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Recommended Citation

de Oca, F. Montes and Zeeman, M. L., "Balancing Survival and Extinction in Nonautonomous Competitive Lotka-Volterra Systems" (1995). *Mathematics Faculty Publications*. 79.
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JOURNAL OF MATHEMATICAL ANALYSIS AND APPLICATIONS **192**, 360–370 (1995)

Balancing Survival and Extinction in Nonautonomous Competitive Lotka–Volterra Systems

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Received February 22, 1994; revised May 5, 1994

We generalise and unify some recent results about extinction in nth-order nonautonomous competitive Lotka–Volterra systems. For each $r \leq n$, we show that if the coefficients are continuous, bounded by strictly positive constants, and satisfy certain inequalities, then any solution with strictly positive initial values has the property that $n - r$ of its components vanish, whilst the remaining r components asymptotically approach a canonical solution of an r-dimensional restricted system. In other words, r of the species being modeled survive whilst the remaining $n - r$ are driven to extinction. © 1995 Academic Press, Inc.

1. INTRODUCTION

This paper generalises and unifies some recent results of Ahmad and Lazer [1–3], Tineo [6], and these authors [5, 7] about classical Lotka–Volterra systems.

Consider a community of n mutually competing species modeled by the nonautonomous Lotka–Volterra system

$$\dot{x}_i(t) = x_i(t)\Big(b_i(t) - \sum_{j=1}^{n} a_{ij}(t)x_j(t)\Big), \qquad i = 1, \ldots, n, \tag{1}$$

0022-247X/95 $6.00
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where $x_i(t)$ is the population size of the ith species at time t, $\dot{x}_i$ denotes dx_i/dt, and for all i and j the functions $a_{ij}(t)$ and $b_i(t)$ are continuous on R and bounded above and below by strictly positive reals.

Each k-dimensional coordinate subspace of R^n is invariant under system (1) ($k \in \{1 \cdots n\}$), and we adopt the tradition of restricting attention to the closed positive cone R^n_+. We denote the open positive cone by $\mathring{R}^n_+$, and call a vector x *positive* if $x \in R^n_+$, *strictly* positive if $x \in \mathring{R}^n_+$.

The restriction of system (1) to the ith coordinate axis is the nonautonomous logistic equation

$$\dot{x}_i(t) = x_i(t)(b_i(t) - a_{ii}(t)x_i). \tag{2}$$

Let $x_i^*(t)$ denote the unique bounded solution of Eq. (2) on the strictly positive x_i-axis. Then x_i^* is bounded below by a strictly positive constant and all other solutions of (2) with strictly positive initial condition converge to x_i^*. See Ahmad [1] and Coleman [4].

Given a function g defined on R, denote the infimum and supremum of g on R by

$$g^l = \inf_t g(t), \qquad g^u = \sup_t g(t).$$

In [5] the authors show the following.

THEOREM 1.1. *Given system* (1), *suppose that*

$$\forall k > 1, \exists i_k < k \ni \forall j \le k, \frac{b_k^u}{a_{kj}^l} < \frac{b_{i_k}^l}{a_{i_kj}^u}. \tag{3}$$

Then every trajectory with initial condition in $\mathring{R}^n_+$ *is asymptotic to* x_1^*.

In other words, under inequalities (3), for all strictly positive initial conditions, species $x_2, \ldots, x_n$ are driven to extinction, whilst species x_1 stabilises at x_1^*.

See Section 3 of [5] for a geometric interpretation of inequalities (3), in terms of thickened nullclines of system (1), which should help to unravel the subscripts.

In [2], Ahmad and Lazer considered system (1) for the autonomous case, where the functions a_{ij} and b_i are positive constants. They proved the following.

THEOREM 1.2 (Ahmad and Lazer [2]). *Given* (*autonomous*) *system* (1), *suppose that*

$$b_k > \sum_{j=1, j\neq k}^{n} a_{kj}\left(\frac{b_j}{a_{jj}}\right), \qquad \forall k < n \tag{4}$$

$$b_n < \sum_{j=1}^{n-1} a_{kj} u_j^*, \tag{5}$$

$$0 < \det(a_{ij}). \tag{6}$$

Then the linear system

$$b_k = \sum_{j=1}^{n-1} a_{kj} u_j, \qquad k < n,$$

has a unique positive solution $u^* = (u_1^*, \ldots, u_{n-1}^*)$, *and* $(u_1^*, \ldots, u_{n-1}^*, 0)$ *is globally attracting for (autonomous) system* (1) *on the open positive cone* $\overset{\circ}{R}{}^n_+$.

In other words, under inequalities (4)–(6), for all strictly positive initial conditions, species x_n is driven to extinction, whilst species $x_1, \ldots, x_{n-1}$ coexist stably at u^*.

In this paper we bridge the gap between these two results, generalising Theorem 1.2 to the nonautonomous case and combining the two sets of inequalities (3)–(6) to find algebraic criteria that guarantee the survival of species $x_1, \ldots, x_r$ and the extinction of species $x_{r+1}, \ldots, x_n$.

In Section 2 we state our main result (Theorem 2.1), which is then proved in Sections 3–5.

2. Statement of Result

In order to discuss the survival of species $x_1, \ldots x_r$, we develop the following notation. Let H^r denote the r-dimensional coordinate subspace on which $x_{r+1}, \ldots x_n$ vanish. Then H^r_+, $(\overset{\circ}{H}{}^r_+)$ denote the closed (open) positive cones in H^r, as usual. We use the variable u to denote the restriction of system (1) to H^r,

$$\dot{u}_i(t) = u_i(t)\left(b_i(t) - \sum_{j=1}^{r} a_{ij}(t) u_j(t)\right), \qquad i = 1, \ldots, r. \tag{7}$$

And we shall refer to this restricted system as the *small* system.

In Section 4 we collect together some recent results of Ahmad and Lazer [3] and Tineo [6] which state that inequality (8) of Theorem 2.1, below, implies that the small system has a unique strictly positive solution $u^*(t)$ which is bounded for all time, and that all other trajectories of the small system with strictly positive initial condition are asymptotic to u^*.

Theorem 2.1 states that if, in addition, we assume inequality (9), then all trajectories of the full n-dimensional system with strictly positive initial conditions are asymptotic to u^*. Note that we are employing a slight abuse of notation, allowing u^* to denote both the trajectory $(u_1^*(t), \ldots, u_r^*(t))$ of system (7) in H^r, and the trajectory $(u_1^*(t), \ldots, u_r^*(t), 0, \ldots, 0)$ of system (1) in R^n.

THEOREM 2.1. *Given system* (1), *suppose that*

$$\forall i \leq r, \qquad b_i^l > \sum_{j=1, j \neq i}^{n} a_{ij}^u \left(\frac{b_j^u}{a_{jj}^l}\right), \tag{8}$$

$$\forall k > r, \exists i_k < k \ni \forall j \leq k, \qquad \frac{b_k^u}{a_{kj}^l} < \frac{b_{i_k}^l}{a_{i_k j}^u}. \tag{9}$$

Then system (7) *has a unique bounded strictly positive solution* $u^*(t)$ *defined on* R, *and every trajectory of system* (1) *with initial condition in* $\mathring{R}_+^n$ *is asymptotic to* u^*.

In other words, under inequalities (8) and (9), for all strictly positive initial conditions, species $x_{r+1}, \ldots, x_n$ are driven to extinction, whilst species $x_1, \ldots, x_r$ stabilise at u^*.

Once again, see Section 3 of [5] for a geometric interpretation of inequalities (9), to help unravel the subscripts.

We prove Theorem 2.1 in Sections 3–5, discussing the extinction of species $x_r, \ldots, x_n$ Section 3, the existence of u^* in Section 4, and the convergence of trajectories to u^* in Section 5.

Allowing for relabeling of the axes by a permutation ϕ, let H^ϕ denote the r-dimensional subspace on which species $\phi^{-1}(r+1), \ldots, \phi^{-1}(n)$ all vanish. Then we have the following.

COROLLARY 2.2. *If there is a permutation* ϕ *of the indices* $\{1, \ldots, n\}$, *after which system* (1) *satisfies inequalities* (8) *and* (9), *then every trajectory with initial condition in* $\mathring{R}_+^n$ *is asymptotic to* u_ϕ^* *under the original system, where* u_ϕ^* *is the unique bounded globally attracting solution of the restriction of system* (1) *to* H^ϕ.

3. EXTINCTION OF $x_{r+1}, \ldots, x_n$

THEOREM 3.1. *If system* (1) *satisfies inequalities* (9) *and* $x(t)$ *is a solution of system* (1) *with* $x(t_0) \in \mathring{R}_+^n$ *for some* t_0, *then for all* $i > r$,

(a) $x_i(t) \to 0$ *as* $t \to \infty$, *and*

(b) $\int_{t_0}^{\infty} x_i(t)\, dt < \infty$.

Proof. Theorem 3.1 is the special case of Theorem 5.1 in [5] for which $r = 2$. Since the method of proof in [5] is to first prove conclusions (a) and (b) for x_n, and then to work from x_n down to x_2 by induction, the proof of Theorem 3.1 here is a subset of the proof of Theorem 5.1 in [5].

4. Existence of u^*

In this section we collect together some recent results concerning the small system (7) on the coordinate space H^r.

THEOREM 4.1 (Ahmad and Lazer [3]; Tineo [6]). *Given system* (7), *suppose that*

$$b_i^l > \sum_{j=1, j \neq i}^{r} a_{ij}^u \left(\frac{b_j^u}{a_{jj}^l} \right), \qquad \forall i = 1, \ldots, r. \tag{10}$$

Then

(a) *System* (7) *has a solution* $u^*(t)$ *defined on* R, *each coordinate of which is bounded above and below by strictly positive constants.*

(b) *The solution* u^* *is unique.*

(c) *Every trajectory with initial condition in* $\overset{\circ}{H}{}^r_+$ *is asymptotic to* u^* *as* $t \to \infty$.

(d) *There exists* $c = (c_1, \ldots, c_r) \in \overset{\circ}{H}{}^r_+$ *and* $m > 0$ *such that*

$$c_i a_{ii}(t) \geq m + \sum_{j=1, j \neq i}^{r} c_j a_{ji}(t) \qquad \forall i \leq r \; \forall t. \tag{11}$$

Proof. (a) See Ahmad and Lazer [3].

(b), (c) See Tineo [6, Theorem 1.2].

(d) See Tineo [6, Theorem 2.2 and Corollary 2.3].

Remark. Note that inequality (10) follows directly from inequality (8).

5. Convergence to u^*

THEOREM 5.1. *If system* (1) *satisfies inequalities* (8) *and* (9) *and* $x(t)$ *is a solution of system* (1) *with* $x(t_0) \in \overset{\circ}{R}{}^n_+$ *for some* t_0, *then for all* $i \leq r$, $x_i(t) \to u_i^*(t)$ *as* $t \to \infty$.

To prove Theorem 5.1 we combine the methods of Tineo [6, Theorem 1.1], proving that trajectories of the *small* system converge to u^*, with those of these authors [5, Theorem 5.1], proving that all but one of the species are driven to extinction. In particular, the introduction of the function f and Lemma 5.4 follow Tineo quite closely. We include the proof of Lemma 5.4 in full to show how the convergence of trajectories in $\mathring{H}^r_+$ has been generalised to the convergence of trajectories in $\mathring{R}^n_+$.

Let $x(t) = (x_1(t), \ldots, x_n(t)) \in \mathring{R}^n_+$ and $u(t) = (u_1(t), \ldots, u_r(t)) \in \mathring{H}^r_+$ be positive solutions of systems (1) and (7), respectively, such that for some t_0, we have $x_i(t_0) > u_i(t_0)$ for all $i \leq r$. We define a continuous function f on R by

$$f(t) = f(x(t), u(t)) = \sum_{j=1}^{r} c_j \left| \ln \left(\frac{x_j(t)}{u_j(t)} \right) \right|, \tag{12}$$

where $c = (c_1, \ldots, c_r)$ is given by Theorem 4.1(d).

Remark. It is easy to show (see Tineo [6, Theorem 1.1]) that f is continuously differentiable on $R \backslash D$, where D is a discrete set, defined as follows. Let $D_j = \{t \in R : x_j(t) = u_j(t) \text{ and } \dot{x}_j(t) \neq \dot{u}_j(t)\}$, and then define $D = \bigcup_{j=1}^{r} D_j$. Hence df/dt is Riemann integrable and obeys the fundamental theorem of calculus.

The next lemma uses a simple compact attracting region to give coarse bounds on the components of solutions to system (1), from which we can deduce that f is bounded.

LEMMA 5.2. *If system* (1) *satisfies inequalities* (8) *and $x(t)$ is a solution of system* (1) *with initial condition in $\mathring{R}^n_+$, then there exist $k_i > 0$ for each $i = 1, \ldots, r$; $\varepsilon > 0$, and $T \in R$ such that for all $t > T$,*

$$\varepsilon < x_i(t) \leq k_i \qquad \forall i = 1, \ldots, r.$$

Proof. See the proof of Lemma A in Ahmad and Lazer [2] which is easily adapted to prove Lemma 5.2.

COROLLARY 5.3. *If system* (1) *satisfies inequalities* (8) *and* (9) *then f is bounded on $[t_0, \infty) \backslash D$.*

Proof. Corollary 5.3 follows directly from Theorem 4.1(a) and (c), and Lemma 5.2.

LEMMA 5.4. *If system* (1) *satisfies inequalities* (8) *and* (9) *then for all $t \in [t_0, \infty) \backslash D$,*

$$\dot{f}(t) \leq -m \|u(t) - \bar{x}(t)\|_r + g(t), \tag{13}$$

where $g \to 0$ as $t \to \infty$ and $\int_{t_0}^{\infty} g(t) < \infty$.

Here $\|\cdot\|_r$ is the l_1 norm in H^r; $\bar{x} = (x_1, \ldots, x_r)$, and the dot denotes differentiation with respect to time, as usual. The proof of Lemma 5.4 follows the proof of Theorem 5.1.

Proof of Theorem 5.1. By Lemma 5.4

$$\|u(t) - \bar{x}(t)\|_r \leq -\frac{1}{m}(\dot{f} - g(t)).$$

Integrating this inequality we have

$$\begin{aligned}\int_{t_0}^{t} \|u(s) - \bar{x}(s)\|_r \, ds &\leq -\frac{1}{m}\left(\int_{t_0}^{t} \dot{f}(s)\, ds - \int_{t_0}^{t} g(s)\, ds\right)\\ &= -\frac{1}{m}\left(f(t) - f(t_0) - \int_{t_0}^{t} g(s)\, ds\right)\\ &= K < \infty,\end{aligned}$$

where K is some constant independent of t, since $f(t)$ is bounded by positive constants (Corollary 5.3) and $\int_{t_0}^{\infty} g(t)\, dt < \infty$ (Lemma 5.4). Thus

$$\int_{t_0}^{\infty} \|u(t) - \bar{x}(t)\|_r \, dt < \infty,$$

and so for all $i \leq r$,

$$x_i(t) \to u_i(t) \qquad \text{as } t \to \infty,$$

since $\|u(t) - \bar{x}(t)\|_r$ is a nonnegative a.e. differentiable function of t, and for all $i \leq r$ the functions u_i, x_i are everywhere differentiable with bounded derivative on $[t_0, \infty)$. Moreover, by Theorem 4.1(c), for all $i \leq r$,

$$u_i(t) \to u_i^*(t) \qquad \text{as } t \to \infty$$

and, hence,

$$x_i(t) \to u_i^*(t) \qquad \text{as } t \to \infty. \qquad \text{Q.E.D.}$$

In order to estimate the derivative of f and prove Lemma 5.4, it is convenient to group the indices as follows. For each fixed $t \in [t_0, \infty)\backslash D$, define

$$S_+(t) = \{j \le r : u_j(t) > x_j(t)\}$$
$$S_0(t) = \{j \le r : u_j(t) = x_j(t)\}$$
$$S_-(t) = \{j \le r : u_j(t) < x_j(t)\}.$$

Now define $S(t) = S_+(t) \cup S_-(t)$. The next lemma shows that for all $t \in [t_0, \infty)\backslash D$, $S(t) \ne \phi$. It is perhaps not strictly necessary, but is included for its independent interest. Note that from here on we shall suppress the t and simply write S_+, S_-, S for $S_+(t)$, $S_-(t)$, and $S(t)$, respectively.

LEMMA 5.5. *Suppose that $x(t)$ is a solution of system (1) with $x(t_0) \in \mathring{R}^n_+$ for some t_0; $u(t)$ is a solution of system (7) with $u(t_0) \in \mathring{H}^r_+$ and for all $i \le r$, $u_i(t_0) > x_i(t_0)$. Then for all $t > t_0$, there exists $i \le r$ such that $u_i(t) \ne x_i(t)$.*

Proof of Lemma 5.5. Suppose, for contradiction, that there exists $s > t_0$ such that for all $i \le r$, $u_i(s) = x_i(s)$. Then

$$\begin{aligned}\dot{u}_i(s) &= u_i(s)\left(b_i(s) - \sum_{j=1}^{r} a_{ij}(s)u_j(s)\right)\\ &= x_i(s)\left(b_i(s) - \sum_{j=1}^{r} a_{ij}(s)x_j(s)\right)\\ &> x_i(s)\left(b_i(s) - \sum_{j=1}^{n} a_{ij}(s)x_j(s)\right)\\ &= \dot{x}_i(s).\end{aligned}$$

Therefore,

$$\frac{d}{dt}(u_i - x_i)(s) > 0, \qquad \forall i \le r.$$

In other words, for each $i \le r$ the function $(u_i - x_i)$ has a zero at s at which it is strictly increasing. But $(u_i - x_i)$ is positive at t_0, so the function $(u_i - x_i)$ must have at least one more zero in (t_0, s). Indeed, for each $i \le r$, there exists $t_i \in (t_0, s)$ such that

$$(u_i - x_i)(t_i) = 0, \tag{14}$$

$$\frac{d}{dt}(u_i - x_i)(t_i) \le 0, \tag{15}$$

$$(u_i - x_i)(t_i) \le 0, \qquad \forall t \in (t_i, s). \tag{16}$$

Now define k by $t_k = \max_{i \le r}\{t_i\}$. Then $u_k(t_k) = x_k(t_k)$, and for all $i \neq k$, $u_i(t_k) \le x_i(t_k)$. So

$$\begin{aligned}
\dot{u}_k(t_k) &= u_k(t_k)\left(b_k(t_k) - \sum_{j=1}^{r} a_{kj}(t_k)u_j(t_k)\right)\\
&= x_k(t_k)\left(b_k(t_k) - \sum_{j=1}^{r} a_{kj}(t_k)u_j(t_k)\right)\\
&\ge x_k(t_k)\left(b_k(t_k) - \sum_{j=1}^{r} a_{kj}(t_k)x_j(t_k)\right)\\
&> x_k(t_k)\left(b_k(t_k) - \sum_{j=1}^{n} a_{kj}(t_k)x_j(t_k)\right)\\
&= \dot{x}_k(t_k).
\end{aligned}$$

Hence $(d/dt)(u_k - x_k)(t_k) > 0$, but this contradicts inequality (15).

Q.E.D.

Proof of Lemma 5.4. Fix $t \in [t_0, \infty)\backslash D$. From the definition of D we see that

$$\frac{d}{dt}\left|\ln \frac{x_j(t)}{u_j(t)}\right| = 0, \qquad \forall j \in S_0.$$

And from Lemma 5.5, $S \neq \phi$. Consequently,

$$\begin{aligned}
\dot{f}(t) &= \frac{d}{dt}\left(-\sum_{j\in S_+} c_j \ln\left(\frac{x_j(t)}{u_j(t)}\right) + \sum_{j\in S_-} c_j \ln\left(\frac{x_j(t)}{u_j(t)}\right)\right)\\
&= -\sum_{j\in S_+} c_j\left(\sum_{i=1}^{r} a_{ji}(t)(u_i(t) - x_i(t)) - \sum_{i=r+1}^{n} a_{ji}(t)x_i(t)\right)\\
&\quad + \sum_{j\in S_-} c_j\left(\sum_{i=1}^{r} a_{ji}(t)(u_i(t) - x_i(t)) - \sum_{i=r+1}^{n} a_{ji}(t)x_i(t)\right)\\
&= -\sum_{j\in S_+} c_j\left(\sum_{i\in S_+} a_{ji}(t)(u_i(t) - x_i(t)) + \sum_{i\in S_-} a_{ji}(t)(u_i(t) - x_i(t))\right)\\
&\quad + \sum_{j\in S_-} c_j\left(\sum_{i\in S_+} a_{ji}(t)(u_i(t) - x_i(t)) + \sum_{i\in S_-} a_{ji}(t)(u_i(t) - x_i(t))\right)\\
&\quad + \sum_{j\in S_+}\left(\sum_{i=r+1}^{n} c_j a_{ji}(t)x_i(t)\right) - \sum_{j\in S_-}\left(\sum_{i=r+1}^{n} c_j a_{ji}(t)x_i(t)\right).
\end{aligned}$$

Interchanging the order of summation and regrouping terms, we have

$$\dot{f}(t) = \sum_{i\in S_+}\left(\left(-\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t)\right)(u_i(t) - x_i(t))\right) \tag{17}$$

$$+ \sum_{i\in S_-}\left(\left(-\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t)\right)(u_i(t) - x_i(t))\right) + g(t), \tag{18}$$

where

$$g(t) = \sum_{i=r+1}^{n}\left(\left(\sum_{j\in S_+} c_j a_{ji}(t) - \sum_{j\in S_-} c_j a_{ji}(t)\right) x_i(t)\right).$$

Consider first the case when $i \in S_+$; then we have $(u_i(t) - x_i(t)) > 0$ and we can estimate the first summation in inequality (18) as

$$\begin{aligned} -\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t) &= -c_i a_{ii}(t) - \sum_{j\in S_+, j\neq i} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t) \\ &\leq -c_i a_{ii}(t) + \sum_{j=1, j\neq i}^{r} c_j a_{ji}(t) \\ &\leq -m \qquad \text{by Theorem 4.1(d).} \end{aligned}$$

And, hence,

$$\begin{aligned} &\sum_{i\in S_+}\left(\left(-\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t)\right)(u_i(t) - x_i(t))\right) \\ &\leq \sum_{i\in S_+} - m(u_i(t) - x_i(t)) \\ &= -m \sum_{i\in S_+} |(u_i(t) - x_i(t))|. \end{aligned}$$

Similarly, in the case when $i \in S_-$, then we have $(u_i(t) - x_i(t)) < 0$ and we can estimate the second summation in inequality (18) by

$$-\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t) \geq m,$$

so that

$$\begin{aligned} &\sum_{i\in S_-}\left(\left(-\sum_{j\in S_+} c_j a_{ji}(t) + \sum_{j\in S_-} c_j a_{ji}(t)\right)(u_i(t) - x_i(t))\right) \\ &\leq \sum_{i\in S_+} m(u_i(t) - x_i(t)) \\ &= -m \sum_{i\in S_-} |(u_i(t) - x_i(t))|. \end{aligned}$$

Therefore,

$$\dot{f}(t) \leq -m \sum_{i \in S_+} |(u_i(t) - x_i(t))| - m \sum_{i \in S_-} |(u_i(t) - x_i(t))| + g(t)$$

$$\leq -m \sum_{i=1}^{r} |(u_i(t) - x_i(t))| + g(t)$$

$$= -m\|u(t) - \bar{x}(t)\|_r + g(t).$$

Finally, we can estimate $g(t)$ by

$$\sum_{i=r+1}^{n} \Big(\sum_{j \in S_+} c_j a_{ji}^l x_i(t) - \sum_{j \in S_-} c_j a_{ji}^u x_i(t) \Big)$$

$$\leq g(t) \leq \sum_{i=r+1}^{n} \Big(\sum_{j \in S_+} c_j a_{ji}^u x_i(t) - \sum_{j \in S_-} c_j a_{ji}^l x_i(t) \Big).$$

So, by Theorem 3.1,

$$g(t) \to 0 \qquad \text{as } t \to \infty; \quad \int_{t_0}^{\infty} g(t)\, dt < \infty. \tag{19}$$

Q.E.D.

Theorem 2.1 is now a corollary of Theorems 3.1 and 5.1.

Acknowledgments

We thank Shair Ahmad and Dmitry Gokhman for helpful discussions.

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