Токуо J. Матн. Vol. 28, No. 1, 2005

Partial Survival and Extinction of Species in Discrete Nonautonomous Lotka-Volterra Systems

Yoshiaki MUROYA1

Waseda University

Abstract. In this paper, we consider the partial survival and extinction of species in model governed by the following discrete model of nonautonomous Lotka-Volterra type:

$$\begin{cases} N_i(p+1) = N_i(p) \exp\{c_i(p) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l)\}, & p \ge 0, \ 1 \le i \le n, \\ N_i(p) = N_{ip} \ge 0, \ p \le 0, & \text{and} \quad N_{i0} > 0, \ 1 \le i \le n, \end{cases}$$

where each $c_i(p)$ and $a_{ij}^l(p)$ are bounded for $p \ge 0$ and

$$\sum_{l=0}^{m} (\inf_{p\geq 0} a_{ii}^{l}(p)) > 0, \quad a_{ij}^{l}(p) \geq 0, \quad i \leq j \leq n, \ 1 \leq i \leq n, \ k_{l} \geq 0, \ 0 \leq l \leq m.$$

To the above discrete system, we extend results on the *principle of competitive exclusion* in nonautonomous Lotka-Volterra differential systems which has been established by Shair Ahmad (1999, *Proceedings of the American Mathematical Society* **127**, 2905–2910), that is, if the coefficients satisfy certain inequalities, then any solution with positive components at some point will have all of its last n - 1 components tend to zero, while the first one will stabilize at a certain solution of a discrete logistic equation.

1. Introduction

Consider the following nonautonomous Lotka-Volterra competitive differential system

$$x'_{i}(t) = x_{i}(t)\{c_{i}(t) + p_{i}(t) - \sum_{j=1}^{n} a_{ij}(t)x_{j}(t)\}, \quad 1 \le i \le n,$$
(1.1)

where $a_{ij}(t)$ is continuous and bounded above and below by positive constants, $c_i(t)$ is continuous and *T*-periodic, $p_i(t)$ is continuous (not necessarily periodic) and $|p_i(t)| \le \delta_i e^{-\gamma_i t}$, where δ_i and γ_i are positive constants. It is not assumed that the growth rate $c_i(t)$ is positive; instead it is assumed that the average $\bar{c}_i = \frac{1}{T} \int_{t_0}^{t_0+T} c_i(t) dt$ is positive for some $t_0 \ge 0$. To this

Received April 3, 2003; revised January 7, 2004; revised February 7, 2005

¹Research partially supported by Waseda University Grant for Special Research Projects 203A-573, and Scientific Research (c), No.16540207 of Japan Society for the Promotion of Science.

Key words. extinction of species; discrete model of nonautonomous Lotka-Volterra type 2000 Mathematics Subject Classification. 34K20, 92D25

differential system, Ahmad [2] showed that if for each $i = 2, 3, \dots, n$, there exist numbers $\lambda_{i1}, \lambda_{i2}, \dots, \lambda_{i,i-1} \ge 0, \ \lambda_{i1} + \lambda_{i2} + \dots + \lambda_{i,i-1} > 0$, such that

$$\frac{\bar{c}_i}{a_{ij}(t)} < \frac{\lambda_{i1}\bar{c}_1 + \lambda_{i2}\bar{c}_2 + \dots + \lambda_{i,i-1}\bar{c}_{i-1}}{\lambda_{i1}a_{1j}(t) + \lambda_{i2}a_{2j}(t) + \dots + \lambda_{i,i-1}a_{i-1,j}(t)}, \quad \text{for } j = 1, 2, \dots, i, \qquad (1.2)$$

and $t \ge t_0$ for some t_0 , then, $x_i(t) \to 0$, $2 \le i \le n$ and $x_1(t) \to x^*(t)$, where x^* is the unique positive solution of the logistic equation

$$x'(t) = x(t)\{c_1(t) - a_{11}(t)x(t)\}.$$
(1.3)

Earlier, Gopalsamy [9,10] had studied the existence and stability of periodic solutions for system (1.1) under the assumption that the growth rates are positive and periodic, and the rest of the coefficients are positive constants with $p_i(t) \equiv 0$, $1 \le i \le n$. Alvarez and Lazer [7] extended this result to the case where all the coefficients were assumed to be positive and periodic (see also Tineo and Alvarez [18]). Ahmad [1] first extended *principle of competitive exclusion* from autonomous systems to nonautonomous systems for two species, that is, under some algebraic inequalities, there can be no coexistence of the two species; one of them will be driven to extinction while the other will stabilize at a certain solution of a logistic equation. Ahmad and Lazer [3, 4], Ahmad and Oca [6], Battauz and Zanolin [8], Ortega and Tineo [15], Redheffer [16, 17], and Oca and Zeeman [14] have extended the result in Ahmad [1] and obtained other similar studies. In particular, Oca and Zeeman [14] have shown that if the coefficients are continuous and bounded above and below by positive constants, and if for each $i = 2, 3, \dots, n$, there exists an integer k_i such that

$$1 \le k_i < i \text{ and } \frac{c_{iM}}{a_{ijL}} < \frac{c_{k_iL}}{a_{k_ijM}}, \quad j = 1, 2, \cdots, i,$$
 (1.4)

then $x_i(t) \to 0$ exponentially for $2 \le i \le n$, and $x_1(t) \to x^*(t)$, where $x^*(t)$ is a certain solution of a logistic equation. Here, as in earlier studies, given a function f(t), f_M and f_L denote $\sup_{t\ge t_0} f(t)$ and $\inf_{t\ge t_0} f(t)$, respectively for some $t_0 \ge 0$. Note that the inequalities (1.4) imply (1.2), since one can take $\lambda_{i1} = 1$ and $\lambda_{ij} = 0$ for $2 \le j \le i - 1$.

For a fairly nice and detailed geometric interpretation of (1.4), the reader is referred to [14]. Some of Ahmad and Lazer's results in [3–5] were extended by the author to discrete models in [11] and to cases with delays in [12]. Applying the similar techniques in [11, 12], the author [13] gave some extentions of the result in Ahmad [2] to delay differential systems.

This paper is a discrete version of [13]. Motivated the above results, we extend results for partial survival and extinction of species in Ahmad [2] to discrete nonautonomous Lotka-Volterra systems.

Consider the following discrete model of nonautonomous Lotka-Volterra type.

$$\begin{cases} N_i(p+1) = N_i(p) \exp\{c_i(p) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l)\}, & p \ge 0, \\ N_i(p) = N_{ip} \ge 0, & p \le 0, & \text{and} & N_{i0} > 0, & 1 \le i \le n, \end{cases}$$
(1.5)

where each $c_i(p)$ and $a_{ij}^l(p)$ are bounded for $p \ge 0$ and

$$\sum_{l=0}^{m} \left(\inf_{p \ge 0} a_{ii}^{l}(p) \right) > 0, \quad a_{ij}^{l}(p) \ge 0, \quad i \le j \le n,$$

$$1 \le i \le n, \quad k_{l} \ge 0, \quad 0 \le l \le m.$$
(1.6)

Let

$$\begin{cases} \bar{a}_{i}(p) = \sum_{l=0}^{m} a_{ii}^{l}(p), \quad \bar{a}_{ii}^{l}(p) \equiv 0, \quad \bar{a}_{ij}^{l}(p) = a_{ij}^{l}(p), \quad j \neq i, \quad 0 \leq l \leq m, \\ \bar{a}_{iL} = \sum_{l=0}^{m} \left(\inf_{p \geq 0} a_{ii}^{l}(p) \right), \quad \bar{a}_{iM} = \sum_{l=0}^{m} \left(\sup_{p \geq 0} a_{ii}^{l}(p) \right), \quad c_{iL} = \inf_{p \geq 0} c_{i}(p), \\ c_{iM} = \sup_{p \geq 0} c_{i}(p), \quad \bar{a}_{ij}^{l-}(p) = \min(0, \bar{a}_{ij}^{l}(p)), \quad \bar{a}_{ij}^{l+}(p) = \max(0, \bar{a}_{ij}^{l}(p)), \\ \bar{b}_{ijL}^{-} = \sum_{l=0}^{m} \left(\inf_{p \geq 0} \bar{a}_{ij}^{l-}(p) \right), \quad \text{and} \quad \bar{b}_{ijM}^{+} = \sum_{l=0}^{m} \left(\sup_{p \geq 0} \bar{a}_{ij}^{l+}(p) \right), \quad 1 \leq i, j \leq n, \\ m[c_{i}] = \lim_{p \to \infty} \inf \left\{ \frac{1}{p_{2} - p_{1}} \sum_{q = p_{1}}^{p_{2} - 1} c_{i}(q) \middle| 0 \leq p_{1} < p_{2} \text{ and } p_{2} - p_{1} \geq p \right\}, \\ \text{and} \\ M[c_{i}] = \lim_{p \to \infty} \sup \left\{ \frac{1}{p_{2} - p_{1}} \sum_{q = p_{1}}^{p_{2} - 1} c_{i}(q) \middle| 0 \leq p_{1} < p_{2} \text{ and } p_{2} - p_{1} \geq p \right\}, \\ 1 \leq i \leq n. \end{cases}$$

$$(1.7)$$

Note that $\bar{b}_{iiL}^- = \bar{b}_{iiM}^+ = 0$ and $c_{iL} \le m[c_i] \le M[c_i] \le c_{iM}, \ 1 \le i \le n$.

Put

$$\begin{split} \bar{k} &= \max_{0 \le l \le m} k_l ,\\ \bar{k}_i &= \max\{k_l \mid a_{ii}^l(p) \ne 0, \text{ for some } p \ge 0, \ 0 \le l \le m\}, \ 1 \le i \le n,\\ \tilde{N}_1 &= \frac{c_{1M}}{\bar{a}_{1L}}, \quad \bar{N}_1 = \tilde{N}_1 \exp(c_{1M}\bar{k}_1),\\ \tilde{N}_i &= \left(c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^- \bar{N}_j\right) \Big/ \bar{a}_{iL}, \quad \bar{N}_i = \tilde{N}_i \exp\left\{\left(c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^- \bar{N}_j\right) \bar{k}_i\right\}, \end{split}$$
(1.8)
$$\begin{aligned} &\qquad 2 \le i \le n-1,\\ \tilde{N}_n &= \left(c_{nM} - \sum_{j=1}^{n-1} \bar{b}_{njL}^- \bar{N}_j\right) \Big/ \bar{a}_{nL}, \quad \bar{N}_n = \tilde{N}_n \exp\left\{\left(c_{nM} - \sum_{j=1}^{n-1} \bar{b}_{njL}^- \bar{N}_j\right) \bar{k}_n\right\}, \end{split}$$

and assume

$$c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^- \bar{N}_j > 0, \quad 1 \le i \le n.$$
 (1.9)

Then,

$$\bar{N}_i \ge \tilde{N}_i > 0, \quad 1 \le i \le n.$$
(1.10)

The following theorems are our main results.

THEOREM 1.1 (Cf. Lemma 2.3 in Muroya [11]). For (1.7) and (1.8), assume (1.9). Then, for solutions $N_i(p)$, $1 \le i \le n$ of the system (1.5)–(1.6),

$$\limsup_{p \to \infty} N_i(p) \le \bar{N}_i , \quad 1 \le i \le n .$$
(1.11)

Moreover, suppose that there exists a nonempty subset $Q \subset \{1, 2, \dots, n\}$ *such that*

$$c_{iL} - \sum_{j \notin Q} b^+_{ijM} \bar{N}_j > 0, \quad for \ any \ i \in Q,$$

$$(1.12)$$

then partial survival holds, that is,

$$\liminf_{p \to \infty} \sum_{i \in Q} N_i(p) > 0.$$
(1.13)

THEOREM 1.2. For (1.7) and (1.8), assume (1.9) and (1.12). If there exist numbers $n_d \in \{1, 2, \dots, n-1\}$ and $\lambda_{r1}, \lambda_{r2}, \dots, \lambda_{r,i-1}, r = n, n-1, \dots, n_d + 1$, such that

$$\lim_{p \to \infty} \inf\{a_{rj}^{l}(p) - \sum_{i=1}^{r-1} \lambda_{ri} a_{ij}^{l}(p)\} > 0, \quad 1 \le j \le n, \quad 0 \le l \le m, \\
c_{r}(p) \le \sum_{i=1}^{r-1} \lambda_{ri} c_{i}(p), \quad r = n, \quad n-1, \cdots, n_{d} + 1, \quad p \ge 0.$$
(1.14)

Then,

$$N_i(p) \to 0$$
 exponentially for $i = n, n - 1, \dots, n_d + 1$,
and $\liminf_{p \to \infty} \sum_{i=1}^{n_d} N_i(p) > 0$. (1.15)

In particular, if $n_d = 1$, then

$$N_1(p) \to N^*(p) \quad as \quad p \to \infty,$$
 (1.16)

where $N^*(p)$ is the unique positive solution of the discrete logistic equation

$$N(p+1) = N(p) \exp\left\{c_1(p) - \sum_{l=0}^m a_{11}^l(p)N(p-k_{11}^l)\right\}.$$
 (1.17)

The organization of this paper is as follows. In Section 2, using the same techniques in Ahmad and Lazer [1] and Muroya [11], we prove that $(1.9) \Rightarrow (1.11)$, and (1.11) and $(1.12) \Rightarrow (1.13)$, and (1.13) and $(1.14) \Rightarrow (1.15)$ and in particular, if $n_d = 1$, then (1.16) holds.

2. Partial survival and extinction of species

Consider the partial survival and extinction of species in discrete models governed by nonautonomous Lotka-Volterra type (1.5) and (1.6).

We have a lemma.

LEMMA 2.1. For the system (1.5) and (1.6) and $1 \le i \le n$,

$$N_i(p) = N_i(0) \exp\left(\sum_{q=0}^{p-1} \left\{ c_i(q) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(q) N_j(q-k_l) \right\} \right), \quad p \ge 0,$$
(2.1)

and every solutions $N_i(p)$, $1 \le i \le n$, exist and remain positive for all $p \ge 0$.

PROOF. From (1.5), we have for any $p \ge 0$,

$$N_i(p+1) = N_i(p) \exp\left(\sum_{q=0}^p \left\{c_i(q) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(q) N_j(q-k_l)\right\}\right) = 0, \quad 1 \le i \le n,$$

from which we get the conclusion.

We have the following lemma (cf. Theorem 1 in Muroya [12]).

LEMMA 2.2. For (1.7) and (1.8), assume (1.9). Then, any solutions $N_i(p)$, $1 \le i \le n$ of the system (1.5) and (1.6), are bounded above and

$$\limsup_{p \to \infty} N_i(p) \le \bar{N}_i , \quad 1 \le i \le n .$$
(2.2)

PROOF. If for some $p \ge 0$, $N_1(p+1) - N_1(p) \ge 0$, then by (1.5) and (1.6), there exists a nonnegative integer \bar{l}_{1p} such that $0 \le \bar{l}_{1p} \le m$ and $N_1(p - k_{\bar{l}_{1p}}) \le \frac{c_{1M}}{\bar{a}_{1L}} = \tilde{N}_1$.

Because, if

$$\min_{0 \le l \le m} N_1(p - k_l) > \frac{c_{1M}}{\bar{a}_{1L}},$$

then

$$c_1(p) - \sum_{j=1}^n \sum_{l=0}^m a_{1j}^l(p) N_j(p-k_l) \le c_{1M} - \bar{a}_{1L}(\min_{0 \le l \le m} N_1(p-k_l)) < 0$$

which implies $N_1(p + 1) < N_1(p)$, by (1.5).

Therefore, by (2.1), $N_1(p+1) \le N_1(p-k_{\bar{l}_{1p}}) \exp(c_{1M}k_{\bar{l}_{1p}}) \le \bar{N}_1$. Thus, if $N_1(p) > \bar{N}_1$ for some $p \ge 0$, then we have

$$N_1(p+1) < N_1(p)$$
.

Now, let us consider the case that $N_1(p)$ is eventually decreasing and bounded below by \bar{N}_1 . Then, $\lim_{p\to\infty} N_1(p)$ exists. Set $\beta = \lim_{p\to\infty} N_1(p) - \bar{N}_1 \ge 0$. We will show that $\beta = 0$.

Indeed, suppose $\beta > 0$. Let take any positive constant η . Then, there exists $\tilde{p}_0 \ge 0$ such that

$$\beta \leq N_1(q) - \bar{N}_1 \leq \beta + \eta$$
, for $q \geq \tilde{p}_0$,

since $N_1(p) - \overline{N}_1$ eventually decreases to β . Thus, we have

$$N_1(p+1) \le N_1(p) \exp\left\{c_{1M} - \sum_{j=1}^n \sum_{l=0}^m a_{11}^l(p) N_1(p-k_l)\right\}$$

$$\le N_1(p) \exp(-\bar{a}_{1L}\beta), \quad \text{for } p \ge \tilde{p}_1 \equiv \tilde{p}_0 + \bar{k}.$$

Therefore, we have

$$N_1(p+1) \le N_1(\tilde{p}_1) \exp\left\{-\beta \sum_{q=\tilde{p}_1}^{p-1} \bar{a}_{1L}\right\},\$$

which in turn implies, due to $\sum_{q=\tilde{p}_1}^{\infty} \bar{a}_{1L} = +\infty$, $\lim_{p\to\infty} N_1(p) = 0$. This contradicts $N_1(p) \ge \bar{N}_1 + \beta > 0$. Thus, $\lim_{p\to\infty} N_1(p) = \bar{N}_1$.

Hence, we have

$$\limsup_{p \to \infty} N_1(t) \le \bar{N}_1 \, .$$

Then, for any fixed positive constant ε , there exists a constant $\bar{p}_1 \ge \bar{p}_0 = 0$ such that $N_1(p) \le \bar{N}_1$, for any $p \ge \bar{p}_1 - \bar{k}$.

Next, for some $2 \le i \le n$, suppose inductively that for any fixed positive constant ε , there exists a constant $\bar{p}_{i-1} \ge \bar{p}_{i-2}$ such that

$$N_j(p) \le \overline{N}_j + \varepsilon$$
, for any $p \ge \overline{p}_{i-1} - \overline{k}$, $1 \le j \le i - 1$.

If for some $p \ge \bar{p}_i$, $N_i(p+1) \ge N_i(p)$, then there exists a nonnegative integer \underline{l}_{ip} such that $0 \le \underline{l}_{ip} \le m$ and

$$N_{i}(p - k_{\underline{l}_{ip}}) \leq \left\{ c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^{-}(\bar{N}_{j} + \varepsilon) \right\} / \bar{a}_{iL} \leq \tilde{N}_{i} + \left\{ \left(-\sum_{j=1}^{i-1} \bar{b}_{ijL}^{-} \right) / \bar{a}_{iL} \right\} \varepsilon.$$

Because, if

$$\min_{0\leq l\leq m} N_i(p-k_l) > \left(c_{iM} - \sum_{j=1}^n \bar{b}_{ijL}^-(\bar{N}_j + \varepsilon)\right) / \bar{a}_{iL},$$

then

$$\begin{split} c_i(p) &- \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l) \leq c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^-(\bar{N}_j + \varepsilon) \\ &- \bar{a}_{iL} \bigg(\min_{0 \leq l \leq m} (N_i(p-k_l)) \bigg) < 0 \,, \end{split}$$

which implies $N_i(p+1) < N_i(p)$, by (1.5).

Therefore, by (2.1),

$$N_{i}(p+1) \leq N_{i}(p-k_{\underline{l}_{ip}}) \exp\left\{\left(c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^{-}(\bar{N}_{j}+\varepsilon)\right)k_{\underline{l}_{ip}}\right\}$$
$$\leq \bar{N}_{i}^{\varepsilon} \equiv \left[\bar{N}_{i} + \left\{\left(-\sum_{j=1}^{i-1} \bar{b}_{ijL}^{-}\right)/\bar{a}_{iM}\right\}\varepsilon \exp\left\{\left(c_{iM} - \sum_{j=1}^{i-1} \bar{b}_{ijL}^{-}\bar{N}_{j}\right)k_{\underline{l}_{ip}}\right\}\right]$$
$$\times \exp\left\{\left(-\sum_{j=1}^{i-1} \bar{b}_{ijL}^{-}\right)\varepsilon k_{\underline{l}_{ip}}\right\}.$$

Thus, if there exists a constant $\tilde{p}_i \ge \bar{p}_{i-1}$ such that $N_i(p) > \bar{N}_i^{\varepsilon}$ for some $p \ge \tilde{p}_i$, then

$$N_i(p+1) < N_i(p) \,.$$

If $N_i(p)$ is eventually decreasing and bounded below by \bar{N}_i^{ε} . Then, as similar to the above discussions of i = 1, we see $\lim_{p \to \infty} N_i(p) = \bar{N}_i^{\varepsilon}$.

Since $\varepsilon > 0$ is any positive constant, we have that by inductions of $i = 1, 2, \dots, n$,

$$\limsup_{p\to\infty} N_i(p) \le \bar{N}_i, \ 1 \le i \le n \,.$$

This completes the proof.

Now, we prove Theorems 1.1 and 1.2.

PROOF OF THEOREM 1.1. By assumptions to (1.5)–(1.6), there exist positive constants $\underline{\gamma}$, \overline{b}_l , $0 \le l \le m$ such that for $i \in Q$ and $p \ge 0$,

$$c_{iL} - \sum_{j \notin Q} \bar{b}^+_{ijM} \bar{N}_j > \underline{\gamma}$$
, and $a^l_{ij}(p) \le \bar{b}_l$, $j \in Q$, $0 \le l \le m$.

By (1.7), it follows that for $i \in Q$ and a sufficiently large integer $p_0 \ge 0$,

$$N_i(p+1) \ge N_i(p) \exp\left\{c_i(p) - \sum_{j \notin Q} \sum_{l=0}^m a_{ij}^{l+}(p) N_j(p-k_l) - \sum_{j \in Q} \sum_{l=0}^m a_{ij}^{l}(p) N_j(p-k_l)\right\}$$

$$\geq N_i(p) \exp\left\{\underline{\gamma} - \sum_{l=0}^m \bar{b}_l \sum_{j \in Q} N_j(p-k_l)\right\}, \quad p \geq p_0.$$

This shows that if

$$V(p) = \sum_{j \in Q} N_j(p) \,,$$

then

$$V(p+1) \ge V(p) \exp\left\{\underline{\gamma} - \sum_{l=0}^{m} \bar{b}_l V(p-k_l)\right\}, \quad p \ge p_0.$$
(2.3)

Now, suppose that $\liminf_{p\to\infty} V(p) = 0$. Then, there exists a sequence $\{p_q\}_{q=1}^{\infty}$ such that

$$V(p_q+1) \le V(p_q)$$
, and $\lim_{q \to \infty} V(p_q) = 0$.

Since V(p) > 0 and for $V^* = \underline{\gamma}/(\sum_{l=0}^m \overline{b}_l) > 0$,

$$V(p+1) \ge V(p) \exp\left\{\sum_{l=0}^{m} \bar{b}_{l}(V^{*} - V(p-k_{l}))\right\},\$$

it holds that for each $q \ge 1$, there exists an $l_q \in \{0, 1, 2, \dots, m\}$ such that

$$V(p_q - k_{l_q}) \ge V^* \,.$$

Similar to (2.1), it follows from (2.3) that

$$V(p_q) \ge V(p_q - k_{l_q}) \exp\left(\sum_{r=k_q-k_{l_q}}^{p_q-1} \left\{ \underline{\gamma} - \sum_{l=0}^m \bar{b}_l V(r-k_l) \right\} \right).$$

By Lemma 2.2 and assumptions, there is a positive constant \bar{V} such that for $V(p) \leq \bar{V}$, $p \geq 0$ and for $\bar{k} = \max_{0 \leq l \leq m} k_l$, we have that

$$V(p_q) \ge \beta \equiv V^* \exp\left(\bar{k} \min\left\{\underline{\gamma} - \sum_{l=0}^m \bar{b}_l \bar{V}, 0\right\}\right) > 0, \quad q \ge 1,$$

which is a contradiction.

Therefore,

$$\liminf_{p\to\infty} V(p) > 0\,,$$

and hence, (1.13) holds.

PROOF OF THEOREM 1.2. First, let us consider the case $n_d = n - 1$ in (1.14). Eq. (1.5) can be written as

$$\ln\left(\frac{N_i(p+1)}{N_i(p)}\right) = c_i(p) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l), \quad 1 \le i \le n-1,$$
(2.4)

and

$$\ln\left(\frac{N_n(p+1)}{N_n(p)}\right) = c_n(p) - \sum_{j=1}^n \sum_{l=0}^m a_{nj}^l(p) N_j(p-k_l).$$
(2.5)

Thus, similar to the proof of Theorem 3.1 in Ahmad [2], (2.5) and multiplying Eq. (2.4) by λ_{ni} and summing over $1 \le i \le n - 1$, and subtracting, we obtain

$$\ln\left(\frac{N_{n}(p+1)}{N_{n}(p)}\right) - \sum_{i=1}^{n-1} \lambda_{ni} \ln\left(\frac{N_{i}(p+1)}{N_{i}(p)}\right) = \left(c_{n}(p) - \sum_{i=1}^{n-1} \lambda_{ni}c_{i}(p)\right) - \sum_{l=0}^{m} \sum_{j=1}^{n} \left(a_{nj}^{l}(p) - \sum_{i=1}^{n-1} \lambda_{ni}a_{ij}^{l}(p)\right) N_{j}(p-k_{l}),$$
(2.6)

In view of Eqs. (1.13) and (1.14), there exist positive numbers α and β such that for $p \ge 0$,

$$\begin{cases} \sum_{j=1}^{n} N_{j}(p-k_{l}) \geq \alpha ,\\ a_{nj}^{l}(p) - \sum_{i=1}^{n-1} \lambda_{ni} a_{ij}^{l}(p) \geq \beta , \quad 1 \leq j \leq n , \quad 0 \leq l \leq m . \end{cases}$$
(2.7)

Then, for a constant $\gamma = (m + 1)\alpha\beta > 0$, one can write

$$\ln\left(\frac{N_{n}(p+1)}{N_{n}(p)}\right) - \sum_{i=1}^{n-1} \lambda_{ni} \ln\left(\frac{N_{i}(p+1)}{N_{i}(p)}\right) \le -\beta \sum_{l=0}^{m} \sum_{j=1}^{n} N_{j}(p-k_{l}) \le -\gamma , \quad \text{for } p \ge 0.$$
(2.8)

Summating both sides from 0 to p - 1, we obtain

$$\ln \frac{N_n(p)}{\prod_{i=1}^{n-1} N_i^{\lambda_{ni}}(p)} \le -\gamma p \,. \tag{2.9}$$

Therefore,

$$N_n(p) \le \left(\prod_{i=1}^{n-1} N_i^{\lambda_{ni}}(p)\right) e^{-\gamma p} \,. \tag{2.10}$$

Since by (1.12), there is a positive constant δ such that $0 < N_i(p) \le \delta$ for $p \ge 0, 1 \le i \le n-1$, it follows that $N_n(p) \to 0$, exponentially, as $p \to \infty$.

Next, we need to show that $N_i(p) \rightarrow 0$ exponentially for $i = 2, 3, \dots, n-1$. We accomplish this by rewriting the system Eq. (1.5) as

$$N_i(p+1) = N_i(p) \exp\left\{c_i(p) - \sum_{j=1}^{n-1} \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l)\right\},\$$

$$i = 1, 2, \cdots, \quad n-1.$$
(2.11)

We note that the inequalities in (1.14) are independent of the smaller system Eq. (2.11) still satisfy inequalities (1.14). Hence, applying the induction hypothesis to the smaller system Eq. (2.11), it follows that for $n_d + 1 \le i \le n - 1$, $N_i(p) \to 0$ exponentially, as $p \to \infty$.

Now, we need to show that the theorem holds for $1 \le i \le n_d$. For $1 \le i \le n_d$, similar to the proof of Theorem 3.1 in Ahmad [2], the system (1.5) reduces to the following discrete Lotka-Volterra smaller system

$$N_i(p+1) = N_i(p) \exp\left\{c_i(p) - \sum_{j=1}^{n_d} \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l)\right\}, \quad 1 \le i \le n_d.$$
(2.12)

Hence, by Theorem 1.1, we obtain $\liminf_{p\to\infty} \sum_{i=1}^{n_d} N_i(p) > 0$.

In particular, suppose that $n_d = 1$. Then, by assumptions, we have that $Q = \{1\}, (1.11)$ and (1.13) hold. Thus, similar to the proof of Lemma 2.8 in Muroya [11], we can show that $N_1(p) \rightarrow N^*(p)$ as $p \rightarrow \infty$, where $N^*(p)$ is the unique positive solution of the discrete logistic equation (1.17). The proof of theorem is now complete.

Consider the system

$$\begin{cases} N_i(p+1) = N_i(p) \exp\{c_i(p) - \sum_{j=1}^n \sum_{l=0}^m a_{ij}^l(p) N_j(p-k_l)\}, & p \ge 0, \\ N_i(p) = N_{ip} \ge 0, & p \le 0, & \text{and} & N_{i0} > 0, & 1 \le i \le n, \end{cases}$$
(2.13)

where each $a_{ij}^l(p)$ are bounded for $p \ge 0$ and (1.6) holds. The growth rate $c_i(p)$ is bounded but we do not assume $c_i(p)$ is positive; instead we assume that

$$\begin{cases} \bar{c}_i = \lim_{p \to \infty} \frac{1}{p} \sum_{q=0}^{p-1} c_i(q) > 0, & 1 \le i \le n \text{ exist} \\ \text{and } R_i(p) = \sum_{q=0}^{p-1} (c_i(q) - \bar{c}_i) \text{ is bounded for } p \ge 0. \end{cases}$$
(2.14)

If $c_i(p) = b_i(p) + q_i(p)$ and $b_i(p)$ is bounded and *T*-periodic, $q_i(p)$ is bounded (not necessarily periodic) and $|q_i(p)| \le \delta_i e^{-\gamma_i p}$ for $p \ge 0$, where δ_i and γ_i are positive constants, then (2.14) is satisfied (see Ahmad [2]).

If $c_i(p) = \overline{c}_i + (p+1)^s$ and s < -1, then (2.14) is also satisfied.

Therefore, condition (2.14) is an extension of the case in Ahmad [2] to discrete cases. We easily obtain the following lemma (see the proof of Lemma 2.2 in Ahmad [2]).

LEMMA 2.3. For the system (2.13), assume (2.14). Letting $Q_i(p) = e^{R_i(p)}$ and making the transformation $N_i(p) = Q_i(p)M_i(p)$ in (2.13) leads to the system:

$$M_i(p+1) = M_i(p) \exp\left\{\bar{c}_i - \sum_{j=1}^n \sum_{l=0}^m \bar{a}_{lj}^l(p) M_j(p-k_l)\right\},$$
(2.15)

where the coefficients $\bar{a}_{ij}^l(p) = a_{ij}^l(p)Q(p-k_l)$ are bounded above and below by positive constants.

Thus, by applying Theorem 1.1 to the system (2.15), we obtain the following corollary (cf. Lemma 2.2 in Ahmad [2]).

COROLLARY 2.1. For system (2.13), assume (2.14). If $col(N_1(p), N_2(p), \dots, N_n(p))$ is a solution of (2.13) such that $N_i(0) > 0$, $1 \le i \le n$, then there exist positive numbers δ and Δ such that $\delta \le \sum_{i=1}^n N_i(p) \le \Delta$ for all $p \ge 0$.

PROOF. For the system (2.15), by (2.14), the corresponding conditions (1.9) and (1.11) for $Q = \{1, 2, \dots, n\}$ are satisfied. Thus, by Theorem 1.1, we obtain the conclusion of this corollary.

By Lemma 2.3, Corollary 2.1 and Theorem 1.2, we obtain the following corollary (cf. Theorem 2.3 in Ahmad [2]).

COROLLARY 2.2. For the system (2.13), assume the condition (1.14) and (2.14) holds. If $col(N_1(p), N_2(p), \dots, N_n(p))$ is any solution of (2.13) such that $N_i(0) > 0$, $1 \le i \le n$, then $N_i(p) \to 0$ for $i = 2, 3, \dots, n$, and $N_1(p) \to N^*(p)$ as $p \to \infty$, where $\{N^*(p)\}_{p=0}^{\infty}$ is the unique positive solution of (1.17).

ACKNOWLEDGEMENT. The author wishes to thank the anonymous referee for his/her valuable comments.

References

- S. AHMAD, On the nonautonomous Volterra-Lotka competition equations, Proc. Amer. Math. Soc. 117 (1993), 199–204.
- S. AHMAD, Extinction of species in nonautonomous Lotka-Volterra systems, Proc. Amer. Math. Soc. 127 (1999), 2905–2910.
- [3] S. AHMAD and A. C. LAZER, On the nonautonomous N-competing species problem, Applicable Anal. 57 (1995), 209–323.
- [4] S. AHMAD and A. C. LAZER, Necessary and sufficient average growth in a Lotka-Volterra system, Nonlinear Analysis TMA 34 (1998), 191–228.
- [5] S. AHMAD and A. C. LAZER, Average conditions for global asymptotic stability in a nonautonomous Lotka-Volterra system, Nonlinear Analysis TMA 40 (2000), 37–49.

- [6] S. AHMAD and F. MONTES DE OCA, Extinction in nonautonomous T-periodic competitive Lotka-Volterra systems, Appl. Math. Comput. 90 (1998), 155–166.
- [7] C. ALVAREZ and A. C. LAZER, An application of topological degree to the periodic competing species problem, J. Austral. Math. Soc. Ser. B 28 (1986), 202–219.
- [8] A. BATTAUZ and F. ZANOLIN, Coexistence states for periodic competitive Kolmogorov systems, J. Math. Anol. Appl. 219 (1998), 179–199.
- [9] K. GOPALSAMY, Exchange of equilibria in two species Lotka-Volterra competition models, J. Austral. Math. Soc. Ser B 24 (1982), 160–170.
- [10] K. GOPALSAMY, Global asymptotic stability in a periodic Lotka-Volterra system, J. Austral. Math. Soc. Ser B 27 (1985), 66–72.
- [11] Y. MUROYA, Persistence and global stability for discrete models of nonautonomous Lotka-Volterra type, J. Math. Anal. Appl. 273 (2002), 492–511.
- [12] Y. MUROYA, Averaged growth and global stability in nonautonomous Lotka-Volterra system with delays, Communications on Applied Nonlinear Analysis 10 (2003), 35–54.
- [13] Y. MUROYA, Partial survival and extinction of species in nonautonomous Lotka-Volterra systems with delays, Dynamic Systems and Applications 12 (2003), 295–306.
- [14] F. MONTES DE OCA and M. L. ZEEMAN, Extinction in nonautonomous competitive Lotka-Volterra systems, Proc. Amer. Math. Soc. 124 (1996), 3677–3687.
- [15] R. ORTEGA and A. TINEO, An exclusion principle for periodic competitive Lotka-Volterra systems in three dimensions, Nonlinear Anal. TMA 31 (1998), 883–893.
- [16] R. REDHEFFER, Nonautonomous Lotka-Volterra system I, J. Differential Equations 127 (1996), 519-540.
- [17] R. REDHEFFER, Nonautonomous Lotka-Volterra system II, J. Differential Equations 127 (1996), 1–20.
- [18] A. TINEO and C. ALVAREZ, A different consideration about the globally asymptotically stable solution of the periodic n-competing species problem, J. Math. Anal. Appl. 159 (1991), 44–60.

Present Address: DEPARTMENT OF MATHEMATICAL SCIENCES, WASEDA UNIVERSITY, 3–4–1 OHKUBO SHINJUKU-KU, TOKYO, 169–8555 JAPAN. *e-mail*: ymuroya@waseda.jp