

Dynamics of a non-autonomous ratio-dependent predator–prey system

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We investigate a non-autonomous ratio-dependent predator–prey system, whose autonomous versions have been analysed by several authors. For the general non-autonomous case, we address such properties as positive invariance, permanence, non-persistence and the globally asymptotic stability for the system. For the periodic and almost-periodic cases, we obtain conditions for existence, uniqueness and stability of a positive periodic solution, and a positive almost-periodic solution, respectively.

1. Introduction

The traditional Lotka–Volterra-type predator–prey model with Michaelis–Menten or Holling type-II functional response has received great attention from both theoretical and mathematical biologists, and has been well studied. The model is described by the following system of ordinary differential equations

$$x' = x[a - bx] - cy \frac{x}{m + x}, \quad y' = -dy + fy \frac{x}{m + x}, \quad (1.1)$$

where $x(t)$ and $y(t)$ stand for the densities of the prey and the predator, respectively, a , c , d and f are the prey intrinsic growth rate, capture rate, death rate of the predator and the conversion rate, respectively, a/b gives the carrying capacity of the prey and m is the half saturation constant. Here, the functional response $x/(m+x)$ is prey dependent only.

Recently, models with such a prey-dependent-only response function have been facing challenges from biology and physiology communities (see, for example, [1–5, 11, 12]). Based on growing biological and physiological evidence, some biologists have argued that, in many situations, especially when predators have to search for food (and therefore have to share or compete for food), the functional response in a prey–predator model should be ratio dependent, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. This has been strongly supported by numerous field and laboratory experiments and observations. Starting from this argument and the

traditional prey-dependent-only model (1.1), Arditi and Ginzburg [2] first proposed the following ratio-dependent predator–prey model:

$$x' = x[a - bx] - \frac{cxy}{my + x}, \quad y' = y \left[-d + \frac{fx}{my + x} \right]. \tag{1.2}$$

Note that (1.2) is a result of replacing the prey-dependent functional response $x/(m + x)$ in (1.1) by a ratio-dependent response $(x/y)/(m + x/y)$. For detailed justifications of (1.2) and its merits versus (1.1), see [2,8,17]. For the mathematical aspect, since Arditi and Ginzburg [2], system (1.2) has been studied by several authors and much richer dynamics have been obtained (see, for example, [7, 9, 13–16, 18]).

Ratio-dependent models have not yet been well studied, in the sense that most results are for models with constant environment. This means that the models have been assumed to be autonomous, that is, all biological or environmental parameters have been assumed to be constant in time. However, this is rarely the case in real life, as many biological and environmental parameters do vary in time (e.g. are naturally subject to seasonal fluctuations). When this is taken into account, a model must be non-autonomous, which is, of course, more difficult to analyse in general. But, in doing so, one can and should also take advantage of the properties of those varying parameters. For example, one may assume that the parameters are periodic or almost periodic for seasonal reasons.

In this paper, we will incorporate the varying property of the parameters into the model and consider the following non-autonomous version of (1.2),

$$x' = x[a(t) - b(t)x] - \frac{c(t)xy}{m(t)y + x}, \quad y' = y \left[-d(t) + \frac{f(t)x}{m(t)y + x} \right], \tag{1.3}$$

where all the variables and parameters have the same biological meanings as in (1.2), except that the parameters are now time dependent. In §2, we will address some basic problems for (1.3), such as positive invariance, permanence, non-persistence, extinction, dissipativity and globally asymptotic stability. Section 3 is devoted to the case when all parameters are periodic of the same period, and the main concern of this section is to establish criteria for the existence of a unique positive periodic solution of system (1.3) that is globally asymptotically stable. Section 4 is for the case when all parameters are almost periodic, and in this section we provide sufficient conditions for the existence and globally asymptotic stability of a unique positive almost-periodic solution of system (1.3). The methods used in this paper will be comparison theorems, coincidence degree theory and Lyapunov functions.

2. General case

In this section, we present some preliminary results including boundedness of solutions, permanence, non-persistence and the globally asymptotic stability of system (1.3). In the following discussion, we always assume that $a(t)$, $b(t)$, $c(t)$, $d(t)$, $m(t)$ and $f(t)$ are all continuous and bounded above and below by positive constants.

Let $R_+^2 := \{(x, y) \in R^2 \mid x \geq 0, y \geq 0\}$. For a bounded continuous function $g(t)$ on R , we use the following notation:

$$g^u := \sup_{t \in R} g(t), \quad g^l := \inf_{t \in R} g(t).$$

LEMMA 2.1. *Both the non-negative and positive cones of R^2 are positively invariant for system (1.3).*

Proof. Note that system (1.3) is equivalent to

$$\begin{aligned} x(t) &= x(t_0) \exp \left\{ \int_{t_0}^t \left[a(s) - b(s)x(s) - \frac{c(s)y(s)}{m(s)y(s) + x(s)} \right] ds \right\}, \\ y(t) &= y(t_0) \exp \left\{ \int_{t_0}^t \left[-d(s) + \frac{f(s)x(s)}{m(s)y(s) + x(s)} \right] ds \right\}. \end{aligned}$$

The assertion of the lemma follows immediately for all $t \geq t_0$. This completes the proof. □

In the remainder of this paper, for biological reasons, we only consider solutions $(x(t), y(t))$ with $x(t_0) > 0$ and $y(t_0) > 0$.

DEFINITION 2.2. The solution of system (1.3) is said to be ultimately bounded if there exist $B > 0$ such that, for every solution $(x(t), y(t))$ of (1.3), there exists $T > 0$ such that $\|(x(t), y(t))\| \leq B$ for all $t \geq t_0 + T$, where B is independent of the particular solution, while T may depend on the solution.

DEFINITION 2.3. System (1.3) is said to be permanent if there exist positive constants δ, Δ , with $0 < \delta < \Delta$, such that

$$\begin{aligned} \min \left\{ \liminf_{t \rightarrow +\infty} x(t), \liminf_{t \rightarrow +\infty} y(t) \right\} &\geq \delta, \\ \max \left\{ \limsup_{t \rightarrow +\infty} x(t), \limsup_{t \rightarrow +\infty} y(t) \right\} &\leq \Delta \end{aligned}$$

for all solutions of (1.3) with positive initial values. System (1.3) is said to be non-persistent if there is a positive solution $(x(t), y(t))$ of (1.3) satisfying

$$\min \left\{ \liminf_{t \rightarrow +\infty} x(t), \liminf_{t \rightarrow +\infty} y(t) \right\} = 0.$$

THEOREM 2.4. *If $f^1 > d^u, m^1 a^1 > c^u$, then the set Γ_ε defined by*

$$\Gamma_\varepsilon := \{(x, y) \in R^2 \mid m_1^\varepsilon \leq x \leq M_1^\varepsilon, m_2^\varepsilon \leq y \leq M_2^\varepsilon\} \tag{2.1}$$

is positively invariant with respect to system (1.3), where

$$\left. \begin{aligned} M_1^\varepsilon &:= \frac{a^u}{b^l} + \varepsilon, & M_2^\varepsilon &:= \frac{(f^u - d^l)M_1^\varepsilon}{d^l m^1}, \\ m_1^\varepsilon &:= \frac{m^1 a^1 - c^u}{m^1 b^u} - \varepsilon, & m_2^\varepsilon &:= \frac{(f^1 - d^u)m_1^\varepsilon}{m^u d^u}, \end{aligned} \right\} \tag{2.2}$$

and $\varepsilon \geq 0$ is sufficiently small so that $m_1^\varepsilon > 0$.

Proof. Let $(x(t), y(t))$ be the solution of (1.3) through $(x(t_0), y(t_0))$, with

$$m_1^\varepsilon \leq x(t_0) \leq M_1^\varepsilon \quad \text{and} \quad m_2^\varepsilon \leq y(t_0) \leq M_2^\varepsilon.$$

From the prey equation in (1.3) and the positivity of the solutions of (1.3), it follows that

$$x'(t) \leq x(t)[a^u - b^l x(t)] \leq b^l x(t) \left[\frac{a^u}{b^l} + \varepsilon - x(t) \right] = b^l x(t)[M_1^\varepsilon - x(t)], \quad t \geq t_0. \tag{2.3}$$

A standard comparison argument shows that

$$0 < x(t_0) \leq M_1^\varepsilon \quad \Rightarrow \quad x(t) \leq M_1^\varepsilon, \quad t \geq t_0,$$

which, together with the predator equation in (1.3), produces

$$y'(t) \leq y(t) \left[-d^l + \frac{f^u M_1^\varepsilon}{m^l y(t) + M_1^\varepsilon} \right] = \frac{m^l d^l y(t)}{m^l y(t) + M_1^\varepsilon} [M_2^\varepsilon - y(t)], \quad t \geq t_0, \tag{2.4}$$

and hence

$$0 < y(t_0) \leq M_2^\varepsilon \quad \Rightarrow \quad y(t) \leq M_2^\varepsilon, \quad t \geq t_0.$$

Similarly, the prey equation of system (1.3) also yields

$$\begin{aligned} x'(t) &\geq x(t) \left[a^l - b^u x(t) - \frac{c^u y(t)}{m^l y(t) + x(t)} \right] \\ &\geq x(t) \left[a^l - b^u x(t) - \frac{c^u}{m^l} \right] \\ &= b^u x(t) \left[\frac{m^l a^l - c^u}{m^l b^u} - x(t) \right] \\ &\geq b^u x(t) [m_1^\varepsilon - x(t)], \quad t \geq t_0, \end{aligned} \tag{2.5}$$

and therefore

$$x(t_0) \geq m_1^\varepsilon \quad \Rightarrow \quad x(t) \geq m_1^\varepsilon, \quad t \geq t_0.$$

Moreover, by the predator equation of system (1.3), we have

$$\begin{aligned} y'(t) &\geq y(t) \left[-d^u + \frac{f^l x(t)}{m^u y(t) + x(t)} \right] \\ &\geq y(t) \left[-d^u + \frac{f^l m_1^\varepsilon}{m^u y(t) + m_1^\varepsilon} \right] \\ &= \frac{m^u d^u y(t)}{m^u y(t) + m_1^\varepsilon} [m_2^\varepsilon - y(t)], \quad t \geq t_0, \end{aligned} \tag{2.6}$$

which implies

$$y(t_0) \geq m_2^\varepsilon \quad \Rightarrow \quad y(t) \geq m_2^\varepsilon, \quad t \geq t_0.$$

Thus Γ_ε is positively invariant for (1.3), and the proof is completed. □

LEMMA 2.5. *Let $(x(t), y(t))$ be a solution of system (1.3) with $x(t_0) > 0$ and $y(t_0) > 0$. Then we have $\lim_{t \rightarrow +\infty} \sup x(t) \leq M_1^0$. Moreover, if $m^l a^l > c^u$, then $\lim_{t \rightarrow +\infty} \inf x(t) \geq m_1^0$.*

Proof. Noting that (2.3) and (2.5) are valid, the conclusion follows from a standard comparison arguments directly. □

For the predator population, we can also have some estimates.

LEMMA 2.6. *If $f^l > d^u$, $m^l a^l > c^u$, then*

$$\liminf_{t \rightarrow +\infty} y(t) \geq m_2^0, \quad \limsup_{t \rightarrow +\infty} y(t) \leq M_2^0.$$

Proof. Since $\lim_{t \rightarrow +\infty} \sup x(t) \leq M_1^0$, for any sufficient small $\varepsilon > 0$, there is some $t_1 > t_0$ such that, for $t \geq t_1$,

$$x(t) < M_1^0 + \varepsilon.$$

Then, from the predator equation of system (1.3), it follows that

$$y'(t) \leq y(t) \left[-d^l + \frac{f^u M_1^\varepsilon}{m^l y(t) + M_1^\varepsilon} \right] = \frac{m^l d^l y(t)}{m^l y(t) + M_1^\varepsilon} \left[\frac{(f^u - d^l) M_1^\varepsilon}{m^l d^l} - y(t) \right]$$

for $t \geq t_1$. Hence, by using the comparison theorem of ordinary differential equations and the arbitrariness of ε , we have

$$\limsup_{t \rightarrow +\infty} y(t) \leq M_2^0.$$

By a similar argument, we can easily show that

$$\liminf_{t \rightarrow +\infty} y(t) \geq m_2^0.$$

This completes the proof. □

Lemmas 2.5 and 2.6 immediately lead to the following.

THEOREM 2.7. *If $f^l > d^u$, $m^l a^l > c^u$, then system (1.3) is permanent.*

From the proofs of lemmas 2.5 and 2.6, one can actually easily obtain the ultimate boundedness of Γ_ε with $\varepsilon > 0$ sufficiently small, as stated in the following theorem.

THEOREM 2.8. *If $f^l > d^u$, $m^l a^l > c^u$, then the set Γ_ε with $\varepsilon > 0$ defined by (2.1) is an ultimately bounded region of system (1.3).*

The following theorem gives conditions under which (1.3) is non-persistent.

THEOREM 2.9. *If $f^u < d^l$ or $c^l/m^u > a^u + d^u$, then system (1.3) is not persistent.*

Proof. If $f^u < d^l$, then, by the predator equation of (1.3), it is not difficult to show that

$$y'(t) \leq y(t)[-d^l + f^u],$$

which implies that $\lim_{t \rightarrow +\infty} y(t) = 0$.

If $c^l/m^u > a^u + d^u$, then there exists an $\alpha > 0$ such that

$$\frac{c^l}{m^u + \alpha} = a^u + d^u.$$

Let $\delta = x(t_0)/y(t_0) < \alpha$, we claim that

$$\frac{x(t)}{y(t)} < \alpha \quad \text{for all } t \geq t_0 \quad \text{and} \quad \lim_{t \rightarrow +\infty} x(t) = 0.$$

Otherwise, there exists a first time t_1 such that

$$\frac{x(t_1)}{y(t_1)} = \alpha \quad \text{and} \quad \frac{x(t)}{y(t)} < \alpha \quad \text{for all } t \in [t_0, t_1).$$

Then, for any $t \in [t_0, t_1]$, we have

$$x'(t) \leq x \left[a^u - \frac{c^l}{m^u + x(t)/y(t)} \right] \leq x \left[a^u - \frac{c^l}{m^u + \alpha} \right] = -d^u x(t),$$

which implies that

$$x(t) \leq x(t_0) \exp\{-d^u(t - t_0)\}. \tag{2.7}$$

However, for all $t \geq t_0$, we have

$$y' \geq -d^u y(t).$$

Then

$$y(t) \geq y(t_0) \exp\{-d^u(t - t_0)\},$$

which, together with (2.7), shows that

$$\frac{x(t)}{y(t)} \leq \frac{x(t_0)}{y(t_0)} = \delta < \alpha \quad \text{for all } t \in [t_0, t_1].$$

This is a contradiction to the existence of t_1 , which proves the claim. This, in turn, implies that

$$x(t) \leq x(t_0) \exp\{-d^u(t - t_0)\} \quad \text{for all } t \geq t_0,$$

and hence

$$\lim_{t \rightarrow +\infty} x(t) = 0.$$

This completes the proof. □

THEOREM 2.10. *If $c^l/m^u > a^u + d^u$, then there exists a positive solution $(x(t), y(t))$ of (1.3) satisfying $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 0)$.*

Proof. If $f^u \leq d^l$, then the conclusion directly follows from the previous arguments that led to theorem 2.9. In the rest of the proof, we assume that $f^u > d^l$. Let $\alpha = c^l/(a^u + d^u) - m^u$ and let $(x(t), y(t))$ be the solution of system (1.3) with $x(t_0)/y(t_0) < \alpha$. Then, by the proof of theorem 2.9, we know that

$$\frac{x(t)}{y(t)} < \alpha \quad \text{for all } t \geq t_0 \quad \text{and} \quad \lim_{t \rightarrow +\infty} x(t) = 0.$$

Next, we show $\lim_{t \rightarrow +\infty} y(t) = 0$. Since $y(t)$ is positive and bounded, we have

$$0 \leq \liminf_{t \rightarrow +\infty} y(t) \leq \limsup_{t \rightarrow +\infty} y(t) =: s < +\infty.$$

So we only need to show $s = 0$. Assume $s > 0$. Since $\lim_{t \rightarrow +\infty} x(t) = 0$, there exists a t_1 such that

$$x(t) < \frac{m^1 d^1 s}{2(f^u - d^l)} \quad \text{for all } t \geq t_1.$$

On the other hand, by the definition of $s > 0$, there must exist a $t_2 > t_1$ such that

$$y(t_2) > \frac{1}{2}s \quad \text{and} \quad y'(t_2) > 0.$$

However, $y'(t_2) > 0$ implies that

$$d(t_2)m(t_2)y(t_2) < x(t_2)(f(t_2) - d(t_2)) \leq x(t_2)(f^u - d^l),$$

and hence

$$x(t_2) > \frac{d(t_2)m(t_2)y(t_2)}{f^u - d^l} \geq \frac{m^1 d^1 s}{2(f^u - d^l)},$$

which is a contradiction. Thus we must have $s = 0$. This completes the proof. \square

REMARK 2.11. The above results generalize the corresponding results obtained by Kuang and Beretta [16] for the autonomous system (1.2). Note also that the first case in theorem 2.8 and the invariance property in theorem 2.4 were not explored in [16].

DEFINITION 2.12. A bounded non-negative solution $(\hat{x}(t), \hat{y}(t))$ of (1.3) is said to be globally asymptotically stable (or globally attractive) if, for any other solution $(x(t), y(t))^T$ of (1.3) with positive initial values, the following holds:

$$\lim_{t \rightarrow +\infty} (|x(t) - \hat{x}(t)| + |y(t) - \hat{y}(t)|) = 0.$$

REMARK 2.13. In general, if the above property holds for any two solutions with positive initial values, then we say system (1.3) is globally asymptotically stable. One can easily show that if system (1.3) has a bounded positive solution that is globally asymptotically stable, then system (1.3) is globally asymptotically stable, and vice versa.

The following lemma is from [6] and will be employed in establishing the globally asymptotic stability of (1.3).

LEMMA 2.14. Let h be a real number and f be a non-negative function defined on $[h, +\infty)$ such that f is integrable on $[h, +\infty)$ and is uniformly continuous on $[h, +\infty)$. Then $\lim_{t \rightarrow +\infty} f(t) = 0$.

THEOREM 2.15. Let $(\hat{x}(t), \hat{y}(t))$ be a bounded positive solution of system (1.3). If $f^1 > d^u$, $m^1 a^1 > c^u$ and

$$\inf_{t \in \mathbb{R}} \left\{ b(t) - \frac{[c(t) + m(t)f(t)]\hat{y}(t)}{[m(t)m_2^\varepsilon + m_1^\varepsilon][m(t)\hat{y}(t) + \hat{x}(t)]} \right\} > 0, \quad \inf_{t \in \mathbb{R}} \{m(t)f(t) - c(t)\} > 0, \tag{2.8}$$

where m_i^ε , M_i^ε , $i = 1, 2$, are defined in (2.2), then $(\hat{x}(t), \hat{y}(t))$ is globally asymptotically stable.

Proof. Let $(x(t), y(t))^T$ be any solution of (1.3) with positive initial value. Since Γ_ε is an ultimately bounded region of (1.3) (theorem 2.4), there exists a $T_1 > 0$ such that $(x(t), y(t)) \in \Gamma_\varepsilon$ and $(\hat{x}(t), \hat{y}(t)) \in \Gamma_\varepsilon$ for all $t \geq t_0 + T_1$.

Consider a Lyapunov function defined by

$$V(t) = |\ln\{x(t)\} - \ln\{\hat{x}(t)\}| + |\ln\{y(t)\} - \ln\{\hat{y}(t)\}|, \quad t \geq t_0. \tag{2.9}$$

A direct calculation of the right derivative $D^+V(t)$ of $V(t)$ along the solutions of (1.3) produces

$$\begin{aligned} D^+V(t) &= \operatorname{sgn}\{x(t) - \hat{x}(t)\} \\ &\quad \times \left[-b(t)[x(t) - \hat{x}(t)] - \left(\frac{c(t)y(t)}{m(t)y(t) + x(t)} - \frac{c(t)\hat{y}(t)}{m(t)\hat{y}(t) + \hat{x}(t)} \right) \right] \\ &\quad + \operatorname{sgn}\{y(t) - \hat{y}(t)\} \left[\frac{f(t)x(t)}{m(t)y(t)x(t)} - \frac{f(t)\hat{x}(t)}{m(t)\hat{y}(t) + \hat{x}(t)} \right] \\ &= -b(t)|x(t) - \hat{x}(t)| \\ &\quad - \operatorname{sgn}\{x(t) - \hat{x}(t)\} \frac{c(t)[\hat{x}(t)y(t) - x(t)\hat{y}(t)]}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} \\ &\quad + \operatorname{sgn}\{y(t) - \hat{y}(t)\} \frac{f(t)m(t)[x(t)\hat{y}(t) - \hat{x}(t)y(t)]}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} \\ &= -b(t)|x(t) - \hat{x}(t)| \\ &\quad - \operatorname{sgn}\{x(t) - \hat{x}(t)\} \frac{c(t)\hat{x}(t)[y(t) - \hat{y}(t)] + c(t)\hat{y}(t)[\hat{x}(t) - x(t)]}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} \\ &\quad + \operatorname{sgn}\{y(t) - \hat{y}(t)\} \\ &\quad \quad \times \frac{m(t)f(t)\hat{y}(t)[x(t) - \hat{x}(t)] + m(t)f(t)\hat{x}(t)[\hat{y}(t) - y(t)]}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} \\ &\leq - \left[b(t) - \frac{[c(t) + m(t)f(t)]\hat{y}(t)}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} \right] |x(t) - \hat{x}(t)| \\ &\quad + \frac{(c(t) - m(t)f(t))\hat{x}(t)}{[m(t)\hat{y}(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} |y(t) - \hat{y}(t)| \\ &\leq - \left[b(t) - \frac{[c(t) + m(t)f(t)]\hat{y}(t)}{[m(t)M_2^\varepsilon + M_1^\varepsilon][m(t)\hat{y}(t) + \hat{x}(t)]} \right] |x(t) - \hat{x}(t)| \\ &\quad + \frac{(c(t) - m(t)f(t))\hat{x}(t)}{[m(t)y(t) + x(t)][m(t)\hat{y}(t) + \hat{x}(t)]} |y(t) - \hat{y}(t)|, \end{aligned}$$

$t \geq t_0 + T_1.$
(2.10)

From (2.8), it follows that there exists a positive constant $\mu > 0$ such that

$$D^+V(t) \leq -\mu[|x(t) - \hat{x}(t)| + |y(t) - \hat{y}(t)|], \quad t \geq t_0 + T_1. \tag{2.11}$$

Integrating on both sides of (2.11) from $t_0 + T_1$ to t produces

$$V(t) + \mu \int_{t_0+T_1}^t [|x(s) - \hat{x}(s)| + |y(s) - \hat{y}(s)|] ds \leq V(t_0 + T_1) < +\infty, \quad t \geq t_0 + T_1.$$

Then

$$\int_{t_0+T_1}^t [|x(s) - \hat{x}(s)| + |y(s) - \hat{y}(s)|] ds \leq \mu^{-1}V(t_0 + T_1) < +\infty, \quad t \geq t_0 + T_1,$$

and hence $|x(t) - \hat{x}(t)| + |y(t) - \hat{y}(t)| \in L^1([t_0 + T_1, +\infty))$.

The boundedness of $\hat{x}(t)$ and $\hat{y}(t)$ and the ultimate boundedness of $x(t)$ and $y(t)$ imply that $x(t)$, $y(t)$, $\hat{x}(t)$ and $\hat{y}(t)$ all have bounded derivatives for $t \geq t_0 + T_1$ (from the equations satisfied by them). Then it follows that $|x(t) - \hat{x}(t)| + |y(t) - \hat{y}(t)|$ is uniformly continuous on $[t_0 + T_1, +\infty)$. By lemma 2.14, we have

$$\lim_{t \rightarrow +\infty} (|x(t) - \hat{x}(t)| + |y(t) - \hat{y}(t)|) = 0.$$

This completes the proof. □

COROLLARY 2.16. *Let $(\hat{x}(t), \hat{y}(t))$ be a bounded positive solution of system (1.3). If $f^1 > d^u$, $m^1 a^1 > c^u$ and one of the following conditions holds,*

$$\begin{aligned} & \inf_{t \in \mathbb{R}} \left\{ b(t) - \frac{(c(t) + m(t)f(t))M_2^\varepsilon}{(m(t)m_2^\varepsilon + m_1^\varepsilon)^2} \right\} > 0, & \inf_{t \in \mathbb{R}} \{f(t)m(t) - c(t)\} > 0, \\ & \inf_{t \in \mathbb{R}} \left\{ b(t) - \frac{c(t)\hat{y}(t) + m(t)f(t)M_2^\varepsilon}{[m(t)m_2^\varepsilon + m_1^\varepsilon][m(t)\hat{y}(t) + \hat{x}(t)]} \right\} > 0, & \inf_{t \in \mathbb{R}} \{m(t)f(t)m_1^\varepsilon - c(t)\hat{x}(t)\} > 0, \\ & \inf_{t \in \mathbb{R}} \left\{ b(t) - \frac{c(t)M_2^\varepsilon + m(t)f(t)\hat{y}(t)}{[m(t)m_2^\varepsilon + m_1^\varepsilon][m(t)\hat{y}(t) + \hat{x}(t)]} \right\} > 0, & \inf_{t \in \mathbb{R}} \{m(t)f(t)\hat{x}(t) - c(t)M_1^\varepsilon\} > 0, \\ & \inf_{t \in \mathbb{R}} \left\{ b(t) - \frac{[c(t) + m(t)f(t)]M_2^\varepsilon}{[m(t)m_2^\varepsilon + m_1^\varepsilon][m(t)\hat{y}(t) + \hat{x}(t)]} \right\} > 0, & \inf_{t \in \mathbb{R}} \{m(t)f(t) - c(t)\} > 0, \end{aligned}$$

where m_i^ε , M_i^ε , $i = 1, 2$, are defined by (2.2), then $(\hat{x}(t), \hat{y}(t))$ is globally asymptotically stable.

3. Periodic case

In this section, we will confine ourselves to the case when the parameters in system (1.3) are periodic of some common period. The assumption of periodicity of the parameters is a way of incorporating the periodicity of the environment. The periodic oscillation of the parameters seems reasonable in view of seasonal factors, e.g. mating habits, availability of food, weather conditions, harvesting and hunting, etc. A very basic and important problem in the study of a population-growth model with a periodic environment is the global existence and stability of positive periodic solution, which plays a similar role as a globally stable equilibrium does in an autonomous model. Thus it is reasonable to seek conditions under which the resulting periodic non-autonomous system would have a positive periodic solution that is globally asymptotically stable.

In the sequel, we will always assume that the parameters in system (1.3) are periodic in t of period $\omega > 0$ and will study the existence and stability of a positive periodic solution to system (1.3).

LEMMA 3.1 (Brouwer fixed-point theorem). *Let σ be a continuous operator that maps a closed bounded convex subset $\Omega \subset R^n$ into itself. Then Ω contains at least one fixed point of the operator σ , i.e. there exists an $x^* \in \Omega$ such that $\sigma(x^*) = x^*$.*

THEOREM 3.2. *If $f^1 > d^u$, $m^1 a^1 > c^u$, then (1.3) has at least one positive periodic solution of period ω , say $(x^*(t), y^*(t))$, which lies in Γ_ε , i.e. $m_1^\varepsilon \leq x^*(t) \leq M_1^\varepsilon$, $m_2^\varepsilon \leq y^*(t) \leq M_2^\varepsilon$, where $m_i^\varepsilon, M_i^\varepsilon, i = 1, 2$, are defined in (2.1).*

Proof. Define a shift operator, also known as a Poincaré mapping $\sigma : R^2 \rightarrow R^2$, by

$$\sigma((x_0, y_0)) = (x(\omega, t_0, (x_0, y_0)), y(\omega, t_0, (x_0, y_0))), \quad (x_0, y_0) \in R^2,$$

where $(x(t, t_0, (x_0, y_0)), y(t, t_0, (x_0, y_0)))$ denotes the solution of (1.3) through the point $(t_0, (x_0, y_0))$. Theorem 2.8 tells us that the set Γ_ε defined by (2.3) is positive invariant with respect to system (1.3), and hence the operator σ defined above maps Γ_ε into itself, i.e. $\sigma(\Gamma_\varepsilon) \subset \Gamma_\varepsilon$. Since the solution of (1.3) is continuous with respect to the initial value, the operator σ is continuous. It is not difficult to show that Γ_ε is a bounded closed convex set in R^2 . By lemma 3.1, σ has at least one fixed point in Γ_ε , i.e. there exists a $(x^*, y^*) \in \Gamma_\varepsilon$ such that

$$(x^*, y^*) = (x(\omega, t_0, (x^*, y^*)), y(\omega, t_0, (x^*, y^*))).$$

Therefore, there exists at least one positive periodic solution, say $(x^*(t), y^*(t))$, and the invariance of Γ_ε assures that $(x^*(t), y^*(t)) \in \Gamma_\varepsilon$. This completes the proof. \square

The conditions in theorem 3.2 are given in terms of the supremum and infimum of the parameters. Next, we will employ an alternative approach, that is, a continuation theorem in coincidence degree theory, to establish some criteria for the same problem but in terms of the averages of the related parameters over an interval of the common period. To this end, we need some preparation as below.

Let X, Z be normed vector spaces, $L : \text{Dom } L \subset X \rightarrow Z$ be a linear mapping and $N : X \rightarrow Z$ be a continuous mapping. The mapping L will be called a Fredholm mapping of index zero if $\dim \text{Ker } L = \text{codim Im } L < +\infty$ and $\text{Im } L$ is closed in Z . If L is a Fredholm mapping of index zero and there exist continuous projectors $P : X \rightarrow X$ and $Q : Z \rightarrow Z$ such that $\text{Im } P = \text{Ker } L, \text{Im } L = \text{Ker } Q = \text{Im}(I - Q)$, it follows that $L|_{\text{Dom } L \cap \text{Ker } P} : (I - P)X \rightarrow \text{Im } L$ is invertible. We denote the inverse of that map by K_P . If Ω is an open bounded subset of X , the mapping N will be called L -compact on $\bar{\Omega}$ if $QN(\bar{\Omega})$ is bounded and $K_P(I - Q)N : \bar{\Omega} \rightarrow X$ is compact. Since $\text{Im } Q$ is isomorphic to $\text{Ker } L$, there exists an isomorphism $J : \text{Im } Q \rightarrow \text{Ker } L$. The following lemma is from [10].

LEMMA 3.3 (continuation theorem). *Let L be a Fredholm mapping of index zero and N be L -compact on $\bar{\Omega}$. Suppose that the following hold.*

- (a) *For each $\lambda \in (0, 1)$, every solution x of $Lx = \lambda Nx$ is such that $x \notin \partial\Omega$.*
- (b) *$QNx \neq 0$ for each $x \in \partial\Omega \cap \text{Ker } L$ and the Brouwer degree*

$$\text{deg}\{JQN, \Omega \cap \text{Ker } L, 0\} \neq 0.$$

Then the operator equation $Lx = Nx$ has at least one solution lying in $\text{Dom } L \cap \bar{\Omega}$.

For a continuous and periodic function $g(t)$ with period ω , denote by \bar{g} the average of $g(t)$ over an interval of length ω , i.e.

$$\bar{g} := \frac{1}{\omega} \int_0^\omega g(t) dt.$$

Then we have the following lemma.

LEMMA 3.4. *If $\bar{f} > \bar{d}$, $\bar{a} > \overline{(c/m)}$, then the system of algebraic equations*

$$\bar{a} - \bar{b}v_1 - \frac{1}{\omega} \int_0^\omega \frac{c(t)v_2}{m(t)v_2 + v_1} dt = 0, \quad \bar{d} - \frac{1}{\omega} \int_0^\omega \frac{f(t)v_1}{m(t)v_2 + v_1} dt = 0 \quad (3.1)$$

has a unique solution $(v_1^*, v_2^*)^* \in R^2$ with $v_i^* > 0$.

Proof. Consider the function

$$f(u) = \bar{d} - \frac{1}{\omega} \int_0^\omega \frac{f(t)}{m(t)u + 1} dt, \quad u \geq 0.$$

One can easily see that

$$f(0) = \bar{d} - \bar{f} < 0, \quad \lim_{u \rightarrow +\infty} f(u) = \bar{d} > 0.$$

Then, from the zero point theorem and the monotonicity of $f(u)$, it follows that there exists a unique $u^* > 0$ such that $f(u^*) = 0$.

Now we can claim that $v_2^* = u^*v_1^*$, if (v_1^*, v_2^*) is a solution of (3.1). Substitute $v_2^* = u^*v_1^*$ into the first equation of (3.1) and simplify. We have

$$\begin{aligned} v_1^* &= \frac{1}{\bar{b}} \left(\bar{a} - \frac{1}{\omega} \int_0^\omega \frac{c(t)u^*}{m(t)u^* + 1} dt \right) \\ &\geq \frac{1}{\bar{b}} \left(\bar{a} - \frac{1}{\omega} \int_0^\omega \frac{c(t)u^*}{m(t)u^*} dt \right) \\ &= \frac{1}{\bar{b}} \left(\bar{a} - \overline{\left(\frac{c}{m} \right)} \right) > 0 \end{aligned}$$

and

$$v_2^* = u^*v_1^* > 0.$$

This completes the proof. □

THEOREM 3.5. *If $\bar{f} > \bar{d}$ and $\bar{a} > \overline{(c/m)}$, then system (1.3) has at least one positive ω -periodic solution, say $(x^*(t), y^*(t))$, and there exist positive constants $\alpha_i \geq m_i^\varepsilon$, $0 < \beta_i \leq M_i^\varepsilon$, $i = 1, 2$, such that*

$$\alpha_1 \leq x^*(t) \leq \beta_1, \quad \alpha_2 \leq y^*(t) \leq \beta_2.$$

Proof. Making the change of variables

$$x(t) = \exp\{\tilde{x}(t)\}, \quad y(t) = \exp\{\tilde{y}(t)\},$$

system (1.3) is reformulated as

$$\left. \begin{aligned} \tilde{x}'(t) &= a(t) - b(t) \exp\{\tilde{x}(t)\} - \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}}, \\ \tilde{y}'(t) &= -d(t) + \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}}. \end{aligned} \right\} \tag{3.2}$$

Let

$$X = Z = \{(\tilde{x}, \tilde{y})^T \in C(R, R^2) \mid \tilde{x}(t + \omega) = \tilde{x}(t), \tilde{y}(t + \omega) = \tilde{y}(t)\}$$

and

$$\|(\tilde{x}, \tilde{y})\| = \max_{t \in [0, \omega]} |\tilde{x}(t)| + \max_{t \in [0, \omega]} |\tilde{y}(t)|, \quad (\tilde{x}, \tilde{y}) \in X \text{ (or } Z).$$

Then X, Z are both Banach spaces when they are endowed with the above norm $\|\cdot\|$.

Let

$$N \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} a(t) - b(t) \exp\{\tilde{x}(t)\} - \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \\ -d(t) + \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \end{bmatrix}$$

and

$$L \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \tilde{x}' \\ \tilde{y}' \end{bmatrix}, \quad P \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = Q \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega} \int_0^\omega \tilde{x}(t) dt \\ \frac{1}{\omega} \int_0^\omega \tilde{y}(t) dt \end{bmatrix}, \quad \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} \in X.$$

Then

$$\begin{aligned} \text{Ker } L &= \{(\tilde{x}, \tilde{y}) \in X \mid (\tilde{x}, \tilde{y}) = (h_1, h_2) \in R^2\}, \\ \text{Im } L &= \left\{ (\tilde{x}, \tilde{y}) \in Z \mid \int_0^\omega \tilde{x}(t) dt = 0, \int_0^\omega \tilde{y}(t) dt = 0 \right\} \end{aligned}$$

and

$$\dim \text{Ker } L = 2 = \text{codim Im } L.$$

Since $\text{Im } L$ is closed in Z , L is a Fredholm mapping of index zero. It is easy to show that P, Q are continuous projectors such that

$$\text{Im } P = \text{Ker } L, \quad \text{Im } L = \text{Ker } Q = \text{Im}(I - Q).$$

Furthermore, the generalized inverse (to L) $K_P : \text{Im } L \rightarrow \text{Dom } L \cap \text{Ker } P$ exists and is given by

$$K_P \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \int_0^t \tilde{x}(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t \tilde{x}(s) ds dt \\ \int_0^t \tilde{y}(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t \tilde{y}(s) ds dt \end{bmatrix}.$$

Thus

$$QN \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega} \int_0^\omega \left[a(t) - b(t) \exp\{\tilde{x}(t)\} - \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \right] dt \\ \frac{1}{\omega} \int_0^\omega \left[-d(t) + \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \right] dt \end{bmatrix}$$

and

$$K_P(I - Q)N \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \int_0^t N_1(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t N_1(s) ds dt - \left(\frac{t}{\omega} - \frac{1}{2} \right) \int_0^\omega N_1(t) dt \\ \int_0^t N_2(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t N_2(s) ds dt - \left(\frac{t}{\omega} - \frac{1}{2} \right) \int_0^\omega N_2(t) dt \end{bmatrix}.$$

Obviously, QN and $K_P(I - Q)N$ are continuous. Using the Arzela–Ascoli theorem, it is not difficult to show that $K_P(I - Q)N(\bar{\Omega})$ is compact for any open bounded set $\Omega \subset X$. Moreover, $QN(\bar{\Omega})$ is bounded. Thus N is L -compact on $\bar{\Omega}$ with any open bounded set $\Omega \subset X$.

Now we reach the position to search for an appropriate open bounded subset Ω for the application of the continuation theorem. Corresponding to the operator equation $L\tilde{x} = \lambda N\tilde{x}$, $\lambda \in (0, 1)$, we have

$$\left. \begin{aligned} \tilde{x}'(t) &= \lambda \left[a(t) - b(t) \exp\{\tilde{x}(t)\} - \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \right], \\ \tilde{y}'(t) &= \lambda \left[-d(t) + \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \right]. \end{aligned} \right\} \quad (3.3)$$

Suppose that $(\tilde{x}(t), \tilde{y}(t)) \in X$ is an arbitrary solution of system (3.2) for a certain $\lambda \in (0, 1)$. Integrating on both sides of (3.3) over the interval $[0, \omega]$, we obtain

$$\left. \begin{aligned} \bar{a}\omega &= \int_0^\omega \left[b(t) \exp\{\tilde{x}(t)\} + \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} \right] dt, \\ \bar{d}\omega &= \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} dt. \end{aligned} \right\} \quad (3.4)$$

It follows from (3.3) and (3.4) that

$$\left. \begin{aligned} \int_0^\omega |\tilde{x}'(t)| dt &\leq \lambda \left[\int_0^\omega a(t) dt + \int_0^\omega b(t) \exp\{\tilde{x}(t)\} dt \right. \\ &\quad \left. + \int_0^\omega \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} dt \right] \\ &< 2\bar{a}\omega, \\ \int_0^\omega |\tilde{y}'(t)| dt &\leq \lambda \left[\int_0^\omega d(t) dt + \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} dt \right] \\ &< 2\bar{d}\omega. \end{aligned} \right\} \quad (3.5)$$

Since $(\tilde{x}(t), \tilde{y}(t)) \in X$, there exist $\xi_i, \eta_i \in [0, \omega]$, $i = 1, 2$, such that

$$\left. \begin{aligned} \tilde{x}(\xi_1) &= \min_{t \in [0, \omega]} \tilde{x}(t), & \tilde{x}(\eta_1) &= \max_{t \in [0, \omega]} \tilde{x}(t), \\ \tilde{y}(\xi_2) &= \min_{t \in [0, \omega]} \tilde{y}(t), & \tilde{y}(\eta_2) &= \max_{t \in [0, \omega]} \tilde{y}(t). \end{aligned} \right\} \tag{3.6}$$

From the first equation of (3.4) and (3.6), we obtain

$$\bar{a}\omega \geq \int_0^\omega b(t) \exp\{\tilde{x}(\xi_1)\} dt = \bar{b}\omega \exp\{\tilde{x}(\xi_1)\},$$

which reduces to

$$\tilde{x}(\xi_1) \leq \ln\left\{\frac{\bar{a}}{\bar{b}}\right\},$$

and hence

$$\tilde{x}(t) \leq \tilde{x}(\xi_1) + \int_0^\omega |\tilde{x}'(t)| dt \leq \ln\left\{\frac{\bar{a}}{\bar{b}}\right\} + 2\bar{a}\omega := H_1. \tag{3.7}$$

On the other hand, from the first equation of (3.4) and (3.6), we also have

$$\bar{a}\omega \leq \int_0^\omega \left[b(t) \exp\{\tilde{x}(\eta_1)\} + \frac{c(t)}{m(t)} \right] dt = \left(\frac{\bar{c}}{\bar{m}}\right)\omega + \bar{b}\omega \exp\{\tilde{x}(\eta_1)\}.$$

Then

$$\tilde{x}(\eta_1) \geq \ln\left\{\frac{\bar{a} - \overline{(c/m)}}{\bar{b}}\right\}.$$

Therefore,

$$\tilde{x}(t) \geq \tilde{x}(\eta_1) - \int_0^\omega |\tilde{x}'(t)| dt \geq \ln\left\{\frac{\bar{a} - \overline{(c/m)}}{\bar{b}}\right\} - 2\bar{a}\omega := H_2,$$

which, together with (3.7), leads to

$$\max_{t \in [0, \omega]} |\tilde{x}(t)| \leq \max\{|H_1|, |H_2|\} := B_1.$$

From the second equation of (3.4) and (3.6), we obtain

$$\begin{aligned} \bar{d}\omega &\leq \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\}} dt \\ &\leq \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(\xi_2)\}} dt \\ &= \frac{1}{\exp\{\tilde{y}(\xi_2)\}} \frac{\bar{a}}{\bar{b}} \overline{\left(\frac{f}{m}\right)} \exp\{2\bar{a}\omega\}\omega. \end{aligned}$$

Then

$$\tilde{y}(\xi_2) \leq \ln\left\{\frac{\bar{a}}{\bar{b}\bar{d}} \overline{\left(\frac{f}{m}\right)}\right\} + 2\bar{a}\omega.$$

Consequently,

$$\tilde{y}(t) \leq \tilde{y}(\xi_2) + \int_0^\omega |\tilde{y}'(t)| dt \leq \ln\left\{\frac{\bar{a}}{\bar{b}\bar{d}} \overline{\left(\frac{f}{m}\right)}\right\} + 2(\bar{a} + \bar{d})\omega := H_3. \tag{3.8}$$

The second equation of (3.4) also produces

$$\begin{aligned} \bar{d}\omega &= \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}} dt \\ &\geq \int_0^\omega \frac{f(t) \exp\{\tilde{x}(t)\}}{m^u \exp\{\tilde{y}(\eta_2)\} + \exp\{\tilde{x}(t)\}} dt \\ &\geq \int_0^\omega \frac{f(t)[(\bar{a} - \overline{(c/m)})/\bar{b}] \exp\{-2\bar{a}\omega\}}{m^u \exp\{\tilde{y}(\eta_2)\} + [(\bar{a} - \overline{(c/m)})/\bar{b}] \exp\{-2\bar{a}\omega\}} dt. \end{aligned}$$

Then it follows that

$$\tilde{y}(\eta_2) \geq \ln \left\{ \frac{(\bar{f} - \bar{d})(\bar{a} - \overline{(c/m)})}{m^u \bar{b} \bar{d}} \right\} - 2\bar{a}\omega,$$

and hence

$$\tilde{y}(t) \geq \tilde{y}(\eta_2) - \int_0^\omega |\tilde{y}'(t)| dt \geq \ln \left\{ \frac{(\bar{f} - \bar{d})(\bar{a} - \overline{(c/m)})}{m^u \bar{b} \bar{d}} \right\} - 2(\bar{a} + \bar{d})\omega := H_4,$$

which, together with (3.8), leads to

$$\max_{t \in [0, \omega]} |\tilde{y}(t)| \leq \max\{|H_3|, |H_4|\} := B_2.$$

Clearly, B_1 and B_2 are independent of λ . Take $B = B_1 + B_2 + B_3$, where $B_3 > 0$ is taken sufficiently large such that $\|(\ln\{v_1^*\}, \ln\{v_2^*\})\| = |\ln\{v_1^*\}| + |\ln\{v_2^*\}| < B_3$, where (v_1^*, v_2^*) is the unique solution of (3.1) with $v_1^* > 0, v_2^* > 0$.

Let $\Omega = \{(\tilde{x}, \tilde{y})^T \in X \mid \|(\tilde{x}, \tilde{y})\| < B\}$. Then it is clear that Ω verifies requirement (a) of lemma 3.3. When $(\tilde{x}, \tilde{y}) \in \partial\Omega \cap \text{Ker } L = \partial\Omega \cap R^2$, (\tilde{x}, \tilde{y}) is a constant vector in R^2 with $\|(\tilde{x}, \tilde{y})\| = |\tilde{x}| + |\tilde{y}| = B$. Then

$$QN \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = \begin{bmatrix} \bar{a} - \bar{b} \exp\{\tilde{x}\} - \frac{1}{\omega} \int_0^\omega \frac{c(t) \exp\{\tilde{y}\}}{m(t) \exp\{\tilde{y}\} + \exp\{\tilde{x}\}} dt \\ -\bar{d} + \frac{1}{\omega} \int_0^\omega \frac{f(t) \exp\{\tilde{x}\}}{m(t) \exp\{\tilde{y}\} + \exp\{\tilde{x}\}} dt \end{bmatrix} \neq \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

Moreover, direct calculation produces

$$\text{deg}(JQN, \Omega \cap \text{Ker } L, 0) = \text{sgn} \left\{ \frac{\bar{b}}{\omega} \int_0^\omega \frac{m(t)f(t)v_1^*}{(m(t)v_2^* + v_1^*)^2} dt \right\} \neq 0,$$

where $\text{deg}(\cdot, \cdot, \cdot)$ is the Brouwer degree and J is the identity mapping, since $\text{Im } Q = \text{Ker } L$. By now we have proved that Ω verifies all requirements of lemma 3.3. Then

$$L \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} = N \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix}$$

has at least one solution in $\text{Dom } L \cap \bar{\Omega}$, i.e. system (3.2) has at least one ω -periodic solution in $\text{Dom } L \cap \bar{\Omega}$, say $(\tilde{x}^*(t), \tilde{y}^*(t))^T$. Set

$$x^*(t) = \exp\{\tilde{x}^*(t)\}, \quad y^*(t) = \exp\{\tilde{y}^*(t)\}.$$

Then $(x^*(t), y^*(t))^T$ is an ω -periodic solution of system (1.3) with strictly positive components. The existence of positive constants $\alpha_1, \alpha_2, \beta_1, \beta_2$ directly follows from corollary 2.16 and the above discussion. This completes the proof. \square

Note that $f^l > d^u, m^l a^l > c^u$ imply that $\bar{f} > \bar{d}, \bar{a} > \overline{(c/m)}$. Together with theorem 2.15, it is not difficult to show the following.

COROLLARY 3.6. *Let all the assumptions in theorem 2.15 hold. Then system (1.3) has a unique positive ω -periodic solution, which is globally asymptotically stable.*

REMARK 3.7. If all the parameters in system (1.3) are positive constants, then (1.3) is the system considered in [16], and the assumptions in theorems 3.2 and 3.5 both reduce to $f > d, ma > c$, which ensure that system (1.1) has a unique positive equilibrium $E^* = (x^*, y^*)$, where

$$x^* = \frac{cd + f(ma - c)}{bm_f} = \frac{cd}{bm_f} + m_1, \quad y^* = \frac{f - d}{dm} x^*.$$

Assumption (2.8) in theorem 2.7 guarantees that E^* is globally asymptotically stable. In addition, in [16], Kuang and Beretta have proved that system (1.1) has no non-trivial positive periodic solutions. Now we can conclude that when system (1.3) reduces to (1.1) (as $\omega \rightarrow 0$), the positive periodic solution claimed above degenerated to a trivial positive periodic solution, i.e. the positive equilibrium $E^* = (x^*, y^*)$.

REMARK 3.8. Theorems 3.2 and 3.5 tell us that system (1.3) admits one positive periodic solution, provided that the (average) growth rate of prey is greater than the (average) consumption rate of prey and the (average) conversion rate that the prey provide for conversion into predator birth is greater than the (average) death rate of predator.

The following theorem explores the boundary periodic solution of (1.3).

THEOREM 3.9. *System (1.3) always has a periodic solution $(x_*(t), 0)$, where*

$$x_*(t) = \left(\exp \left\{ \int_0^\omega a(s) ds \right\} - 1 \right) \left(\int_t^{t+\omega} b(s) \exp \left\{ - \int_s^t a(\tau) d\tau \right\} ds \right)^{-1}. \quad (3.9)$$

Moreover, if

$$d(t) - \frac{c(t)}{m(t)} - f(t) > 0 \quad \text{for } t \in [0, \omega],$$

then $(x_*(t), 0)$ is globally asymptotically stable, i.e. $(x_*(t), 0)$ attracts all the solutions of (1.3) with positive initial values.

Proof. One can easily show that $(x_*(t), 0)$ is a solution of system (1.3) and $x_*(t + \omega) = x_*(t)$, i.e. $(x_*(t), 0)$ is a periodic solution of (1.3). Let $(x(t), y(t))$ be any solution of (1.3) with $x(t_0) > 0$ and $y(t_0) > 0$. In order to show that $(x_*(t), 0)$ is globally asymptotically stable, we only need to prove that

$$\lim_{t \rightarrow +\infty} |x(t) - x^*(t)| = 0,$$

since, from the predator equation in (1.3) and the assumption that $d(t) - c(t)/m(t) - f(t) \geq 0$ for $t \in [0, \omega]$, one can easily derive that $\lim_{t \rightarrow +\infty} y(t) = 0$.

Consider the Lyapunov function defined by

$$V(t) = |\ln\{x(t)\} - \ln\{x_*(t)\}| + |\ln\{y(t)\}|, \quad t \geq t_0.$$

Calculating the upper-right derivative of $V(t)$ along the solution of (1.2) produces

$$\begin{aligned} D^+V(t) &\leq -b(t)|x(t) - x_*(t)| + \frac{c(t)y}{m(t)y + x} - d(t) + \frac{f(t)x}{m(t)y + x} \\ &\leq -b(t)|x(t) - x_*(t)| + \frac{c(t)}{m(t)} - d(t) + f(t) \\ &\leq -b(t)|x(t) - x_*(t)| \\ &\leq -b^1|x(t) - x_*(t)|, \quad t \geq t_0, \end{aligned}$$

The rest of the proof is exactly the same as that carried out in theorem 2.15, and hence we omit the details here. □

COROLLARY 3.10. *The logistic equation with periodic coefficients*

$$x' = x[a(t) - b(t)x]$$

has a unique positive periodic solution $x^*(t)$, which is globally asymptotically stable, and $x^*(t)$ is given by (3.9).

The next result shows that the condition $\bar{f} > \bar{d}$ in theorem 3.5 is a necessary one.

THEOREM 3.11. *If system (1.3) admits a positive ω -periodic solution $(x^*(t), y^*(t))$, then $\bar{f} > \bar{d}$.*

The conclusion follows directly from the predator equation in (1.3) and the periodicity of $y^*(t)$.

REMARK 3.12. Theorems 3.5 and 3.11 raise an interesting but challenging problem: is the condition $\bar{a} > (c/m)$ also necessary? We leave this as an open problem.

4. Almost-periodic case

In some situations, the varying parameters $a(t)$, $b(t)$, $c(t)$, $d(t)$, $f(t)$ and $m(t)$ in (1.3) may not all be periodic, but fall into a more general class, i.e. the class of *almost-periodic* functions. For the definition and properties of almost-periodic functions, we refer to [19]. In this section, we consider such a situation and are concerned with the existence, uniqueness and stability of positive almost-periodic solution of (1.3). Throughout this section, in addition to the assumptions in § 2, we further assume that $a(t)$, $b(t)$, $c(t)$, $d(t)$, $f(t)$ and $m(t)$ are all almost periodic. Thus all the theorems in § 2 remain valid.

Let

$$x(t) = \exp\{\tilde{x}(t)\}, \quad y(t) = \exp\{\tilde{y}(t)\}.$$

Then system (1.3) becomes

$$\left. \begin{aligned} \tilde{x}'(t) &= a(t) - b(t) \exp\{\tilde{x}(t)\} - \frac{c(t) \exp\{\tilde{y}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}}, \\ \tilde{y}'(t) &= -d(t) + \frac{f(t) \exp\{\tilde{x}(t)\}}{m(t) \exp\{\tilde{y}(t)\} + \exp\{\tilde{x}(t)\}}. \end{aligned} \right\} \tag{4.1}$$

By theorem 2.8, it is not difficult to prove the following result.

THEOREM 4.1. *If $f^1 > d^u$, $m^1 a^1 > c^u$, then the set*

$$\Gamma_\varepsilon^* := \{(x, y) \in R^2 \mid \ln\{m_1^\varepsilon\} \leq x \leq \ln\{M_1^\varepsilon\}, \ln\{m_2^\varepsilon\} \leq y \leq \ln\{M_2^\varepsilon\}\}$$

is a positively invariant and ultimately bounded region of system (4.1), where m_i^ε , M_i^ε , $i = 1, 2$, are defined in (2.2).

In order to prove the main result of this section, we shall first introduce a useful lemma. Consider the ordinary differential equation

$$x' = f(t, x), \quad f(t, x) \in C(R \times D, R^n), \tag{4.2}$$

where D is an open set in R^n and $f(t, x)$ is almost periodic in t uniformly with respect to $x \in D$.

In order to discuss the existence of an almost-periodic solution of (4.2), we consider the product system of (4.2),

$$x' = f(t, x), \quad y' = f(t, y). \tag{4.3}$$

LEMMA 4.2 (cf. theorem 19.1 of [19]). *Suppose that there exists a Lyapunov function $V(t, x, y)$ defined on $[0, +\infty) \times D \times D$ that satisfies the following conditions.*

- (i) $\alpha(\|x - y\|) \leq V(t, x, y) \leq \beta(\|x - y\|)$, where $\alpha(\gamma)$ and $\beta(\gamma)$ are continuous, increasing and positive-definite.
- (ii) $|V(t, x_1, y_1) - V(t, x_2, y_2)| \leq K\{\|x_1 - x_2\| + \|y_1 - y_2\|\}$, where $K > 0$ is a constant.
- (iii) $V'_{(4.3)}(t, x, y) \leq -\mu V(|x - y|)$, where $\mu > 0$ is a constant.

Moreover, suppose that system (4.2) has a solution that remains in a compact set $S \subset D$ for all $t \geq t_0 \geq 0$. Then system (4.2) has a unique almost-periodic solution in S , which is uniformly asymptotically stable in D .

THEOREM 4.3. *If $f^1 > d^u$, $m^1 a^1 > c^u$ and*

$$\inf_{t \in R} \left\{ b(t) + \frac{(c(t) - f(t)m(t))M_2^\varepsilon}{(m(t)m_2^\varepsilon + m_1^\varepsilon)^2} \right\} > 0, \quad \inf_{t \in R} \{f(t)m(t) - c(t)\} > 0, \tag{4.4}$$

where m_i^ε , M_i^ε , $i = 1, 2$, are defined in (2.2), then system (1.3) has a unique positive almost-periodic solution, which is globally asymptotically stable, and, especially, is uniformly globally asymptotically stable in Γ_ε .

Proof. For $(x, y)^T \in \text{Int } R^2_+$, we define $\|(x, y)^T\| = x + y$. In order to prove that system (1.3) has a unique positive almost-periodic solution, which is uniformly asymptotically stable in Γ , it is equivalent to show that system (4.1) has a unique almost-periodic solution to be uniformly asymptotically stable in Γ^*_ε .

Consider the product system of (4.1),

$$\left. \begin{aligned} \tilde{x}'_1(t) &= a(t) - b(t) \exp\{\tilde{x}_1(t)\} - \frac{c(t) \exp\{\tilde{y}_1(t)\}}{m(t) \exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\}}, \\ \tilde{y}'_1(t) &= -d(t) + \frac{f(t) \exp\{\tilde{x}_1(t)\}}{m(t) \exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\}}, \\ \tilde{x}'_2(t) &= a(t) - b(t) \exp\{\tilde{x}_2(t)\} - \frac{c(t) \exp\{\tilde{y}_2(t)\}}{m(t) \exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\}}, \\ \tilde{y}'_2(t) &= -d(t) + \frac{f(t) \exp\{\tilde{x}_2(t)\}}{m(t) \exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\}}. \end{aligned} \right\} \quad (4.5)$$

Now we define a Lyapunov function on $[0, +\infty) \times \Gamma^*_\varepsilon \times \Gamma^*_\varepsilon$ as follows:

$$V(t, \tilde{x}_1, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2) = |\tilde{x}_1(t) - \tilde{x}_2(t)| + |\tilde{y}_1(t) - \tilde{y}_2(t)|.$$

Then condition (i) of lemma 4.2 is satisfied for $\alpha(\gamma) = \beta(\gamma) = \gamma$ for $\gamma \geq 0$. In addition,

$$\begin{aligned} &|V(t, \tilde{x}_1, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2) - V(t, \tilde{x}_3, \tilde{y}_3, \tilde{x}_4, \tilde{y}_4)| \\ &= (|\tilde{x}_1(t) - \tilde{x}_2(t)| + |\tilde{y}_1(t) - \tilde{y}_2(t)|) - (|\tilde{x}_3(t) - \tilde{x}_4(t)| + |\tilde{y}_3(t) - \tilde{y}_4(t)|) \\ &\leq |\tilde{x}_1(t) - \tilde{x}_3(t)| + |\tilde{y}_1(t) - \tilde{y}_3(t)| + |\tilde{x}_2(t) - \tilde{x}_4(t)| + |\tilde{y}_2(t) - \tilde{y}_4(t)| \\ &\leq \|(\tilde{x}_1(t), \tilde{y}_1(t)) - (\tilde{x}_3(t), \tilde{y}_3(t))\| + \|(\tilde{x}_2(t), \tilde{y}_2(t)) - (\tilde{x}_4(t), \tilde{y}_4(t))\|, \end{aligned} \quad (4.6)$$

which shows that condition (ii) of lemma 4.2 is also satisfied.

Let $(\tilde{x}_i(t), \tilde{y}_i(t))^T, i = 1, 2$, be any two solutions of (4.1) defined on $[0, +\infty) \times \Gamma^*_\varepsilon \times \Gamma^*_\varepsilon$.

Calculating the right derivative $D^+V(t)$ of $V(t)$ along the solutions of (4.1), we have

$$\begin{aligned} &D^+V(t) \\ &= \left[-b(t)(\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}) \right. \\ &\quad \left. - \left(\frac{c(t) \exp\{\tilde{y}_1(t)\}}{m(t) \exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\}} \right. \right. \\ &\quad \quad \left. \left. - \frac{c(t) \exp\{\tilde{y}_2(t)\}}{m(t) \exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\}} \right) \right] \text{sgn}(\tilde{x}_1(t) - \tilde{x}_2(t)) \\ &\quad + \left[\frac{f(t) \exp\{\tilde{x}_1(t)\}}{m(t) \exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\}} \right. \\ &\quad \quad \left. - \frac{f(t) \exp\{\tilde{x}_2(t)\}}{m(t) \exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\}} \right] \text{sgn}(\tilde{y}_1(t) - \tilde{y}_2(t)) \end{aligned}$$

$$\begin{aligned}
 &= \left[-b(t)(\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}) \right. \\
 &\quad \left. - \left(\frac{c(t)(\exp\{\tilde{x}_2(t) + \tilde{y}_1(t)\} - \exp\{\tilde{x}_1(t) + \tilde{y}_2(t)\})}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \right) \right] \\
 &\quad \times \operatorname{sgn}(\tilde{x}_1(t) - \tilde{x}_2(t)) \\
 &\quad + \left[\frac{f(t)m(t)(\exp\{\tilde{x}_1(t) + \tilde{y}_2(t)\} - \exp\{\tilde{x}_2(t) + \tilde{y}_1(t)\})}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \right] \\
 &\quad \times \operatorname{sgn}(\tilde{y}_1(t) - \tilde{y}_2(t)) \\
 &\leq -b(t)|\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}| \\
 &\quad + \frac{c(t)\exp\{\tilde{x}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \\
 &\quad \times |\exp\{\tilde{y}_1(t)\} - \exp\{\tilde{y}_2(t)\}| \\
 &\quad - \frac{c(t)\exp\{\tilde{y}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \\
 &\quad \times |\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}| \\
 &\quad + \frac{f(t)m(t)\exp\{\tilde{y}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \\
 &\quad \times |\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}| \\
 &\quad - \frac{f(t)m(t)\exp\{\tilde{x}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \\
 &\quad \times |\exp\{\tilde{y}_1(t)\} - \exp\{\tilde{y}_2(t)\}| \\
 &= \left[-b(t) + \frac{(f(t)m(t) - c(t))\exp\{\tilde{y}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \right] \\
 &\quad \times |\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}| \\
 &\quad + \frac{(c(t) - f(t)m(t))\exp\{\tilde{x}_2(t)\}}{(m(t)\exp\{\tilde{y}_1(t)\} + \exp\{\tilde{x}_1(t)\})(m(t)\exp\{\tilde{y}_2(t)\} + \exp\{\tilde{x}_2(t)\})} \\
 &\quad \times |\exp\{\tilde{y}_1(t)\} - \exp\{\tilde{y}_2(t)\}| \\
 &\leq \left[-b(t) + \frac{(f(t)m(t) - c(t))M_2^\varepsilon}{(m(t)m_2^\varepsilon + m_1^\varepsilon)^2} \right] |\exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\}| \\
 &\quad + \frac{(c(t) - f(t)m(t))m_1^\varepsilon}{(m(t)M_2^\varepsilon + M_1^\varepsilon)^2} |\exp\{\tilde{y}_1(t)\} - \exp\{\tilde{y}_2(t)\}|.
 \end{aligned}$$

Note that

$$\begin{cases} \exp\{\tilde{x}_1(t)\} - \exp\{\tilde{x}_2(t)\} = \exp\{\xi(t)\}(\tilde{x}_1(t) - \tilde{x}_2(t)), \\ \exp\{\tilde{y}_1(t)\} - \exp\{\tilde{y}_2(t)\} = \exp\{\eta(t)\}(\tilde{y}_1(t) - \tilde{y}_2(t)), \end{cases} \tag{4.7}$$

where $\xi(t)$ lies between $\tilde{x}_1(t)$ and $\tilde{x}_2(t)$, while $\eta(t)$ lies between $\tilde{y}_1(t)$ and $\tilde{y}_2(t)$.

Then we have

$$\begin{aligned}
 D^+V(t) &\leq - \left[b(t) - \frac{(f(t)m(t) - c(t))M_2^\varepsilon}{(m(t)m_2^\varepsilon + m_1^\varepsilon)^2} \right] m_1^\varepsilon |\tilde{x}_1(t) - \tilde{x}_2(t)| \\
 &\quad - \frac{(f(t)m(t) - c(t))m_1^\varepsilon}{(m(t)M_2^\varepsilon + M_1^\varepsilon)^2} m_2^\varepsilon |\tilde{y}_1(t) - \tilde{y}_2(t)| \\
 &\leq -\mu (|\tilde{x}_1(t) - \tilde{x}_2(t)| + |\tilde{y}_1(t) - \tilde{y}_2(t)|) \\
 &= -\mu \|(\tilde{x}_1(t), \tilde{y}_1(t)) - (\tilde{x}_2(t), \tilde{y}_2(t))\|,
 \end{aligned}
 \tag{4.8}$$

where

$$\mu = \min \left\{ \inf_{t \in R} \left\{ \left[b(t) - \frac{(f(t)m(t) - c(t))M_2^\varepsilon}{(m(t)m_2^\varepsilon + m_1^\varepsilon)^2} \right] m_1^\varepsilon \right\} \right.$$

and

$$\left. \inf_{t \in R} \left\{ \frac{(f(t)m(t) - c(t))m_1^\varepsilon}{(m(t)M_2 + M_1)^2} m_2^\varepsilon \right\} \right\} > 0.$$

Hence condition (iii) of lemma 4.2 is verified as well. Therefore, by theorem 4.1 and lemma 4.2, it follows that system (4.1) has a unique almost-periodic solution in Γ_ε^* , say $(\tilde{x}^*(t), \tilde{y}^*(t))^T$, which is uniformly asymptotically stable in Γ_ε^* . Hence system (1.3) has a unique positive almost-periodic solution $(x^*(t), y^*(t))^T$ in Γ_ε^* , which is uniformly asymptotically stable in Γ_ε^* . By corollary 2.16, we have that $(x^*(t), y^*(t))^T$ is globally asymptotically stable. This completes the proof. \square

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References

- 1 H. R. Akcakaya. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecol. Monogr.* **62** (1992), 119–142.
- 2 R. Arditi and L. R. Ginzburg. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* **139** (1989), 311–326.
- 3 R. Arditi and H. Saiah. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* **73** (1992), 1544–1551.
- 4 R. Arditi, L. R. Ginzburg and H. R. Akcakaya. Variation in plankton densities among lakes: a case for ratio-dependent models. *Am. Naturalist* **138** (1991), 1287–1296.
- 5 R. Arditi, N. Perrin and H. Saiah. Functional response and heterogeneities: an experimental test with cladocerans. *OIKOS* **60** (1991), 69–75.
- 6 I. Barbălat. Systems d’equations differential d’oscillations nonlineaires. *Rev. Roumaine Math. Pure Appl.* **4** (1959), 267–270.
- 7 E. Beretta and Y. Kuang. Global analysis in some delayed ratio-dependent predator–prey systems. *Nonlin. Analysis* **32** (1998), 381–408.
- 8 A. A. Berryman. The origins and evolution of predator–prey theory. *Ecology* **75** (1992), 1530–1535.
- 9 H. I. Freedman and R. M. Mathsen. Persistence in predator–prey systems with ratio-dependent predator influence. *Bull. Math. Biol.* **55** (1993), 817–827.

- 10 R. E. Gaines and J. L. Mawhin. *Coincidence degree and nonlinear differential equations* (Springer, 1977).
- 11 A. P. Gutierrez. The physiological basis of ratio-dependent predator–prey theory: a metabolic pool model of Nicholson’s blowflies as an example. *Ecology* **73** (1992), 1552–1563.
- 12 I. Hanski. The functional response of predator: worries about scale. *TREE* **6** (1991), 141–142.
- 13 S.-B. Hsu, T.-W. Hwang and Y. Kuang. Global analysis of Michaelis–Menten type ratio-dependent predator–prey system. *J. Math. Biol.* **42** (2001), 489–506.
- 14 C. Jost, O. Arino and R. Arditi. About deterministic extinction in ratio-dependent predator–prey models. *Bull. Math. Biol.* **61** (1999), 19–32.
- 15 Y. Kuang. Rich dynamics of Gauss-type ratio-dependent predator–prey systems. *Fields Inst. Commun.* **21** (1999), 325–337.
- 16 Y. Kuang and E. Beretta. Global qualitative analysis of a ratio-dependent predator–prey systems. *J. Math. Biol.* **36** (1998), 389–406.
- 17 P. Lundberg and J. M. Fryxell. Expected population density versus productivity in ratio-dependent and prey-dependent models. *Am. Naturalist* **147** (1995), 153–161.
- 18 D. Xiao and S. Ruan. Global dynamics of a ratio-dependent predator–prey system. *J. Math. Biol.* **43** (2001), 268–290.
- 19 T. Yoshizawa. *Stability theory and the existence of periodic solutions and almost periodic solutions*, pp. 210–223 (Springer, 1975).

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