(2c)} \text{ or } y(t) < e^{-r/(2a)+r^{\varepsilon+1/2}/(2a)}\Big) > 1 - Cr^{-2\varepsilon}. \tag{4.2}$$

The result states that a vast majority of time one of the populations is very small. Note that in view of the inequality (3.29) the populations never get closer than exponentially close to zero: for all $t \geq 0$,

$$x(t) > (1/ef)e^{-r/c}, \qquad y(t) > (1/eb)e^{-r/a}. \tag{4.3}$$

PROOF. By squaring (3.34) we have $\mathrm{Var}^r(\gamma(r)) = \overline{\xi^2}(r) + \overline{\eta^2}(r)$, which by Theorem 5 is asymptotically $(a + c)/2r$. Therefore,

$$\mathrm{Var}^r\big(\gamma(r)\big) \leq Cr. \tag{4.4}$$

Apply now Chebyshev's inequality to γ and take into account $\overline{\gamma}(r) = r$ to obtain

$$P^r\big(|\gamma(t, r) - r| > r^{\varepsilon+1/2}\big) \leq r^{-1-2\varepsilon}\,\mathrm{Var}^r\big(\gamma(r)\big) \leq Cr^{-2\varepsilon}. \tag{4.5}$$

Therefore,

$$P^r\big(|\gamma(t, r) - r| < r^{\varepsilon+1/2}\big) > 1 - Cr^{-2\varepsilon}. \tag{4.6}$$

It is easy to see from the definition of γ (3.33) that the event $\{|\gamma(t, r) - r| < r^{\varepsilon+1/2}\}$ can happen only if the variables are near the coordinates

$$x(t) < (c/f)e^{-r/(2c)+r^{\varepsilon+1/2}/(2c)}$$

or

$$y(t) < (a/b)e^{-r/(2a)+r^{\varepsilon+1/2}/(2a)}. \tag{4.7}$$

□

REMARK. Our result should be compared to that of Rothe (1985) who gives the asymptotics of the times the system spends above and below the equilibrium: if (in his notations) T_{++} is the time when both x and y are above x^*, y^*, and T_{+-}, T_{--} are defined similarly, then as $r \to \infty$ $T_{++} = O(\ln r/r)$, $T_{+-} = O(\ln r)$, and $T_{--} = O(r)$.

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