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The effect of diffusion on giant pandas that live in complex patchy environments*

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Abstract. The habitat loss and fragmentation is almost the greatest threat to the survival of the wild giant panda. In this paper, we construct a mathematical model to consider the effect of diffusion on giant pandas that live in complex patchy environments. Our discussion includes the studying of a diffusive n-dimensional single species model, sufficient conditions are derived for the permanence and extinction of the giant panda species. Especially, we also discuss the situations of diffusion of giant pandas between two patches, and numerical simulations are presented to illustrate the results. Furthermore, we consider the existence, uniqueness, and global stability of the positive periodic solution of the n-dimensional single species model. The implications of these results are significant for giant panda conservation.

Keywords: giant panda, diffusion, patch, permanence, extinction, stability.

1 Introduction

With growing levels of human activity and frequent natural disturbances throughout the world, it is increasingly important that both research and management efforts take into account the widespread landscape fragmentation and its consequences for biodiversity conservation [6]. Giant Panda is a flag species for biodiversity conservation in China.

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Natural disasters (including earthquakes and hurricanes) and human activities (including road construction, urbanization and farming) are the primary causes of habitat loss, fragmentation and degradation [1]. Now they are occurring only in high mountains and steep valleys of the east edge of Qingzang plateau, i.e. Minshan, Qionglaishan, Daxiangling, Xiaoxiangling, Liangshan and Qinling. The giant panda populations living in these mountains have been separated completely. Even in one mountain system, where the giant panda is distributed, fragmentation of habitats and populations is severe. Severe and irreversible habitat fragmentation is a major threat to the survival of the giant panda.

The results of the mathematical model provide us with information on the probability of survival or extinction given certain assumptions on the biology and status of the population. Therefore, we can use mathematical models to develop conservation strategies to reduce the risks of extinction.

As well as we known, each patch has different habitats. For some patch, the number of giant pandas is large, and the reproduction rate of giant pandas is high because they are easy to find spouse. In [9], the authors obtained the birth rate function of captive giant panda by numerical fitting method, and use logistic equation to represent the natural growth law of the giant panda. Therefore, classical logistic equation can be used to describe the changes on the population of the giant panda in the above patch:

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = b(t)x(t) - c(t)x^2(t), \tag{1}$$

where $b(t)$, i.e. the growth rate function makes reference to the function in [9]. The population of giant pandas grows and develops better, giant pandas are able to continue to survive in the patch, we say this patch food-rich patch.

For the common patch, the situation of giant pandas' habitat is in general, the number of giant pandas is small, and it is difficult for giant pandas to find spouses, which results in low reproductive rate. We call the patch normal patch, and use the differential equation with Allee effect to describe the growth mode of the giant panda:

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = \frac{a(t)x^2(t)}{N(t) + x(t)} - b(t)x(t) - c(t)x^2(t). \tag{2}$$

Allee effects play an important role in extinction of already endangered rare or dramatically declining species [3]. We find that in most of the current giant panda population, the growth of giant pandas can comply with the model, where $N(t)$ is the sparse coefficient. When the giant panda population density is low, the population density growth rate and population density are positively correlated, when the population density is less than a certain value, the population density of negative growth causes the ultimate demise of the local population.

There are also some patch, the giant panda's habitat is bad, such as: the giant panda's food is scarce as a result of natural disasters or staple bamboo flowering or lack of water. Thus, the number of giant pandas in the patch is extremely rare, the species will vanish without the contribution from other patches. We still use the logic equation (1) to describe the dynamic changes of the giant panda population in the patch. But the giant panda population growth rate is negative, that is, $b(t) < 0$. We call it a food-poor patch.

According to fieldwork, we know that giant pandas sometimes migrate from one patch to another for finding food, mating, etc. In order to protect the rare species, we should investigate the circumstance of each patch and consider the effect of diffusion on the permanence and extinction of giant pandas that live in different patches. Different from the former studies, we pay attention on the more complicate situations in conservation giant pandas which live in three kinds of patchy environments: food-rich patch, normal patch and food-poor patch. In this case, we consider the system as being composed of patches connected by linear diffusions, each patch being assumed to be occupied by giant pandas,

$$\begin{aligned}\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} &= \frac{a_i(t)x_i^2(t)}{N_i(t)+x_i(t)} - b_i(t)x_i(t) - c_i(t)x_i^2(t) + \sum_{k=1}^{n} D_{ki}(t)x_k(t) \\ &\quad - \sum_{k=1}^{n} D_{ik}(t)x_i(t), \\ \frac{\mathrm{d}x_j(t)}{\mathrm{d}t} &= b_j(t)x_j(t) - c_j(t)x_j^2(t) + \sum_{k=1}^{n} D_{kj}(t)x_k(t) - \sum_{k=1}^{n} D_{jk}(t)x_j(t).\end{aligned} \tag{3}$$

Let $N = \{1, 2, \dots n\}$, I and J are two nonempty subsets of N, $I \cup J = N$, $i \in I$, $j \in J$, $1 \leqslant i < j \leqslant n$, $1 \leqslant k \leqslant n$, $k \in N$, and $x_k(t)$ $(k = 1, 2, \dots, n)$ denotes the giant panda population x in patch k. All coefficients in system (3) are ω-periodic and continuous for $t \geqslant 0$, $N_i(t)$, $a_i(t)$, $b_i(t)$, $D_{ki}(t)$, $D_{ik}(t)$, $D_{kj}(t)$ and $D_{jk}(t)$ are all positive, while $c_i(t)$, $c_j(t)$ are nonnegative. The function $b_j(t)$ is the growth rate for giant panda population $x_j(t)$ in patch j, $N_i(t)$ is sparse coefficient, and $D_{kj}(t)$ is the diffusion coefficient of population $x_j(t)$ from patch k to patch j.

The present paper considers the following interesting problem: To what extent does diffusion lead to the permanence or extinction of the giant panda species which living in three kinds of complicate patchy environments?

The paper is organized as following. In the next section, we present some notations, state two lemmas which will be essential to our proofs. In Section 3, a diffusive n-dimensional single species model is given, and its permanence and extinction are both considered. In order to study how diffusion affects the continual survival of giant panda which lives in different habitats, we also discuss the permanence and extinction for three kinds of 2-dimensional single species models. In Section 4, it is shown that the system has a unique globally asymptotically stable positive periodic solution provided that the n-dimensional system is permanent. The biological meaning of the results obtained in Sections 3 and 4 and the control measures to protect the extinction of giant pandas are discussed in Section 5.

2 Some basic results

In this section, we introduce some definitions and notations and state some results which will be useful in subsequent sections.

Let C denote the space of all bounded continuous function $F : R \to R$. For any continuous ω-periodic function $f(t)$ defined on R, we denote

$$A_w\big(f(t)\big) = \omega^{-1} \int_0^{\omega} f(t)\,\mathrm{d}t, \qquad f^M = \max_{t\in[0,\omega]} f(t), \qquad f^L = \min_{t\in[0,\omega]} f(t). \tag{4}$$

In order to study the permanence of (3), we need the information on the following periodic logistic model:

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = b(t)x(t) - a(t)x^2(t), \tag{5}$$

where $b(t)$ and $a(t)$ are ω-periodic functions, $a^M > 0$. We have the following well-known results.

Lemma 1. (*See* [13].) *If* $A_\omega(b(t)) > 0$*, then* (5) *has a unique globally asymptotically stable positive* ω*-periodic solution*; *if* $A_\omega(b(t)) \leqslant 0$*, then the trivial solution* $x = 0$ *of* (5) *is globally asymptotically stable.*

Lemma 2. (*See* [8].) *Let* $x(t)$ *and* $y(t)$ *be solutions of* $\mathrm{d}x(t)/\mathrm{d}t = F(t,x)$ *and* $\mathrm{d}y(t)/\mathrm{d}t = G(t,y)$*, respectively, where both systems are assumed to have the uniqueness property for initial value problems. Assume both* $x(t)$ *and* $y(t)$ *belong to a domain* $D \subseteq R^n$ *for* $[t_0,t_1]$ *in which one of two systems is cooperative and*

$$F(t,z) \leqslant G(t,z), \quad (t,z) \in [t_0,t_1] \times D.$$

If $x(t_0) \leqslant y(t_0)$*, then* $x(t) \leqslant y(t)$ *for all* t *satisfying* $t_0 \leqslant t \leqslant t_1$*. If* $F = G$ *and* $x(t_0) < y(t_0)$*, then* $x(t) < y(t)$ *for all* t *satisfying* $t_0 \leqslant t \leqslant t_1$*.*

3 Permanence and extinction

Definition 1. The system of differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = F(t,x), \quad x \in R^n,$$

is said to be permanent if there exists a compact set D in the interior of $R^n_+ = \{(x_1, x_2, \dots, x_n) \in R^n \mid x_k \geqslant 0,\ k = 1,2,\dots,n\}$, such that all solutions starting in the interior of R^n_+ ultimately enter D.

Theorem 1. *Given any* $\xi_k > 0$ ($k = 1,2,\dots,n$)*, the initial value problem*

$$\begin{aligned}
\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} &= \frac{a_i(t)x_i^2(t)}{N_i(t) + x_i(t)} - b_i(t)x_i(t) - c_i(t)x_i^2(t) + \sum_{k=1}^n D_{ki}(t)x_k(t) \\
&\quad - \sum_{k=1}^n D_{ik}(t)x_i(t), \\
\frac{\mathrm{d}x_j(t)}{\mathrm{d}t} &= b_j(t)x_j(t) - c_j(t)x_j^2(t) + \sum_{k=1}^n D_{kj}(t)x_k(t) - \sum_{k=1}^n D_{jk}(t)x_j(t), \\
x_k(0) &= \xi_k > 0,
\end{aligned} \tag{6}$$

has a unique solution $x(t) = (x_1(t), x_2(t), \ldots, x_n(t))$ *which exists for all* $t \geqslant 0$. *Moreover, there exist* $M > 0$, $T > 0$ *such that*

$$0 < x_k(t) \leqslant M \quad \textit{for } t \geqslant T, \tag{7}$$

the region $D = \{(x_1, x_2, \ldots, x_n) \mid 0 < x_i \leqslant M,\ i = 1, 2, \ldots, n\}$ *is positively invariant with respect to* (3).

Proof. Obviously, R_+^n is a positively invariant set of (3). Define

$$V\big(x(t)\big) = \max_{1 \leqslant k \leqslant n} \big\{x_k(t)\big\}.$$

For every given $t > 0$, there exists an integer k $(1 \leqslant k \leqslant n)$ such that

$$V(t) = V\big(x(t)\big) = x_k(t).$$

Calculating the upper-right derivative of $V(x(t))$ along the positive solution of (6), we have

$$D^+V(t) \leqslant V(t)\big(b(t) - c(t)V(t)\big),$$

where

$$b(t) = \max_{i \in I, j \in J} \big\{a_i(t) - b_i(t), b_j(t)\big\}, \qquad c(t) = \min_{1 \leqslant k \leqslant n} \big\{c_k(t)\big\}.$$

Denote $M = (|b|^M + \varepsilon)/c^L$, where ε is any positive constant. For any $t^* > 0$, if $V \geqslant M$ for all $t \geqslant t^*$, then $D^+V \leqslant -\varepsilon V$ for all $t \geqslant t^*$, this will lead to a contradiction. Hence, there must exist a $T > t^*$ such that $V(T) \leqslant M$. If $V(t) \leqslant M$ for all $t \geqslant T$, then $V(t)$ is bounded. If not, suppose that $V(t_1) > M$, where $t_1 > T$. Then, from the above discussion, there exist t_1^* and t_1^{**} such that $V(t_1^*) = V(t_1^{**}) = M$ and $V(t) > M$ for all $t_1^* < t < t_1^{**}$. This means $V(t)$ at least has a maximum within $t_1^* \leqslant t \leqslant t_1^{**}$. Now suppose $V(t)$ attains its maximum at t_2. This implies that $D^+V > 0$ for $t_2 - \delta < t < t_2$ and that δ is a positive constant. This is in contradiction with

$$D^+V(t) \leqslant V(t)\big(b(t) - c(t)V(t)\big).$$

Therefore, we have that in any case $V(t) \leqslant M$ for all $t \geqslant T$, i.e. $x_k(t) \leqslant M$ $(k = 1, 2, \ldots, n)$.

But the ultimately boundedness implies that $x(t)$ exists for all $t > 0$. Furthermore,

$$\left.\frac{dx_k(t)}{\mathrm{d}t}\right|_{x_k = M} < M\big(|b|^M - c^L M\big) < 0.$$

Hence, all solutions of (3) initiating in boundary of D enter the region D for $t \geqslant 0$, so D is positively invariant with respect to (3). This completes the proof. □

Theorem 2. *If there exists* $j_0 (j_0 \in J)$ *such that*

$$A_w\left[b_{j_0} - \sum_{k=1}^{n} D_{j_0 k}(t)\right] > 0 \tag{8}$$

holds, then there exist δ_k $(0 < \delta_k < M)$ *and* $T \geqslant 0$ *such that the solution of* (6) *satisfies*

$$x_k(t) \geqslant \delta_k, \quad t \geqslant T,\ k = 1, 2, \dots, n.$$

Proof. Suppose that (8) holds, we have

$$\begin{aligned}\frac{\mathrm{d}x_{j_0}(t)}{\mathrm{d}t} &\geqslant b_{j_0}(t)x_{j_0}(t) - c_{j_0}(t)x_{j_0}^2(t) - \sum_{k=1}^{n} D_{j_0k}x_{j_0}(t) \\ &= \left[b_{j_0}(t) - \sum_{k=1}^{n} D_{j_0k}\right]x_{j_0}(t) - c_{j_0}(t)x_{j_0}^2(t). \end{aligned} \tag{9}$$

By Lemma 1, if condition (8) holds, the logistic equation

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = \left[b_{j_0}(t) - \sum_{k=1}^{n} D_{j_0k}\right]u(t) - c_{j_0}(t)u^2(t)$$

has a unique positive globally asymptotically stable ω-periodic solution $u^*(t)$, and there exist $\varepsilon_{j_0} > 0$ and T_{j_0} such that

$$\left|u(t) - u^*(t)\right| < \varepsilon_{j_0}, \quad t \geqslant T_{j_0}.$$

Let $u(t)$ be the solution of (9) with $u(0) = x_{j_0}(0)$. By Lemma 2, $x_{j_0}(t) \geqslant u(t) > 0$. Then $x_{j_0}(t) \geqslant u(t) > u^*(t) - \varepsilon_{j_0} =: \eta_{j_0}$.

Moreover, for every $j \neq j_0$, we have

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} \geqslant -c_j^M x_j^2 + \left(b_j^L - \sum_{k=1}^{n} D_{jk}^M\right)x_j + D_{j_0j}^L\eta_{j_0} = f(x_j), \quad t \geqslant T_{j_0}.$$

The algebraic equation

$$c_j^M x_j^2 - \left(b_j^L - \sum_{k=1}^{n} D_{jk}^M\right)x_j - D_{j_0j}^L\eta_{j_0} = 0$$

gives us one positive root

$$x_j' = \frac{b_j^L - \sum_{k=1}^{n} D_{jk}^M + \sqrt{(b_j^L - \sum_{k=1}^{n} D_{jk}^M)^2 + 4c_j^M D_{j_0j}^L\eta_{j_0}}}{2c_j^M}.$$

Clearly, $f(x_j) > 0$ for every positive number x_j $(0 \leqslant x_j < x_j')$. Choose δ_j $(0 \leqslant \delta_j < x_j')$,

$$\left.\frac{\mathrm{d}x_j}{\mathrm{d}t}\right|_{x_j=\delta_j} > f(\delta_j) > 0.$$

If $x_j(T_{j_0}) \geqslant \delta_j$, then it also holds for $t \geqslant T_{j_0}$; if $x_j(T_{j_0}) < \delta_j$, then

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} \geqslant \inf\bigl\{f(x_j) \bigm| 0 \leqslant x_j < \delta_j\bigr\} > 0.$$

There must exists a $T_j(\geqslant T_{j_0})$ such that $x_j(t) \geqslant \delta_j$ for $t \geqslant T_j$.

For every i, we have

$$\begin{aligned}\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} &= -b_i(t)x_i(t) - c_i(t)x_i^2(t) - \sum_{k=1}^{n} D_{ik}(t)x_i(t) + D_{j_0 i}x_{j_0}\\ &\geqslant -c_i^M x_i^2(t) - \left(b_i^L + \sum_{k=1}^{n} D_{ik}^L\right)x_i(t) + D_{j_0 i}x_{j_0}.\end{aligned}$$

Similarly as the proof of the above, there exists a T_i such that $x_i(t) \geqslant \delta_i$ for $t \geqslant T_i$. This completes the proof. □

Theorems 1 and 2 have established that under assumption (8), there exist positive constants m and M such that the solution of (3) with positive initial values ultimately enters the region $\Omega = \{(x_1, x_2, \dots, x_n) \mid m \leqslant x_k \leqslant M,\ k = 1, 2, \dots, n\}$. Therefore, the giant panda population is permanent.

Remark 1. According to the proof of Theorems 1 and 2, if the population of the giant panda is permanent in a fixed patch j_0, then it will also be permanent in other patches under some condition.

Let us consider the biological meanings of Theorems 1 and 2. Remember that $b_{j_0}(t)$ is the intrinsic growth rate for the species in patch j_0 and $D_{j_0 k}(t)$ is the diffusion coefficient for the species from patch j_0 to k. Hence $b_{j_0}(t) - \sum_{k=1}^{n} D_{j_0 k}(t)$ represents the net increasing rate for the species in patch j_0, that is, the actual growth rate in patch j_0 minus out-frow from patch k. The assumption $A_w[b_{j_0} - \sum_{k=1}^{n} D_{j_0 k}(t)] > 0$ implies that the above rate is strictly positive on the average, we call such a patch j_0 belongs to J as food-rich patch. In general, all patches belong to J satisfy the condition $A_w[b_j - \sum_{k=1}^{n} D_{jk}(t)] > 0$ are called food-rich patch. On the contrary, the other patches belong to J is called food-poor patches, and the patch $i \in I$ is called normal patch.

According to (8) and Theorem 2, we can obtain that suitable diffusion between food-rich and the other patches implies permanence. That is to say, to be permanent for (6), it is sufficient that each food-poor or normal patch must have a connection with at least one food-rich patch.

Now, we apply the result of Theorem 2 in Qinling's giant panda population. The giant panda in Qinling mountains can be divided into six sub-populations [11], they are Pinghe liang local population, Jinji liang local population, Tianhua mountain local population, Xinglongling-Taibai mountain local population, Niuwei river local population, and Zibai mountain local population from east to west. There are only about 5 giant pandas in Pinghe liang, and this local population is located in the eastern boundary of the wild giant panda population, we call this patch food-poor patch. About 6 pandas are distributed in

Jinji liang local population. In recent years, the implementation of natural forest protection project has enabled the region's vegetation to be well restored, we call this patch normal patch. There are about 12 giant pandas in Tianhua mountain. The density of giant panda is low in this region, and there is great potential for development, we call this patch normal patch. There are about 219 giant pandas in Xinglong ling-Taibai mountain. The density of giant panda is high, and the habitat conditions are good, we call this patch food-rich patch. There are about 29 giant pandas in Niuwei river local population, we call this patch food- rich patch. There are only 3 or 4 giant pandas in Zibai mountain, we call this patch food-poor patch. From the basic features of the distribution pattern for Qinling giant panda population, Qinling pandas exist diffusion between adjacent patches, according to the conclusion of Theorems 1 and 2, Qinling panda population is able to sustain for a long time if it's environment could be kept as current or get better, which verifies the conclusion in [12].

If $n = 2$, let $i = 1$, $j = 2$, then system (3) can be rewritten as

$$\begin{aligned}\frac{\mathrm{d}x_1(t)}{\mathrm{d}t} &= \frac{a_1(t)x_1^2(t)}{N_1(t)+x_1(t)} - b_1(t)x_1(t) - c_1(t)x_1^2(t)\\ &\quad + D_{21}(t)x_2(t) - D_{12}(t)x_1(t),\\ \frac{\mathrm{d}x_2(t)}{\mathrm{d}t} &= b_2(t)x_2(t) - c_2(t)x_2^2(t) + D_{12}(t)x_1(t) - D_{21}(t)x_2(t).\end{aligned} \tag{10}$$

According to the proof of Theorems 1 and 2, we have the following corollary.

Corollary 1. *Suppose that*

$$A_\omega\bigl[b_2(t) - D_{21}(t)\bigr] > 0, \tag{11}$$

then there exist δ and M, $0 < \delta < M$ and $T \geqslant 0$, such that the solution of (10) *with positive initial values satisfies*

$$\delta < x_1(t) < M, \qquad \delta < x_2(t) < M.$$

Remark 2. System (10) considers the survival of giant pandas living in two kinds of habitats, the patch 1 means normal patch, and patch 2 means food-rich patch. If the species of giant panda has positive growth rate $b_2(t)$ in patch 2, i.e. the species of the giant panda lives in a suitable environment, this patch may have adequate food and abundant number of giant pandas, then the giant panda is permanent when the patch is isolate. Theorem 3 implies that if the average of the sum of diffusion rate from patch 2 to patch 1 is less than the intrinsic growth rate of patch 2, then the giant panda is permanent even if the isolated patch 1 is not persistent.

If $n = 2$, let $j = 1, 2$, then the system (3) can be rewritten as

$$\begin{aligned}\frac{\mathrm{d}x_1(t)}{\mathrm{d}t} &= b_1(t)x_1(t) - c_1(t)x_1^2(t) + D_{21}(t)x_2(t) - D_{12}(t)x_1(t),\\ \frac{\mathrm{d}x_2(t)}{\mathrm{d}t} &= b_2(t)x_2(t) - c_2(t)x_2^2(t) + D_{12}(t)x_1(t) - D_{21}(t)x_2(t).\end{aligned} \tag{12}$$

If $c_i(t)$, $D_{12}(t)$ and $D_{21}(t)$ are all positive periodic functions, $b_i(t)$ is the intrinsic growth rate, which may be negative periodic functions in some time intervals. For the diffusion logistic equations, we can obtained the following results from [4, Lemma 2.3].

Corollary 2. *If there exists an integer j ($j = 1$ or 2) such that*

$$A_\omega\big(b_j(t) - D_{jk}(t)\big) > 0, \quad k \neq j, \tag{13}$$

then system (12) *is permanent and there exists a unique positive ω-periodic solution $(x_1^*(t), x_2^*(t))$ which is globally and asymptotically stable.*

Remark 3. System (12) considers the situation of the diffusion of giant pandas between food-rich patch and food-poor patch. Corollary 2 shows that if the average of the sum of diffusion rate from food-rich patch to food-poor patch is less than the actual growth rate of food-rich patch, then the giant panda will be permanent at the two patches.

Remark 4. If $b_i(t)$ and $c_i(t)$ are all positive periodic functions described in system (12), then it is the case of diffusion between the two food-rich patches. From [7], system (12) possesses a globally stable positive periodic solution for any positive diffusive rate $D_{12}(t)$ and $D_{21}(t)$. Which implies that if each patch of giant pandas can continue to survive alone, then they can continue to survive in the two patches with any diffusion rate.

Theorem 3. *Suppose*

$$A_\omega\big[\varphi(t)\big] < 0 \tag{14}$$

holds, then the solution of (3) *satisfies*

$$x_k(t) \to 0, \quad t \to +\infty,\ k = 1, 2, \dots, n, \tag{15}$$

where

$$\varphi(t) = \max_{i \in I, j \in J}\big\{a_i(t) - b_i(t),\, b_j(t)\big\}.$$

Proof. Choose function

$$\rho(t) = x_1(t) + x_2(t) + \cdots + x_n(t).$$

Calculating the derivative of ρ along solution (3), we have

$$\begin{aligned}\frac{\mathrm{d}\rho(t)}{\mathrm{d}t} &= \sum_i \left(\frac{a_i(t)x_i^2(t)}{N_i(t) + x_i(t)} - b_i(t)x_i(t) - c_i(t)x_i^2(t)\right) \\ &\quad + \sum_j \big(b_j(t)x_j(t) - c_j(t)x_j^2(t)\big) \\ &\leqslant \sum_i \big(a_i(t) - b_i(t)\big)x_i(t) + \sum_j b_j(t)x_j(t) \leqslant \varphi(t)\rho(t).\end{aligned}$$

Let $u(t)$ be the solution of the equation

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = \varphi(t)u(t)$$

with $u(0) = \rho(0)$. By comparison theorem of differential equation, we have

$$\rho(t) \leqslant \rho(0)\mathrm{e}^{\int_0^t \varphi(\xi)\,\mathrm{d}\xi}.$$

Since $A_\omega[\varphi(t)] < 0$, $\int_0^t \varphi(\xi)\,\mathrm{d}\xi \to -\infty$ as $t \to \infty$, so $x_k(t) \to 0$ as $t \to \infty$. This completes the proof. □

Corollary 3. *For system* (10)*, if condition*

$$A_\omega\big[\phi(t)\big] < 0 \tag{16}$$

holds, then the solution of (10) *satisfies*

$$x_1(t) \to 0, \quad x_2(t) \to 0 \quad \text{as } t \to \infty,$$

where $\phi(t) = \max\{a_1(t) - b_1(t),\, b_2(t)\}$.

4 Stability of positive periodic solution

In this section, we prove that system (3) has a unique periodic solution and derive sufficient conditions for all positive solutions of (3) to converge to a periodic solution.

Let the following denote the unique solution of periodic system (3) for initial value $x(0, x_0) = x_0 = (x_{10}, x_{20}, \dots, x_{n0})$. Now define Poincaré transformation

$$Ax_0 = x(\omega, x_0),$$

where w is the period of periodic system (3). In this way, the existence of periodic solution of system (3) will be equal to the existence of the fixed point of A.

Lemma 3 (Brouwer fixed-point theorem). (*See* [2].) *Suppose that the continuous operator A maps closed and bounded convex set $Q \subset R^n$ onto itself, then the operator A has at least one fixed point in set Q.*

Theorem 4. *Suppose that* (8) *holds, then system* (3) *has at least one positive ω-periodic solution that lies in $\Omega = \{(x_1, x_2, \dots, x_n) \mid m \leqslant x_k \leqslant M,\ k = 1, 2, \dots, n\}$.*

Proof. Suppose that (8) holds, by Theorems 1 and 2, any solution of (3) with positive initial values ultimately enters the region Ω, and Ω also is a closed bounded convex set. So we have $x_0 \in \Omega \Rightarrow x(t, x_0) \in \Omega$, also, $x(\omega, x_0) \in \Omega$, thus $A\Omega \subset \Omega$. The operator A is continuous because the solution is continuous about the initial value. Using the Brouwer fixed-point theorem, we can obtain that A has at least one fixed point in Ω, then there exists at least one strictly positive w-periodic solution of system (3). This completes the proof of Theorem 4. □

Let $x^*(t) = (x_1^*(t), x_2^*(t), \dots, x_n^*(t))$ be a positive ω-periodic solution of (3), now we consider its uniqueness and stability. We introduce the following definitions.

Definition 2. (See [5].) An operator $U : D \subset R^n \to R^n$ is said to be monotonic if $X_1 = (x_{11}, x_{21}, \dots, x_{n1}) \in D$, $X_2 = (x_{12}, x_{22}, \dots, x_{n2}) \in D$, and $X_1 < X_2$ in the sense $x_{11} < x_{12}, x_{21} < x_{22}, \dots, x_{n1} < x_{n2}$ implies $UX_1 < UX_2$.

Definition 3. (See [5].) An operator $U : D \subset R^n \to R^n$ is said to be positive with respect to a cone K in R^n if $U : K \to K$ and is said to be strictly positive if $UK \subset$ interior of K.

Definition 4. (See [5].) An operator U defined on a cone K in R^n is said to be stongly concave, if, for an arbitrary interior element $X \in K$ and any number $\tau \in (0,1)$, there exists a positive number η such that $U(\tau X) \geqslant (1+\eta)\tau UX$.

Theorem 5. *Suppose that $c_i^L - a_i^M/N_i^L > 0$ and* (8) *hold. Then the operator A corresponding to* (3) *is monotonic, strictly positive, and strictly concave with respect to the cone R_+^n. Moreover, operator A has unique fixed point in R_+^n and the corresponding positive periodic solution is globally asymptotically stable.*

Proof. We rewrite system (3) in the form

$$\frac{\mathrm{d}x_l}{\mathrm{d}t} = f_l(t, x_1, x_2, \dots, x_n), \quad l = 1, 2, \dots, n,$$

then

$$f_l(t, x_1, x_2, \dots, x_{l-1}, 0, x_{l+1}, \dots, x_n) = \sum_{k=1}^{n} D_{kl} x_l.$$

In addition, the function F_l defined by

$$\begin{aligned}
&F_l(t, x_1, x_2, \dots, x_n) = f_l(t, x_1, x_2, \dots, x_n) - \sum_{k=1}^{n} \frac{\partial f_l}{\partial x_k} x_k,\\
&F_i(t, x_1, x_2, \dots, x_n)\\
&\quad = \frac{a_i(t)x_i^2}{N_i(t)+x_i} - b_i(t)x_i - c_i(t)x_i^2 + \sum_{k=1}^{n} D_{ki}(t)x_k - \sum_{k=1}^{n} D_{ik}(t)x_i\\
&\qquad - \left(\frac{2a_i(t)N_i(t)x_i^2 + a_i(t)x_i^3}{(N_i(t)+x_i)^2} - b_i(t)x_i - 2c_i(t)x_i^2 + \sum_{k=1}^{n} D_{ki}x_k - \sum_{k=1}^{n} D_{ik}x_i \right)\\
&\quad = \left(c_i(t) - \frac{a_i(t)N_i(t)x_i^2}{(N_i(t)+x_i)^2} \right) x_i^2 \geqslant \left(c^L - \frac{a_i^M}{N_i^L} \right) x_i^2.
\end{aligned}$$

Moreover,

$$\begin{aligned}
F_j(t, x_1, x_2, \dots, x_n) &= b_j(t)x_j - c_j(t)x_j^2 + \sum_{k=1}^{n} D_{kj}(t)x_k - \sum_{k=1}^{n} D_{jk}(t)x_j\\
&\quad - \left(\sum_{k=1}^{n} D_{kj}(t)x_k + b_j(t)x_j - 2c_j(t)x_j^2 - \sum_{k=1}^{n} D_{jk}(t)x_j \right)\\
&= c_j(t)x_j^2.
\end{aligned}$$

If $c_i^L - a_i^M/N_i^L > 0$ holds, then $F_l(t, x_1, x_2, \dots, x_n)$ is strictly positive for $x_l > 0$ ($l = 1, 2, \dots, n$) and $t \geqslant 0$. Thus, the operator A is monotonic, strongly positive, and strongly concave, follows from Theorem 10.2 and Lemma 3 in [5]. Moreover, it is known by Theorem 10.1 in [5] and Theorem 4 of our present paper that operator A has exactly one positive fixed point in R_+^n, and hence, the periodic solution $x^*(t)$ corresponding to the fixed point of A is unique. The globally asymptotically stability of $x^*(t)$ follows from the Theorem 10.6 in [5] and $\lim_{x\to\infty} x(t) = x^*(t)$ for every solution of (3) with $x(0) \in R_+^n \setminus (0, 0)$. This completes the proof. □

5 Discussion

In this paper, we considered the effect of diffusion on giant pandas that live in different habitat environments. Since more and more habitats of the giant panda have been broken into patches, in some of these patches, giant pandas live a good life style, and in some of these patches, giant pandas will become extinct without contributions from other patches, and in more patches, giant pandas live only at low reproduction rate, then we classified these habitat environments as three categories: food-rich patch, food-poor patch and normal patch. And we use different mathematical models to describe the growth and reproduction of the giant panda in the three types of habitats. In Section 3, the situations of the growth and reproduction of giant pandas that live in n kinds of complex habitat environments are described by model (3). Theorems 1 and 2 present the sufficient conditions which guarantee the permanence of giant pandas. The results imply that if the average of the sum of diffusion rate from patch j to patch k ($k = 1, 2, \dots, n$, $k \neq j$) is less than the actual growth rate of patch j ($j \neq i$), then giant pandas are permanent even if the isolated patch k are not persistent, i.e. in the n kinds of complex patches, if one patch is food-rich patch, no matter how the situations of other patches, the giant panda can persist in n patches. We apply the above results in Qinling's giant panda population. We find that Qinling's giant panda population can be able to sustain for a long time if it's environment could be kept as current or get better. Therefore, we can say the diffusive ability of Qinling's giant panda is amazing, which also verified the speculation on Qinling's panda distribution laws mentioned in the reference [11]. Qinling pandas' north-south distribution is mainly affected by farming and alpine, and east-west distribution has a certain regularity. The east-west distribution of giant pandas, with Xinglong ling-Taibai mountain as the center, gradually spread to the end of both the east and west. The number and density are gradually decreasing. If every suitable habitat patch were seen as an isolated island which is suitable for the survival of giant panda, then this law fits island species biology diffusion law [10]. Hence, migration and dispersal can increase the possibility of the permanence of giant panda in the patchy environment.

Theorem 3 points out sufficient condition which induces the extinction of the giant panda. If condition (14) holds, then giant pandas that live in n kinds of patches will go to extinct ultimately. In fact, this condition implies there is no food-rich patch in this case.

Particulary, we discuss the situations of diffusion on the giant panda in two kinds of patches, and present some useful results for giant panda conservation.

Corollary 1 implies that if the average of the sum of diffusion rate from food-rich patch to normal patch is less than the actual growth rate of food-rich patch, then the giant panda can be permanent in the two patches.

Here we discuss a simple example that illustrates the biological consequence of the result on Corollary 1. In model (10), if we choose the parameter variables as follows: $a_1(t) = (|\cos 2\pi t| - \cos 2\pi t)$, $b_1(t) = 0.4(1 - \sin 2\pi t)$, $c_1(t) = 0.05(1 - \sin 2\pi t)$, $D_{21}(t) = 0.05(1 - \cos 2\pi t)$, $D_{12}(t) = 0.04(1 - \sin 2\pi t)$, $b_2(t) = 0.31(|\cos 2\pi t| - \cos 2\pi t)$, $c_2(t) = 0.002(1 - \sin 2\pi t)$, $N_1(t) = 100(1 - \sin 2\pi t)$, we can easily get that $A_\omega[b_2(t) - D_{21}(t)] = 0.147 > 0$. And system (10) is permanent (see Fig. 1a).

Corollary 2 shows that if the average of the sum of diffusion rate from food-rich patch to food-poor patch is less than the actual growth rate of food-rich patch, then the giant panda will be permanent in the two patches. If we choose the parameter variables of system (12) as follows: $b_1(t) = 0.31(|\cos 2\pi t| - \cos 2\pi t)$, $c_1(t) = 0.05(1 - \sin 2\pi t)$, $D_{21}(t) = 0.02(1 - \cos 2\pi t)$, $D_{12}(t) = 0.08(1 - \sin 2\pi t)$, $b_2(t) = -0.1(|\cos 2\pi t| - \cos 2\pi t)$, $c_2(t) = 0.002(1 - \sin 2\pi t)$, we find that $A_\omega[b_1(t) - D_{12}(t)] = 0.117 > 0$. System (12) is permanent (see Fig. 1b).

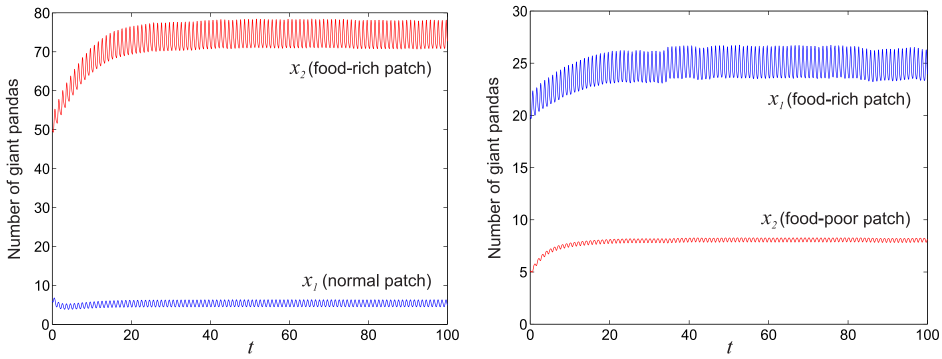
If the two patches are both food-rich patches, the giant panda species will be permanent in the two patches for any positive diffusive rate. If we choose the parameter variables in system (12) as follows: $b_1(t) = 0.4(|\cos 2\pi t| - \cos 2\pi t)$, $c_1(t) = 0.005(1 - \sin 2\pi t)$, $D_{21}(t) = 0.06(1 - \cos 2\pi t)$, $D_{12}(t) = 0.05(1 - \sin 2\pi t)$, $b_2(t) = 0.31(|\cos 2\pi t| - \cos 2\pi t)$, $c_2(t) = 0.005(1 - \sin 2\pi t)$, system (12) is always permanent (see Fig. 2a).

When the two patches are both food-poor patches, the giant panda in this two patches will go to extinct without the contribution from other patches no matter how much is the diffusive rate. If we choose the parameter variables of system (12) as follows: $b_1(t) = -0.4(|\cos 2\pi t| - \cos 2\pi t)$, $c_1(t) = 0.015(1 - \sin 2\pi t)$, $D_{21}(t) = 0.06(1 - \cos 2\pi t)$, $D_{12}(t) = 0.05(1 - \sin 2\pi t)$, $b_2(t) = -0.3(|\cos 2\pi t| - \cos 2\pi t)$, $c_2(t) = 0.005(1 - \sin 2\pi t)$, system (12) is not permanent (see Fig. 2b).

As far as two normal patches, we still are not aware of the conditions that ensure the giant panda to be permanent in the two patches. Numerical simulations show that the situation will be complicated in this case. For example, consider the system

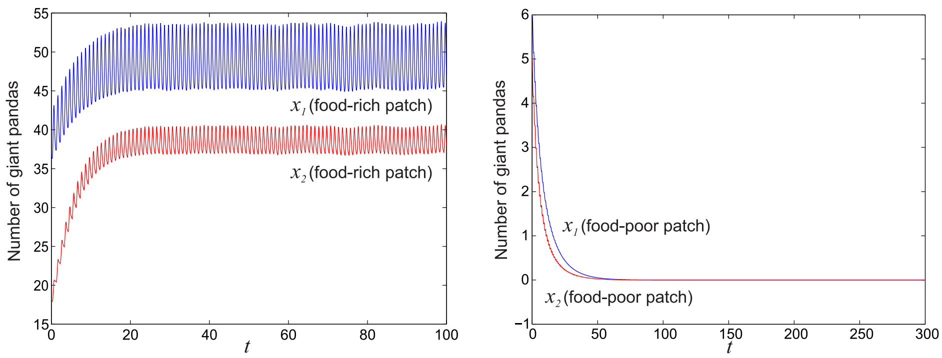
$$\begin{aligned}
\frac{\mathrm{d}x_1(t)}{\mathrm{d}t} &= \frac{a_1(t)x_1^2(t)}{N_1(t) + x_1(t)} - b_1(t)x_1(t) - c_1(t)x_1^2(t) \\
&\quad + D_{21}(t)x_2(t) - D_{12}(t)x_1(t), \\
\frac{\mathrm{d}x_2(t)}{\mathrm{d}t} &= \frac{a_2(t)x_2^2(t)}{N_2(t) + x_2(t)} - b_2(t)x_2(t) - c_2(t)x_2^2(t) \\
&\quad + D_{12}(t)x_1(t) - D_{21}(t)x_2(t).
\end{aligned} \tag{17}$$

If we choose the parameter variables of system (17) as follows: $a_1(t) = 3(|\cos 2\pi t| - \cos 2\pi t)$, $b_1(t) = 0.4(1 - \sin 2\pi t)$, $c_1(t) = 0.015(1 - \sin 2\pi t)$, $D_{21}(t) = 0.03(1 - \cos 2\pi t)$, $D_{12}(t) = 0.01(1 - \sin 2\pi t)$, $a_2(t) = 5(1 - \sin 2\pi t)$, $b_2(t) = 0.2(1 - \sin 2\pi t)$, $c_2(t) = 0.015(|\cos 2\pi t| - \cos 2\pi t)$, $N_1(t) = 100(1 - \sin 2\pi t)$, $N_2(t) = 120(1 - \sin 2\pi t)$, system (17) has a positive periodic solution (see Fig. 3a).



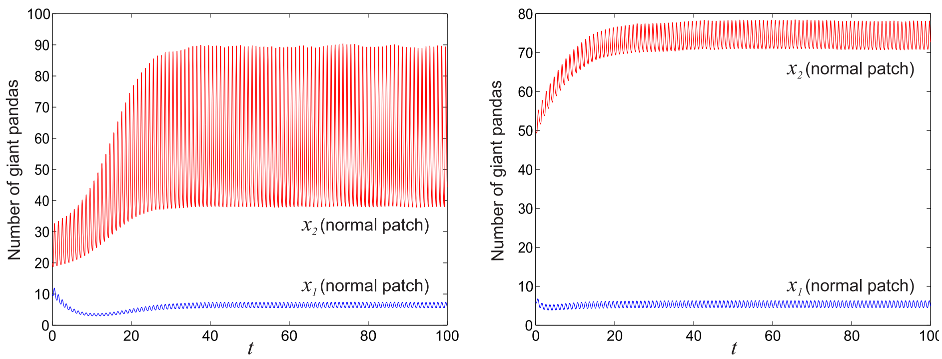
(a) (b)

Fig. 1. Time series diagrams: (a) of system (10); (b) of system (12).



(a) (b)

Fig. 2. Time series diagrams of system (12).



(a) (b)

Fig. 3. Time series diagrams of system (17).

If we choose the parameter variables of system (17) as follows: $a_1(t) = 3(|\cos 2\pi t| - \cos 2\pi t)$, $b_1(t) = 0.4(1 - \sin 2\pi t)$, $c_1(t) = 0.015(1 - \sin 2\pi t)$, $D_{21}(t) = 0.03(1 - \cos 2\pi t)$, $D_{12}(t) = 0.01(1 - \sin 2\pi t)$, $a_2(t) = 2(1 - \sin 2\pi t)$, $b_2(t) = 0.2(1 - \sin 2\pi t)$, $c_2(t) = 0.015(|\cos 2\pi t| - \cos 2\pi t)$, $N_1(t) = 100(1 - \sin 2\pi t)$, $N_2(t) = 120(1 - \sin 2\pi t)$, system (17) is extinct (see Fig. 3b). In practice, this situation is very common, and we will leave them for future investigation.

In order to protect the endanger species, it is very important to study the effect of diffusion of giant pandas that live in local region patches. From the researching results, to protect giant pandas, we must be aware of the distribution circumstance of the giant panda in distribution regions, and understand the habitat situation of the giant panda in every isolated region. Especially, we must understand the situations of the regions that to be protected and implement some recovery protection measures in these regions. For example, we can implement afforestation to increase the types of giant panda staple bamboo. To restore suitable habitat for giant pandas surviving we also should consider the connectivity of adjacent patches, establish ecological corridors between the two regions that are not connected such as: the regions are separated by the railways, rivers and villages, try to maintain the circulation between these regions, promote giant pandas to exchange between various regions.

The article also discusses that under certain conditions model (3) has an unique globally asymptotically stable periodic solutions, i.e. the giant panda population can become permanently stable to survive by diffusion. Which implies that diffusion increases the degree of stability of the system. This also provides a theoretical basis for studying the development of the recovery of the giant panda in the whole distribution areas in the future. As long as the six mountain ranges that constitute the extant geographic distribution of giant pandas can be connected together, and a series of habitat restoration work can be implement to ensure the diffusion rate between the various mountain ranges of the giant panda, the giant panda population will eventually survive in a wider range. Of course, this is an ambitious target, we still have a lot of work to do in the future.

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