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PERMANENCE FOR NON-AUTONOMOUS PREDATOR-PREY SYSTEMS*

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Abstract. The question of permanence is considered for general predator-prey models. It is shown, by using an "average" Liapunov function technique, that a natural average condition on the predator growth rate ensures that permanence holds. Conclusions extending the known results are deduced for the periodic and almost periodic cases.

1. Introduction. The criterion of *permanence* (which is sometimes called uniform persistence [9]) has recently received much attention in studying the long term survival of interacting species in ecology; see [12] for an extensive treatment of ordinary differential equation models, and [13] for a review of more general models. However, the important case of models based on nonautonomous ordinary differential equations appears to have received relatively little attention from this point of view. Our object is to show that at least for two species models, a rather natural condition for permanence may be obtained. Although we concentrate here on a model of predator-prey type, it is clear that the same techniques are applicable for other types of interaction, for example those of competing species type.

We shall consider a model based on the pair of equations

$$\begin{cases} \dot{x}_1 = x_1 F_1(t,x) \\ \dot{x}_2 = x_2 F_2(t,x) \end{cases} \tag{1.1}$$

where $x = (x_1, x_2)$. We write $f_i(t,x) = x_i F_i(t,x)$, and set $F = (F_1, F_2)$, $f = (f_1, f_2)$. The function $F : \mathbb{R} \times \mathbb{R}^2_+ \to \mathbb{R}^2$ is assumed to be smooth (for the precise assumptions see Section 2), so it is obvious that $\mathbb{R}^2_+$, $\operatorname{int} \mathbb{R}^2_+$, and $\partial \mathbb{R}^2_+$ are forward invariant sets. We shall impose conditions yielding dissipativity. Then the system is said to be permanent if there is an $\epsilon > 0$ such that given any $t_0 \in \mathbb{R}_+$ and $x \in \operatorname{int} \mathbb{R}^2_+$ there is a T such that the solution of (1.1) with $x(t_0) = x$ satisfies the condition $x_i(t) \geq \epsilon$ ($i = 1, 2$, $t \geq T$). This condition is attractive from a biological point of view in that it allows complicated asymptotic dynamics while ruling out in a rather strong sense

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the extinction of either species. The condition of *strong persistence* (also sometimes known as persistence, see [7]) is weaker than this, and is obtained by replacing $x_i(t) \geq \epsilon$ by $\liminf_{t\to\infty} x_i(t) > 0$ in the above definition.

Non-autonomous models have been considered in a biological context by a number of authors. Because of the technical difficulties, the analysis has usually been restricted to two species models, exceptions including [8], [4] where a food chain model with n species is discussed, and [5] where an abstract discussion of permanence is given without extensive treatment of specific examples. Even for two species models, progress has been somewhat limited, and our aim here is to show that at least for this case a rather natural condition ensuring permanence may be obtained. Some general references are [3], [10], and [18], while for predator-prey problems the reader is referred to [1], [2], and [7].

To motivate the direction of the present investigation, consider first an autonomous predator-prey model. Then intuitively one expects that if the prey is at its carrying capacity μ (μ being the non-trivial solution of $F_1(\mu,0) = 0$), the system will be permanent if for low predator levels the predator population increases; that is, $F_2(\mu,0) > 0$; it can be proved easily that this is indeed the case. Suppose next that the system has period Ω. Then under reasonable conditions there is a non-trivial Ω-periodic global solution $\mu(t)$ of $\dot{x}_1 = x_1F_1(t,x_1,0)$, see [1]. Here, μ may be regarded as a generalized carrying capacity. We may now hope that analogously permanence holds if the predator increases *on average* near this solution; that is,

$$\frac{1}{\Omega}\int_0^{\Omega} F_2(s,\mu(s),0)\,ds > 0, \tag{1.2}$$

although the simple arguments available in the autonomous case will clearly not generalize readily. We shall show here that even for general F a sort of analogue of this condition, based on a generalized average ensures permanence, and then deduce the sufficiency of (1.2) for the periodic case. In [7] an almost periodic system is considered, and it is shown that the condition $F_2(t,\mu(t),0) > 0$ ($t \in \mathbb{R}$) is sufficient for strong persistence. We shall be able to deduce from our general criterion that the weaker average condition (which also appears more natural),

$$\lim_{t\to\infty}\frac{1}{t}\int_0^{t} F_2(s,\mu(s),0)\,ds > 0,$$

is in fact enough for the stronger criterion of permanence to hold.

The mathematical technique is based on the use of an "average" Liapunov function applied to the skew-product semi-flow generated by (1.1). The average Liapunov function method is reviewed in [12] and [13]. This method seems particularly effective in the present context since the natural criterion for permanence involves an average over a global orbit, the generalized carrying capacity, of the prey equation.

A review of the contents is as follows. In Section 2 a fairly general condition implying dissipativity is given, and the existence of a non-trivial global solution (defined for all $t \in \mathbb{R}$) for the prey equation in the absence of the predator is established. In Section 3 the skew-product semi-flow is introduced. Section 4 contains the main results on permanence.

We conclude Section 4 by showing the existence of a predator orbit in $\operatorname{int}\mathbb{R}^2_+$ for periodic equations when permanence holds; such an orbit may be regarded as a generalization of a coexistence state for the autonomous case. The proof of this result is an immediate consequence of a theorem of Massera [15], and may be compared with the proof of the very similar Theorem 2.2 of [1] based on a bifurcation argument.

2. Preliminary results for the system (1.1). It will be assumed throughout that the following hold:

(C1) $F : \mathbb{R} \times \mathbb{R}^2_+ \to \mathbb{R}^2$ is bounded and uniformly continuous on every set $\mathbb{R} \times K$ for $K \subset \mathbb{R}^2_+$ compact.

(C2) F is locally Lipschitz in x uniformly in t. That is, for every compact K there is a k such that

$$|F(t,x) - F(t,y)| \le k|x-y| \quad (x, y \in K, \quad t \in \mathbb{R}).$$

These conditions are enough to ensure that the theory of skew-product semi-flows is applicable (see Section 3). They also yield local existence and uniqueness of solutions, and global existence will follow if an *a priori* bound can be found. Our first result gives this and somewhat more.

Suppose there exist $h_1, h_2 \in C(\mathbb{R}_+, \mathbb{R}_+)$ and $\alpha \in C(\mathbb{R}_+, (0,\infty))$ such that the following hold:

(H1) $\int_0^p r(s)\,ds \to \infty$ as $p \to \infty$, where $r(s) = \min[h_1(s), h_2(s)]$.

(H2) There exist $M > 0$ such that

$$h_1(x_1)f_1(t,x_1,x_2) + h_2(x_2)f_2(t,x_1,x_2) \le -\alpha(x_1+x_2) \quad (t \in \mathbb{R}, \ x_1 + x_2 \ge M).$$

Remark. The condition (H2) is natural for these systems. Consider the pair

$$\begin{cases} x' = x(a - dx - by) \\ y' = y(-c + kxy) \end{cases}$$

with a, b, c, d, and k continuous non-negative functions of t and $a(t) \le a_0 < \infty$, $b(t) \ge b_0 > 0$, $c(t) \ge c_0 > 0$, $d(t) \ge d_0 > 0$, and $k(t) \le k_0 < \infty$. Let E be a positive constant satisfying $Eb(t) > 2k(t)$ for all t. Then

$$\begin{aligned} Ex' + y'/(1+y) &\le x(aE - dEx - \tfrac{1}{2}bEy) - \tfrac{1}{2}bExy + kxy - cy/(1+y) \\ &\qquad \text{(and for large } x+y\text{)} \\ &\le -x - cy/(1+y) \le -\gamma(x+y)/[1+x+y]. \end{aligned}$$

Theorem 2.1. *Let* (H1) *and* (H2) *hold. Then for each* $x_0 \in \mathbb{R}^2_+$ *and every* $t_0 \in \mathbb{R}$, *every solution* $x(t)$ *of* (1.1) *with* $x(t_0) = x_0$ *exists and is bounded in forward time. Furthermore there is an open set* $U \subset \mathbb{R}^2_+$ *with compact closure such that* U, $\bar{U}$ *are forward invariant, and every solution eventually enters* U.

Proof.: Let $\sigma(t) = x_1(t) + x_2(t)$, and for a solution x and a function $V : \mathbb{R}^2_+ \to \mathbb{R}$ put $V(t) = V(x_1(t), x_2(t))$; thus $\dot{V}$ denotes differentiation along a solution.

Define

$$V(x_1, x_2) = \int_0^{x_1} h_1(s)\,ds + \int_0^{x_2} h_2(s)\,ds.$$

Then by (H2), for $\sigma \geq M$, $t \geq 0$, we have

$$\dot{V}(t) = h_1(x_1)f_1(t, x_1, x_2) + h_2(x_2)f_2(t, x_1, x_2) \leq -\alpha(\sigma). \tag{2.2}$$

It follows that for $t' > t$, if $\sigma(s) \geq M$ for $s \in [t, t']$, then

$$V(t') \leq V(t) - \int_t^{t'} \alpha(\sigma(s))\,ds. \tag{2.3}$$

Set also

$$W_1(p) = \int_0^{p/2} r(s)\,ds, \qquad W_2(p) = \int_0^p [h_1(s) + h_2(s)]\,ds.$$

Then

$$W_1(x_1 + x_2) = \int_0^{(x_1+x_2)/2} r(s)\,ds \leq \int_0^{\max[x_1,x_2]} r(s)\,ds \leq V(x_1, x_2) \leq W_2(x_1 + x_2).$$

Therefore

$$W_1(\sigma) \leq V(x_1, x_2) \leq W_2(\sigma). \tag{2.4}$$

Note also that W_1 and W_2 are non-decreasing, and by (H1) as $\sigma \to \infty$, $W_1(\sigma)$ and $W_2(\sigma) \to \infty$. It follows that given any $p > 0$, there is a $\nu(p) \geq p$ such that $W_2(p) = W_1(\nu(p))$.

The first step is to establish the following *a priori* bound:

$$\sigma(t) \leq \nu(\max[\sigma(t_0), M]). \tag{2.5}$$

The proof for $\sigma(t_0) \geq M$ is as follows, while a minor amendment yields the result for $\sigma(t_0) < M$. If the result is false, there are t_1, t_2 with $t_2 > t_1 \geq t_0$ such that $\sigma(t_0) = \sigma(t_1) \leq \nu(\sigma(t_0)) < \sigma(t_2)$ and $\sigma(t_2) \geq \sigma(t) \geq M$ for $t \in [t_1, t_2]$. Then,

$$\begin{aligned} W_1(\nu(\sigma(t_1))) = W_2(\sigma(t_1)) \geq V(t_1) \quad & \text{(by (2.4))} \\ > V(t_2) \quad & \text{(by (2.2))} \\ \geq W_1(\sigma(t_2)) \quad & \text{(by (2.4))}. \end{aligned}$$

Thus, as $W_1 \nearrow$, $\sigma(t_2) < \nu(\sigma(t_1)) = \nu(\sigma(t_0))$. This contradiction proves (2.5), and existence for $t \geq t_0$ follows from the standard existence theorem.

It is easy to deduce that for any $\sigma(t_0)$, there is a T such that $\sigma(T) \leq M$. For if $\sigma(t) > M$ for $t \geq t_0$, then by (2.5), $M \leq \sigma(t) \leq \nu(\sigma(t_0))$. So from compactness and (H2), there is a $\beta > 0$ such that $\alpha(\sigma(t)) > \beta$ for $t \geq t_0$. Therefore from (2.3), $V(t) \leq V(t_0) - \beta(t - t_0)$, and a contradiction is obtained on choosing t large enough.

To establish the forward invariance, choose any finite $d > \max_{\sigma \leq M} V(x_1, x_2)$, and define

$$U = \{x : V(x_1, x_2) < d\}, \quad U_1 = \{x : V(x_1, x_2) \leq d\}.$$

Clearly, U is open and U_1 is closed in $\mathbb{R}^2_+$. Further, U_1 is bounded (and so is compact) by (2.4) since $W_1(\sigma) \to \infty$ as $\sigma \to \infty$. From (2.3) and (H2), $\dot{V} < 0$ for $V(x_1, x_2) = d$. This establishes the forward invariance, and since orbits with $V(x_1, x_2) = d$ immediately enter U, this shows that $\bar{U} = U_1$. This completes the proof.

We now impose a further set of conditions covering the behavior of one species in the absence of the other

(H3) $F_1(t, x, 0) > a$ for all $t \in \mathbb{R}$ and all $x \in [0, \bar{\epsilon})$ for some $\bar{\epsilon} > 0$ and $a > 0$.

(H4) $F_1(t, \cdot, 0) \in C^1((0, \infty), \mathbb{R})$. There exists $\beta \in C^1((0, \infty), (0, \infty))$ such that given $b > 0$ there is an $a > 0$ with

$$\frac{\partial}{\partial x}[f_1(t, x, 0)\beta(x)] \leq -a \quad \text{for } 0 < x \leq b,\ t \in \mathbb{R}.$$

(H5) Given $\epsilon > 0$, there exists $\delta > 0$ such that

$$f_2(t, 0, x_2) \leq -\delta \quad \text{for } x_2 \geq \epsilon.$$

These conditions are satisfied by most predator-prey models. (H3) implies that the prey population increases at small densities in the absence of the predator, while (H4) implies that the prey population on its own decreases for large densities, and thus models intra-specific competition. However, note that (H4) is considerably weaker than the condition usually imposed; that is, that the per capita prey growth rate is monotone decreasing. (H5) simply states that the predator population tends to zero in the absence of the prey.

As indicated in the introduction, the key condition for permanence is based on a form of time average over a certain non-trivial global solution of the prey equation, and we now establish the existence of this solution.

Lemma 2.2. *There exists a unique global solution μ with $\mu(0) = \bar{\mu}$, say, of the equation $\dot{x} = f_1(t, x, 0)$ with $\liminf_{|t|\to\infty} \mu(t) > 0$, $\limsup_{|t|\to\infty} \mu(t) < \infty$. This solution is uniformly asymptotically stable and attracts all solutions except $x = 0$. That is, for any $x > 0$, $\tau \geq 0$,*

$$\lim_{t\to\infty} |\varphi(f_\tau, x, t) - \mu(t + \tau)| = 0,$$

where $\varphi(f_\tau, x, t)$ denotes the solution of

$$\dot{x} = f_1(t + \tau, x, 0), \quad x(0) = x.$$

Proof: For simplicity in notation write $f_1(t + \tau, x, 0) = g(t, x)$, and consider the equation $\dot{x} = g(t, x)$. From (H3) and (H2) there exist $\bar{x}_1, x_1, x_2, \bar{x}_2, \delta \in (0, \infty)$ with $\bar{x}_1 < x_1 < x_2 < \bar{x}_2$ such that $g(t, x) \geq \delta$ for $\bar{x}_1 \leq x \leq x_1$, and $g(t, x) \leq -\delta$ for $x_2 \leq x \leq \bar{x}_2$ and $t \in \mathbb{R}$. Take $I = (\bar{x}_1, \bar{x}_2)$. Let x_λ denote the solution with $x_\lambda(0) = \lambda$, where $\lambda \in I$, and consider solutions for $t < 0$. Let $(-\beta_\lambda, 0]$ be the maximal interval such that $x_\lambda(t) \in I$.

By uniqueness, solutions cannot cross, so $x_{\lambda_1}(t) > x_{\lambda_2}(t)$ for $t \in \mathbb{R}_-$ if $\lambda_1 > \lambda_2$. It follows that I may be covered by the disjoint intervals I_-, I_0, I_+ lying one above the other, where

$$\begin{aligned} I_- &= \{\lambda : \text{there exists a } \beta_\lambda < \infty \text{ with } x_\lambda(-\beta_\lambda) = \bar{x}_1\}, \\ I_0 &= \{\lambda : x_\lambda(t) \in I \text{ for } t \in \mathbb{R}_-\} \\ I_+ &= \{\lambda : \text{there exists a } \beta_\lambda < \infty \text{ with } x_\lambda(-\beta_\lambda) = \bar{x}_2\}. \end{aligned}$$

We shall show that I_- and I_+ are non-empty and open, from which it will follow that $I_0 \neq \emptyset$. To see that I_+ is non-empty, choose $\lambda \in (x_2, \bar{x}_2)$, note that $\dot{x}_\lambda \leq -\delta$, and reverse time. Then $x_\lambda(-t) \to \infty$ as $t \to \infty$, and the assertion follows. A similar argument applies for I_-. If I_+ is not open, then $I_+ = [\lambda_+, \bar{x}_2)$ for some $\lambda_+ < \bar{x}_2$. Then for some $T > 0$, $x_{\lambda_+}(-\beta_\lambda - T) > \bar{x}_2$. Hence, by continuity there is a neighborhood N of λ_+ such that $x_\lambda(-\beta_\lambda - T) > \bar{x}_2$ for $\lambda \in N$. Therefore there is a $\lambda < \lambda_+$ and $T \in \mathbb{R}$ with $x_\lambda(-T) = \bar{x}_2$. However, this contradicts the definition of I_+. A similar argument applies for I_-. This proves the existence of a global solution μ with the stated properties, since by Theorem 2.1 and (H3) these properties hold for $t \in \mathbb{R}_+$.

Define

$$V(x, y) = \left[\int_x^y \beta(s)\, ds\right]^2 \quad \text{for } \beta \text{ defined in (H4).}$$

By (H3) and Theorem 2.1 there exist $\underline{x}, \bar{x} \in (0, \infty)$ such that every solution $x(t)$ except $x = 0$ satisfies $x(t) \in (\underline{x}, \bar{x})$ for large enough t. Since $\beta > 0$, there exist $D_1, D_2 \in (0, \infty)$ such that

$$D_1^2(x-y)^2 \leq V(x,y) \leq D_2^2(x-y)^2 \quad \text{for } x, y \in (\underline{x}, \bar{x}). \tag{2.6}$$

Let x, y be two nontrivial solutions. As solutions cannot intersect it may be assumed without loss of generality that $x(t) < y(t)$ for $t \in \mathbb{R}$. We have

$$\dot{V}(t) = 2[\beta(y)g(t,y) - \beta(x)g(t,x)] \int_x^y \beta(s)\, ds \leq -2a(y-x) \int_x^y \beta(s)\, ds$$

(by the mean value theorem for derivatives and (H4)) so that

$$\dot{V}(t) \leq -2aD_1(y-x)^2 \quad \text{for } x, y \in (\underline{x}, \bar{x}) \tag{2.7}$$

by (2.6). Here, a is independent of x and y. The uniform asymptotic stability and global attractivity follow from [20; Theorem 15.5] and (2.6) and (2.7).

We have shown that there is a solution μ with the stated properties. Now, let x and y be two solutions with the properties of μ satisfying $x, y \in (\underline{x}, \bar{x})$ for some numbers $0 < \underline{x}, < \bar{x}$ and for $-\infty < t < \infty$. Now (2.6) and (2.7) hold for this pair x, y for all $t \in \mathbb{R}$ and so we have

$$\dot{V}(t) \leq -\gamma V(t), \quad \text{some } \gamma > 0. \tag{2.8}$$

If $x(t) \not\equiv y(t)$, then there is a $t_0 \in \mathbb{R}$ and a $\lambda > 0$ with $y(t_0) - x(t_0) = \lambda > 0$. Then for any $t_1 < t_0$ and $t \in [t_1, t_0]$,

$$V(t) \leq V(t_1)e^{-\gamma(t-t_1)} \leq D_2^2(x(t_1) - y(t_1))^2 e^{-\gamma(t-t_1)} \leq D_2^2 \bar{x}^2 e^{-\gamma(t-t_1)}$$

so that

$$D_1^2 \lambda^2 \leq V(t_0) \leq D_2^2 \bar{x}^2 e^{-\gamma(t_0 - t_1)},$$

a contradiction as $t_1 \to -\infty$. This establishes the uniqueness of μ.

Corollary 2.3. *With U as in Theorem 2.1, let $M^* = \max\{x : (x,0) \in \bar{U}\}$. If $f_1(\cdot, x, 0)$ is almost periodic for each $x \in [0, M^*]$, then μ is almost periodic with module in the module of f. If $f_1(\cdot, x, 0)$ has period Ω for each $x \in [0, M^*]$, then μ has period Ω.*

Proof: From (C1) and [6; Theorem 2.10] f_1 is uniformly almost periodic for $x \in [0, M^*]$. It follows from Theorem 2.1 and [6; Theorem 12.9] that there is a non-trivial almost periodic solution, which must be μ by the uniqueness. In view of (2.8), this result also follows from [19; Theorem 19.1].

3. The skew-product semi-flow.

The analysis of the differential equation (1.1) will be based on the induced skewproduct semi-flow described in [17]. We first introduce this, and then calculate the ω-limit sets corresponding to points on the axes $x_1 = 0$ and $x_2 = 0$ which are crucial in obtaining conditions for permanence.

Let f_τ denote the τ-translate of f; that is, $f_\tau(t, x) = f(t+\tau, x)$. Take the solution of the differential equation (1.1) such that $x(0) = x$ to be $\varphi(f, x, t)$. Equip $C(\mathbb{R} \times \mathbb{R}^2_+, \mathbb{R}^2)$ with the compact open topology, and note that this is metrizable with metric d, say. H^+ will denote the positive hull of f; that is, the closure of the set $\{f_\tau : \tau \geq 0\}$. By [17; Theorem III.7], (C1) implies that H^+ is compact. With U as in Theorem 2.1, the phase space is taken to be $X = H^+ \times \bar{U}$ (with the product topology), which is therefore compact. Define the map $\pi : X \to X$ by setting

$$\pi((f,x),t) = (f_t, \varphi(f,x,t)) \quad \text{for } t \in \mathbb{R}_+.$$

By [17; Theorem 4], (C2), together with Theorem 2.1 ensure that π is a semi-flow, the differential equation $\dot{x} = \tilde{f}(t,x)$ having a unique solution for every $\tilde{f} \in H^+$. Let $\omega(f,x)$ denote the ω-limit set of (f,x). The following result [17; p. 65] will be useful in dealing with the limit equations, that is with those equations coresponding to f^* where $(f^*, y) \in \omega(f,x)$.

Lemma 3.1. *Let $(f^*, y) \in \omega(f,x)$, so that there is a sequence $\{\tau_n\} \to \infty$ such that $f_{\tau_n} \to f^*$ and $\varphi(f,x,\tau_n) \to y$ as $n \to \infty$. Then $\varphi(f_{\tau_n}, \varphi(f,x,\tau_n), t) = \varphi(f,x,\tau_n + t)$ converges uniformly to $\varphi(f^*, y, t)$ on compact t-sets.*

For the one-dimensional system obtained by setting $x_2 = 0$, the global attractivity of the solution μ (Lemma 2.2) enables us to obtain a relatively simple characterization of $\omega(f_\tau, (x_1, 0))$. For convenience we temporarily denote $(\bar{\mu}, 0)$ by $\bar{\mu}$.

Lemma 3.2. *For any x of the form $(x_1, 0)$, with $x_1 > 0$, and any $\tau \in \mathbb{R}_+$, then $\omega(f_\tau, x) = \omega(f, \bar{\mu})$.*

Proof: We have $\mu(t+\tau) = \varphi(f, \bar{\mu}, t+\tau) = \varphi(f_\tau, \bar{\mu}_\tau, t)$ where $\bar{\mu}_\tau = \varphi(f, \bar{\mu}, \tau)$. Hence, by Lemma 2.2, $\lim_{t\to\infty} |\varphi(f_\tau, x, t) - \varphi(f_\tau, \bar{\mu}_\tau, t)| = 0$. Thus, from the definition of π,

$$\lim_{t\to\infty} d(\pi((f_\tau, x), t), \pi((f_\tau, \bar{\mu}_\tau), t) = 0. \tag{3.1}$$

Now if $(h, y) \in \omega(f_\tau, x)$, there is a sequence $\{t_n\} \to \infty$ such that

$$\lim_{n\to\infty} \pi((f_\tau, x), t_n) = (h, y).$$

Therefore by the triangle inequality and (3.1), $(h, y) \in \omega(f_\tau, \bar{\mu}_\tau)$. But

$$\omega(f_\tau, \bar{\mu}_\tau) = \omega(\pi((f, \bar{\mu}), \tau)) = \omega(f, \bar{\mu}).$$

Hence, $(h, y) \in \omega(f, \bar{\mu})$. This completes the proof.

Note finally that by (H5) every solution in the axis $x_2 = 0$ tends to zero. Thus, the ω-limit set of any point $(f_\tau, (0, x_2))$ is of the form $(g, (0, 0))$ for some $g \in H^+$.

4. An average type condition for permanence. We prove here the broad assertion made in the introduction that the key condition for permanence for (1.1) is that an "average" of the per capita predator rate of increase over the global solution μ should be positive. The proof is based on the idea of a so called "average" Liapunov function developed in [16], [11], and [14], and reviewed in [12], [13], see Theorem 4.1 below.

For $u = (g, x) \in X = H^+ \times \bar{U}$, let Q be the projection onto $\bar{U}$ so that $Q(u) = x$. Let $p = x_1^{\beta_1} x_2^{\beta_2}$ for some $\beta_1, \beta_2 > 0$, and define $V(u) = p(Qu)$; $V : X \to \mathbb{R}_+$ is a candidate for an average Liapunov function. In the following we need to consider $(f^*, y) \in \omega(f_\tau, x)$. From the definitions, $(F_1^*, F_2^*) = (f_1^*/x_1, f_2^*/x_2)$. It will be convenient below to contract the notation and use $(F^*, y) \in \omega(F_\tau, x)$ to mean $(f^*, y) \in \omega(f_\tau, x)$. We continue to assume throughout this section that (C1), (C2), and (H1)–(H5) hold.

Theorem 4.1. *Permanence holds for the system* (1.1) *if there exist* $\beta_1, \beta_2 > 0$ *such that*

$$\sup_{t>0} \int_0^t [\beta_1 F_1^*(s, \varphi(F^*, y, s)) + \beta_2 F_2^*(s, \varphi(F^*, y, s))]\, ds > 0 \tag{4.1}$$

for all $(F^*, y) \in \omega(F_\tau, x)$ *with* $\tau \geq 0$ *and* $x \in \bar{U} \cap \partial\mathbb{R}_+^2$.

Proof: Take $X = H^+ \times \bar{U}$, and let S be the compact subset $H^+(\bar{U} \cap \partial\mathbb{R}_+^2)$ of X. The result is a consequence of Corollary 2.3 of [14] which asserts that permanence holds if

$$\sup_{t>0} \liminf_{\substack{v \to u \\ v \in X \setminus S}} V(v \cdot t)/V(v) > \begin{cases} 1, & u \in \omega(S), \\ 0, & u \in S, \end{cases}$$

where $v \cdot t = \pi(v, t)$. To verify that these conditions are satisfied we proceed as follows. Let "dot" denote differentiation along an orbit. Then

$$V(v \cdot t)/V(v) = \exp\left\{ \int_0^t [\dot{V}(v \cdot s)/V(v \cdot s)]\, ds \right\}. \tag{*}$$

With $v = (f, y)$,

$$V(v \cdot s) = p(Q(v \cdot s)) = p(y_1(s), y_2(s)),$$

and

$$\begin{aligned} \dot{V}(v \cdot s)/V(v \cdot s) &= [1/p(y_1(s), y_2(s))](d/ds)p(y_1(s), y_2(s)) \\ &= \beta_1 F_1(s, x) + \beta_2 F_2(s, x) \end{aligned}$$

on carrying out the partial differentiation and using the differential equation (1.1). We then have from (*),

$$V(v \cdot t)/V(v) = \exp\left\{ \int_0^t [\beta_1 F_1(s, \varphi(F, y, s)) + \beta_2 F_2(s, \varphi(F, y, s))]\, ds \right\}.$$

The first condition above, which is required only on $\omega(S)$, is then an immediate consequence of (4.1). The second condition is a simple consequence of continuity.

Theorem 4.2. *Permanence holds for the system* (1.1) *if there exist* $\delta > 0$, α_0 *and a sequence* $\{t_k\} \to \infty$ *such that*

$$\frac{1}{t_k} \int_\alpha^{\alpha + t_k} F_2(s, \mu(s), 0)\, ds > \delta \quad \text{for } \alpha \geq \alpha_0, \quad k \geq 1. \tag{4.2}$$

Proof: The proof is based on showing that (4.1) holds. We continue to denote $(\bar{\mu}, 0)$ by $\bar{\mu}$ to simplify notation. Consider first any $x = (x_1, 0)$ where $x_1 > 0$. Then by Lemma 3.2, $(F^*, y) \in \omega(F, \bar{\mu})$. Therefore, by Lemma 3.1 there is a sequence $\{\tau_n\} \to \infty$ such that as $n \to \infty$

$$F_{\tau_n} \to F^*, \tag{4.3}$$

$$\varphi(F, \bar{\mu}, s + \tau_n) = \varphi(F_{\tau_n}, \varphi(f, \bar{\mu}, \tau_n), s) \to \varphi(F^*, y, s), \tag{4.4}$$

the convergence being uniform for s in compact subsets of $\mathbb{R}$. Now

$$\begin{aligned} &|F_{\tau_n}(s, \varphi(F, \bar{\mu}, s + \tau_n)) - F^*(s, \varphi(F^*, y, s))| \\ \leq &|F(s + \tau_n, \varphi(F, \bar{\mu}, s + \tau_n)) - F(s + \tau_n, \varphi(F^*, y, s))| \\ &+ |F_{\tau_n}(s, \varphi(F^*, y, s)) - F^*(s, \varphi(F^*, y, s))|. \end{aligned} \tag{4.5}$$

Since the range of each solution φ lies in a compact subset of $\mathbb{R}_+^2$, by (C1) and (4.4) the first term on the right-hand side tends to zero uniformly for s in compact subsets of $\mathbb{R}_+$. As the convergence in (4.3) is in the compact open topology, a similar conclusion holds for the other term. We conclude that, given $t \in \mathbb{R}_+$, there is a sequence $\{\epsilon_n(t)\} \to 0$ such that

$$\sup_{s \in [0,t]} |F_{\tau_n}(s, \varphi(F, \bar{\mu}, s + \tau_n)) - F^*(s, \varphi(F^*, y, s))| \leq \epsilon_n(t). \tag{4.6}$$

Consider the integrals in (4.1). From (4.4), for $i = 1, 2$ we have

$$\begin{aligned} \frac{1}{t} \int_0^t F_i^*(s, \varphi(F^*, y, s))\, ds &\geq \frac{1}{t} \int_0^t F_{i\tau_n}(s, \varphi(F, \bar{\mu}, s + \tau_n))\, ds - \epsilon_n(t) \\ &= \frac{1}{t} \int_{\tau_n}^{\tau_n + t} F_i(s, \mu(s), 0)\, ds - \epsilon_n(t). \end{aligned} \tag{4.7}$$

Since μ is a solution of $\dot{\mu} = \mu F_1(t, \mu(t), 0)$,

$$\frac{1}{t} \int_{\tau_n}^{\tau_n + t} F_1(s, \mu(s), 0)\, ds = \frac{1}{t} \log \mu(\tau_n + t)/\mu(\tau_n).$$

Therefore from (4.7)

$$\begin{aligned} &\frac{1}{t_k}\int_0^{t_k} \left[\beta_1 F_1^*(s,\varphi(F^*,y,s)) + \beta_2 F_2^*(s,\varphi(F^*,y,s))\right] ds \\ &\geq \beta_1 t_k^{-1} \log \frac{\mu(\tau_n + t)}{\mu(\tau_n)} + \beta_2 t_k^{-1} \int_{\tau_n}^{\tau_n + t_k} F_2(s,\mu(s),0)\, ds - 2\epsilon_n(t_k). \end{aligned} \tag{4.8}$$

Letting first $n \to \infty$ and then $k \to \infty$ in this inequality, we see that (4.1) follows from (4.2).

For points on the $x_1 = 0$ axis, a simplified version of the above argument is applicable as every solution tends to $(0,0)$. For from (H3) and (H5), choosing $\beta_2 = 1$ and sufficiently large β_1, we immediately obtain (4.1). This completes the proof.

Corollary 4.3. *Assume that $f(\cdot, x)$ is almost periodic for each x. Then the system is permanent if*

$$\lim_{t\to\infty} \frac{1}{t}\int_0^t F_2(s,\mu(s),0)\, ds > 0. \tag{4.9}$$

Proof: By (C1) and [6; Theorem 2.10], $f(t,x)$ is uniformly almost periodic for x in compact subsets of $\mathbb{R}_+^2$. Since $\mu(s) = \varphi(f,\bar{\mu},s)$ is almost periodic (Corollary 2.3), $F(s,\varphi(F,\bar{\mu},s)) = G(s)$, say, is almost periodic [6; Theorem 2.11]. Therefore by [6; Theorem 1.6] its hull is compact in the uniform norm. Hence, for some sequence, still denoted by $\{\tau_n\}$, $F_{\tau_n}(s,\varphi(F,\bar{\mu},s+\tau_n))$ converges in the uniform norm, and its limit must be $F^*(s,\varphi(F^*,y,s))$ by (4.6). Therefore in (4.6) we may replace the interval $[0,t]$ by $\mathbb{R}_+$ and drop the dependence of the ϵ_n on t.

Finally, as $G(s)$ is almost periodic, its averages converge. Thus

$$\begin{aligned} \lim_{t\to\infty} \frac{1}{t}\int_{\tau_n}^{\tau_n+t} G(s)\, ds &= \lim_{t\to\infty} \frac{1}{\tau_n + t}\,\frac{\tau_n + t}{t}\left[\int_0^{\tau_n+t} G(s) ds - \int_0^{\tau_n} G(s) ds\right] \\ &= \lim_{t\to\infty} \frac{1}{t}\int_0^t G(s)\, ds > 0 \quad \text{by (4.9).} \end{aligned}$$

In (4.8) replace τ_k by t; first let $t \to \infty$, and then let $n \to \infty$. This shows that (4.1) holds and completes the proof.

Corollary 4.4. *Assume that $f(\cdot, x)$ has period Ω for each x. Then the system is permanent if*

$$\int_0^\Omega F_2(s,\mu(s),0)\, ds > 0.$$

Proof: This is an obvious consequence of Theorem 4.3 on taking $t_k = k\Omega$.

A result similar to the following is proved in [1] by a global bifurcation argument. However, the concept of permanence enables us to write down the result very simply as we merely remark that it is an immediate consequence of Theorem 4.2 and a result of Massera [15] (see also [19; p. 167]).

Corollary 4.5. *Assume that $f(\cdot, x)$ has period Ω for each x and that*

$$\int_0^\Omega F_2(s, \mu(s), 0)\, ds > 0.$$

Then there is an Ω-periodic solution in the interior of $\mathbb{R}^2_+$.

Remark. Corollary 4.5 is trivial to prove and one would like a similar result in the almost periodic case. But it is most unlikely that such a result holds without drastic additional assumptions. In the one-dimensional case we were able to show the almost periodicity of μ because it was a unique globally stable solution on $-\infty < t < \infty$. The conclusion is then essentially an old result of Favard. Something akin to this would seem to be needed in $\mathbb{R}^2_+$ and that seems to require far more than we are prepared to ask.

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