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Practical persistence in ecological models via comparison methods*

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A basic question in mathematical ecology is that of deciding whether or not a model for the population dynamics of interacting species predicts their long-term coexistence. A sufficient condition for coexistence is the presence of a globally attracting positive equilibrium, but that condition may be too strong since it excludes other possibilities such as stable periodic solutions. Even if there is such an equilibrium, it may be difficult to establish its existence and stability, especially in the case of models with diffusion. In recent years, there has been considerable interest in the idea of uniform persistence or permanence, where coexistence is inferred from the existence of a globally attracting positive set. The advantage of that approach is that often uniform persistence can be shown much more easily than the existence of a globally attracting equilibrium. The disadvantage is that most techniques for establishing uniform persistence do not provide any information on the size or location of the attracting set. That is a serious drawback from the applied viewpoint, because if the positive attracting set contains points that represent less than one individual of some species, then the practical interpretation that uniform persistence predicts coexistence may not be valid. An alternative approach is to seek asymptotic lower bounds on the populations or densities in the model, via comparison with simpler equations whose dynamics are better known. If such bounds can be obtained and approximately computed, then the prediction of persistence can be made practical rather than merely theoretical. This paper describes how practical persistence can be established for some classes of reaction–diffusion models for interacting populations. Somewhat surprisingly, the models need not be autonomous or have any specific monotonicity properties.

1. Introduction

A basic question in mathematical ecology is that of determining whether a model for the dynamics of interacting populations predicts their long-term coexistence. A simple criterion for long-term coexistence is the presence of a globally attracting equilibrium with all populations or population densities positive. However, that criterion may be either too strong or too weak. A model which has a globally attracting periodic orbit on which all populations fluctuate with time but remain quite large probably should be interpreted as predicting coexistence, even in the absence of an attracting equilibrium. On the other hand, it is not reasonable to infer coexistence from a model possessing a globally attracting equilibrium at which the predicted population of one of the species is less than one individual. In recent years, there has been considerable interest in the idea of uniform persistence or permanence,

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where coexistence is inferred from the presence of a globally attracting positive set rather than a single globally attracting equilibrium. The advantages of using the criterion of uniform persistence/permanence to infer long-term coexistence are that it allows the system to have complex dynamics (even a strange attractor) and that often it can be established under more natural conditions than those needed to establish the presence of a globally attracting equilibrium. The disadvantages of using uniform persistence/permanence are that the techniques used to establish uniform persistence/permanence do not usually provide any information on the size or location of the positive attracting set; also, in most cases the model must be cast as a dynamical or semidynamical system, thereby severely restricting the sort of time dependence that may be allowed in the coefficients. In the present paper, we present an alternative approach based on seeking asymptotic lower bounds for the populations or densities in our models, via comparison with simpler equations whose dynamics are better known. Specifically, we shall use diffusive logistic equations with time-periodic coefficients for purposes of comparison. Since the solutions of such equations can often be estimated or approximately computed with a moderate amount of additional effort, our lower bounds can provide computable quantitative information about the long-term dynamics of the models and thus make predictions of persistence which are practical as well as theoretical. The lower bounds are also practical in the sense that they are robust relative to changes in the nonlinearities in the models, which is important in ecological applications since the available data are often limited in quantity or quality. Somewhat surprisingly, we do not need to assume that the original models be autonomous or time-periodic, and we do not need any specific monotonicity hypotheses. The main limitation of our approach is that it requires each species to be subject to logistic self-regulation, which excludes some types of predator–prey models.

The key ingredients in this work are comparison methods, the theory of periodic-parabolic logistic equations, and the associated spectral theory for periodic-parabolic operators. The importance of the work of Peter Hess on those topics cannot be overstated. His results and ideas, collected in [**30**], are the foundation and inspiration for the present paper. Without them, it quite literally could not have been written. We are deeply thankful that we were privileged to know him and learn from him.

The models we consider have the form

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= L_i u_i + f_i(x, t, \vec{u})u_i \qquad \text{in } \Omega \times (0, \infty), \\ B_i u &= 0 \qquad \text{on } \partial\Omega \times (0, \infty), \quad i = 1, \ldots, n, \end{aligned} \tag{1.1}$$

where $\Omega \subseteq \mathbb{R}^m$ is a bounded domain, L_i is a second-order uniformly strongly elliptic operator (possibly with T-periodic time-dependent coefficients), with f_i T-periodic in t, and $B_i u \equiv u$ or $B_i u \equiv \beta_i u + \partial u/\partial \nu$ or some $\beta_i \geqq 0$. In principle, we could allow f_i to have nonlocal dependence on $\vec{u}$ via delays or spatial averages, but we do not consider those situations explicitly. Models such as (1.1) can describe many sorts of interactions between populations and their environment or among populations; they include diffusive Lotka–Volterra models, among many others. There is a large literature on such models; see the discussion and references in [**13–18, 30, 32, 33, 36, 46, 47, 51, 56**].

Since the dependent variables represent population densities, we are interested only in non-negative solutions. The structure of (1.1) ensures that non-negative (respectively positive) initial data will induce non-negative (respectively positive) solutions; when we use terms such as 'globally' attracting, we generally mean globally with respect to positive solutions. The main conditions we impose on the nonlinearities are that the nonlinearity f_n for the last species can be bounded by $f_n \leqq R_n - C_n u_n$, with R_n and C_n possibly dependent on x and T-periodic in t but without reference to $u_1, \ldots, u_{n-1}$; that after we have asymptotic upper bounds on $u_{i+1}, \ldots, u_n$ we can obtain an upper bound $f_i \leqq R_i - C_i u_i$ for large t with R_i and C_i possibly depending on the bounds on $u_{i+1}, \ldots, u_n$; that once we have asymptotic upper bounds on $u_1, \ldots, u_n$ we can obtain a lower bound on f_n of the form $f_n \geqq r_n - c_n u_n$ for large t with r_n and c_n depending on the upper bounds for $u_1, \ldots, u_{n-1}$ and thus can obtain an asymptotic lower bound on u_n; and, finally, we have $f_i \geqq r_i - c_i u_i$ for large t, with r_i and c_i possibly depending on the asymptotic upper bounds for all the components and/or on the asymptotic lower bounds for $u_{i+1}, \ldots, u_n$. Our hypotheses are met by almost all Lotka–Volterra models for competition or predator–prey interactions with self-regulation of each population, but they are also met by many other models, including models with a limited amount of mutualism. A class of models satisfying our structural hypotheses are those satisfying a food pyramid condition [**5, 55**] with self-regulation, that is, where the ith species is a predator on some or all of those with indices $j > i$ but is prey to those with indices $j < i$. We cannot eliminate the hypothesis of self-regulation for each species, which excludes certain predator–prey models. The reasons for that may be deeper than mere technicalities associated with our methods. In [**11**], it is shown that for systems of ordinary differential equations, the presence of self-regulation limits the possible complexity of dynamics in a manner somewhat analogous to the limitations imposed by a competititve or cooperative structure. The essential idea in our analysis is to view each component of (1.1) as a sub- or supersolution to an appropriate logistic equation which admits a positive attracting T-periodic (or temporally constant) steady-state. Related ideas are used in the context of specific systems in [**1, 2, 4, 15, 18, 23, 25, 26, 30, 36, 44, 48, 49, 57**]. By using results of Hess [**30**] on diffusive logistic equations, we can often estimate their steady-states in terms of quantities such as the principal eigenfunctions of associated linear problems—which can be as simple as $\sin(\pi x)$.

There is a substantial literature on models such as (1.1), especially Lotka–Volterra models, and there are several different sorts of results that have been obtained by various authors. Many investigators have concerned themselves with the existence of positive equilibria or periodic steady-states; see for example [**7, 12, 16, 23–27, 30, 34, 36–44, 49**]. In some cases, the equilibria can be approximated or bounded by some type of monotone iteration; see [**25, 26, 36, 48, 57**]. The problem with approaches based on studying equilibria is that it is often very difficult to obtain good uniqueness or global stability results. In any case, the equilibria may not be adequate to describe the asymptotic dynamics of the system. One way of handling these difficulties is to say something about the 'stability' of sets more general than equilibria. An idea that is very useful and elegant in cases where the model induces a monotone semiflow is the concept of compressivity introduced by Hess (see [**30**]). A monotone system is said to be compressive if it admits a globally attracting order interval. Related ideas are the method of contracting rectangles

[**8, 51**] (the basic ideas date back at least to [**45**]) and monotone iteration in the parabolic context based on sub- and supersolutions for the system [**36, 48**]. These approaches typically treat all components simultaneously and often require some sort of monotonicity in either the nonlinearities or the semiflow induced by the model. A related but more general idea is that of uniform persistence/permanence; a system is said to be uniformly persistent if it admits a positive set which is bounded away from zero in each component (i.e. bounded away from the boundary of the positive cone) and which is globally attracting for positive solutions. If in addition the system is also dissipative (i.e. all orbits enter some compact set in finite time), then the system is said to be permanent. The idea of uniform persistence/permanence is discussed in [**9, 10, 16, 29, 31, 32, 53**]. Some nonautonomous models are treated in [**9**]. Typically, the methods for establishing uniform persistence/permanence are 'soft' in that they do not provide any information about the location of the positive attractor. This is in contrast with compressivity, which may lead to bounds on the attracting order interval via estimates on sub- and supersolutions, but which requires some monotonicity. In recent work Cao and Gard [**19, 20**] introduced the idea of practical persistence, which they define as uniform persistence together with some information about the location of the positive attractor. They studied ordinary differential equations with delays using multiple Lyapunov functions. In a sense, we also use multiple Lyapunov functions, but they are of the simplest possible sort—namely the components of the system taken one by one. (We do not consider Lyapunov functions involving several components at once, because we want to allow different differential operators in different components. In the case of ordinary differential equations that is not an issue and Lyapunov methods can be used with great creativity; see for example [**3**].) Our work could also be viewed as an extension of the idea of compressivity to nonmonotone situations, or of contracting rectangles to Banach space.

We have followed the terminology of Cao and Gard [**9, 20**] in referring to our results as yielding practical persistence. There are two major reasons for using the term 'practical'. The first is that many ecologists believe that for any species there is 'minimum viable population' required to avoid extinction via genetic drift or localised environmental catastrophe [**28, 52**]; often the proposed minimum viable population for a given species will number several hundred individuals. Thus, for a model's prediction of long-term persistence to be practical, it must imply a lower bound on the expected population which are larger than the minimum viable population. The second reason why the term 'practical' is appropriate, is that there is almost always error and uncertainty in the construction of models, often together with considerable complexity, but for predictions to be useful in practice they must be robust and simple enough to be understood by ecologists and decision-makers with only a modest knowledge of mathematics. As we shall demonstrate via examples, our methods allow us to obtain robust and simple bounds on the location of a positive attracting set for models which can be quite complicated.

For applied reasons we do not assume that our nonlinearities are time-periodic, but only that they can be bounded appropriately by periodic functions. The sort of situation we envision in the models is one where some important quantity such as temperature or precipitation varies randomly from day to day within a known range, but the range shifts from season to season in a periodic way. We must assume, however, that the elliptic operators in our models are periodic if they have any time dependence at all. This requirement is probably a technicality, but we do not know how to remove it.

We now outline the structure of the remainder of this paper. In Section 2, we introduce the necessary background material and state two reasonably general theorems on practical persistence. The key idea is the method used to prove the main theorems rather than the theorems themselves. In Section 3, we examine some representative examples and see what sort of information can be extracted from the general theory in those particular cases. Again, the methods are probably more important than the specific results, although some of the estimates are new and may be of interest to mathematical ecologists. In Section 4, we consider some less representative examples with interesting mathematical structure and explore some possible extensions and variations of the theory.

2. Mathematical background and general results

The models we shall consider have the form

$$\begin{aligned} u_{i_t} &= L_i u_i + f_i(x, t, \vec{u})u_i && \text{in } \Omega \times (0, \infty), \\ B_i u_i &= 0 && \text{on } \partial\Omega \times (0, \infty), \quad i = 1, \ldots, n. \end{aligned} \tag{2.1}$$

We assume that $\Omega \subseteq \mathbb{R}^m$ is a bounded domain with $\partial\Omega$ smooth and, for each i, L_i is a uniformly strongly elliptic operator of the form

$$L_i u = \sum_{k,l=1}^{m} a_{kl}^i(x, t)u_{x_k x_l} + \sum_{k=1}^{m} b_k^i(x, t)u_{x_k} + c^i(x, t)u,$$

with $\Sigma_{k,l=1}^m a_{kl}^i \zeta_k \zeta_l \geqq a_0^i |\zeta|^2$ for some constant $a_0^i > 0$, where all the coefficients are T-periodic in t and Hölder-continuous in x and t, lying in $C^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ for some $\alpha > 0$, with $a_{kl}^i = a_{lk}^i$ and $c^i \leqq 0$. (There need not actually be any t-dependence.) We also assume that

$$B_i u = u \quad \text{or} \quad B_i u = \frac{\partial u}{\partial \nu} + \beta(x)u,$$

with $\beta(x)$ of class $C^{1+\alpha}$ and $\beta \geqq 0$. By the theory of second-order periodic parabolic problems introduced in [**21, 35**] and developed and described in [**30**] we have that, for T-periodic $R(x, t) \in C^{\alpha,\alpha/2}(\bar{\Omega}, \mathbb{R})$, the problem

$$\begin{aligned} \varphi_t - L_i\varphi - R\varphi &= \sigma\varphi && \text{in } \Omega \times \mathbb{R}, \\ B_i\varphi &= 0 && \text{on } \partial\Omega \times \mathbb{R}, \\ \varphi &\text{ is } T\text{-periodic}, \end{aligned} \tag{2.2}$$

has a principal eigenvalue σ_1 with positive eigenfunction.

For purposes of comparison, we shall use solutions to diffusive logistic equations of the form

$$\begin{aligned} u_t &= L_i u + Ru - Cu^2 && \text{in } \Omega \times (0, \infty), \\ B_i u &= 0 && \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{2.3}$$

where $C = C(x, t)$ is T-periodic, $C(x, t) \geqq C_0 > 0$, and $C \in C^{\alpha,\alpha/2}(\bar{\Omega}, \mathbb{R})$. Since C is strictly positive, any sufficiently large constant is a supersolution to (2.3), so solutions are bounded. By standard arguments based on the maximum principle, any solution with non-negative nontrivial initial data will be strictly positive in Ω for $t>0$, with $u>0$ on $\bar{\Omega}$ in the case of Neumann or Robin boundary conditions and $\partial u/\partial \nu<0$ on $\partial\Omega$ in the case of Dirichlet conditions. We have the following lemma ([**30**, Theorem 28.1]):

LEMMA 2.1. *The problem* (2.3) *admits a positive T-periodic solution* (*which will be denoted by* $\theta(L_i, R, C)$) *if and only if the principal eigenvalue* σ_1 *in* (2.2) *satisfies* $\sigma_1<0$ (*i.e. the solution* $u\equiv 0$ *to* (2.3) *is unstable*). *In that case,* $\theta(L_i, R, C)$ *is a global attractor for solutions of* (2.3) *with non-negative nontrivial initial data.*

REMARK 2.2. If $\sigma_1 \geqq 0$, then non-negative solutions to (2.3) approach 0 as $t\to\infty$. By parabolic regularity theory (alternatively by the smoothing properties of evolution operators) the convergence to θ can be taken in $C^{1+\alpha,\alpha/2}(\bar{\Omega}, (0,\infty))$; see for example [**13, 14, 30, 32**]. In the case of trivial t-dependence in L_i, R and C, the regularity requirements may be relaxed somewhat; see [**13–15**]. Similar generalisations are probably possible in the genuinely periodic-parabolic case as well, but we shall not pursue that question here.

We can now state a reasonably general theorem giving conditions which imply the existence of asymptotic lower bounds on solutions of (2.1). What is really important, however, is not so much the specific theorem but the method used to prove it. The ideas are probably easiest to understand in the context of a food pyramid (see [**5, 55**]) in which the kth species preys upon some or all of the species with higher indices but cannot be preyed upon by them, while it may be preyed upon by some or all of the species with lower indices but cannot prey upon them. (The thereom was formulated with such a situation in mind, but applies to somewhat more general situations.) The method of proof would then be to find an asymptotic upper bound on u_n, the density of the nth species, use that to obtain an upper bound on the $n-1$st species, then use those two bounds to obtain a bound on the $n-2$nd species, etc. Once upper bounds have been obtained for all predator species, those would then be used to obtain an asymptotic lower bound on the nth species. Since the nth species acts as prey for some or all of the others, the lower bound on u_n would then be used to obtain a lower bound on, say, u_{n-1} (or more generally on the species with largest index that preys on the nth species) and those lower bounds would be used to obtain lower bounds on, say, u_{n-2} and so on until lower bounds are obtained for all species. In some cases the process can be refined via further iteration of estimates. We shall discuss some applications of the theorem or its proof in the next section.

THEOREM 2.3. *Let* $\vec{u}=(u_1,\dots,u_n)$ *be a solution to* (2.1) *with* $u_i(x,0)\geqq 0$, $u_i(x,0)\not\equiv 0$ *for* $i=1,\dots,n$.

(i) *Suppose that for* $i=1,\dots,n$ *and for all* $\vec{u}$ *with* $u_i\geqq 0$ *for all i, we have*

$$f_i(x,t,\vec{u}) \leqq R_i(x,t,U_{i+1},\dots,U_n) - C_i(x,t)u_i, \tag{2.4}$$

provided $u_k\leqq U_k$ *for* $k=i+1,\dots,n$ (*so* $R_n=R_n(x,t)$) *where* R_i *and* C_i *are T-periodic in t, Hölder-continuous in x, t of class* $C^{\alpha,\alpha/2}$ *and* R_i *is monotone increasing in* $U_{i+1},\dots,U_n$. *Then solutions to* (2.1) *exist globally in time. Suppose also that the* *principal eigenvalue* σ_1 *for*

$$\varphi_t - L_n\varphi - R_n\varphi = \sigma\varphi, \quad B_n\varphi = 0, \tag{2.5}$$

is negative; define $\bar{\theta}_n \equiv \theta(L_n, R_n, C_n)$, *where* $\theta(L_n, R_n, C_n)$ *is the unique globally attracting positive steady-state solution of*

$$u_t = L_n u + (R_n - C_n u)u, \quad B_n u = 0.$$

(If there is no explicit t dependence in L_n, R_n *and* C_n, *then* θ_n *will be an equilibrium; in general* θ_n *is T-periodic in t.) For any sufficiently small* $\varepsilon > 0$, *define* $\bar{\theta}_i$ *(inductively) by* $\bar{\theta}_i \equiv \theta(L_i, R_i(x, t, (1+\varepsilon)\bar{\theta}_{i+1}, \ldots, (1+\varepsilon)\bar{\theta}_n), C_i)$, *where we suppose that for* $\varepsilon > 0$ *sufficiently small the principal eigenvalue* σ_1 *of*

$$\varphi_t - L_i\varphi - R_i(x, t, (1+\varepsilon)\bar{\theta}_{i+1}, \ldots, (1+\varepsilon)\bar{\theta}_n)\varphi = \sigma\varphi, \quad B_i\varphi = 0, \tag{2.6}$$

is negative for each i so that $\bar{\theta}_i > 0$ *inside* Ω. *Then, for t sufficiently large, we have* $u_i \leqq (1+\varepsilon)\bar{\theta}_i$.

(ii) *Suppose that in addition to* (2.4) *there is, for each i, an index* $k(i) \in \{i, i+1, \ldots, n\}$ *and a function* $r_i(x, t, U_1, \ldots, U_{i-1}, U_{i+1}, \ldots, U_n)$ *with the same periodicity and regularity hypotheses as* R_i, *such that* r_i *is monotone decreasing in* U_k *for* $k \leqq k(i)$ $(k \neq i)$ *and monotone increasing in* U_k *for* $k > k(i)$, *and a Hölder-continuous and T-periodic function* $c_i(x, t) > 0$ *so that*

$$f_i(x, t, \vec{u}) \geqq r_i(x, t, U_1, \ldots, U_{i-1}, U_{i+1}, \ldots, U_n) - c_i(x, t)u_i \tag{2.7}$$

whenever $u_k \geqq U_k$ *for* $k > k(i)$ *and* $u_k \leqq U_k$ *for* $k \leqq k(i)$, $k \neq i$. *Suppose further that the principal eigenvalue for*

$$\varphi_t - L_n\varphi - r_n(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-1})\varphi = \sigma\varphi, \quad B_n\varphi = 0, \tag{2.8}$$

is negative for $\varepsilon > 0$ *sufficiently small and define* $\underline{\theta}_n \equiv \theta(L_n, r_n(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-1}), c_n)$, *then define* $\underline{\theta}_i \equiv \theta(L_i, r_i(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{i-1}, (1+\varepsilon)\bar{\theta}_{i+1}, \ldots, (1+\varepsilon)\bar{\theta}_{k(i)}, (1-\varepsilon)\underline{\theta}_{k(i)+1}, \ldots, (1-\varepsilon)\underline{\theta}_n), c_i)$ *where we suppose that, for* $\varepsilon > 0$ *sufficiently small, the principal eigenvalue of*

$$\varphi_t - L_i\varphi - r_i(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{k(i)}, (1-\varepsilon)\underline{\theta}_{k(i)+1}, \ldots, (1-\varepsilon)\underline{\theta}_n)\varphi = \sigma\varphi, \quad B_i\varphi = 0, \tag{2.9}$$

is negative. Then, for any sufficiently small $\varepsilon > 0$, *we have* $u_i \geqq (1-\varepsilon)\underline{\theta}_i$ *for all i when t is sufficiently large.*

REMARK 2.4. For upper bounds the eigenvalue condition in (2.6) is not really necessary. If the eigenvalue in (2.6) is positive for some i, the implication is that $u_i \to 0$ as $t \to \infty$, so for large t we may view the species represented by u_i to be absent and reapply the theorem to the remaining components in the system. In this sense, the proof of the theorem yields results on extinction as well as persistence in certain cases. The significance of the index $k(i)$ in (ii) is that it permits consideration of cases where the ith species competes against those with higher indices and cases where the ith species is a predator on those below. For example, if $n=3$ and $f_3(\vec{u})=a_3-b_{31}u_1-b_{32}u_2-b_{33}u_3$, $f_2(\vec{u})=a_2-b_{21}u_1-b_{22}u_2-b_{23}u_3$, then $k(2)=3$ since to obtain a lower bound on $f_2(\vec{u})$ we will need an upper bound on u_3. If $f_3(\vec{u})=a_3-b_{31}u_1-b_{32}u_2-b_{33}u_3$ and $f_2(\vec{u})=a_3-b_{21}u_1-b_{22}u_2+b_{23}u_3$, then we would use $k(2)=2$ since now a lower bound on u_3 will yield a better lower bound on u_2 than could be obtained otherwise.

The proof of Theorem 2.3 is structured so that we first obtain all upper bounds and then obtain lower bounds, so that hypothesis (2.7) of part (ii) need only hold for $0 \leqq U_i \leqq \sup(1+\varepsilon)\bar{\theta}_i$ for the conclusions to be valid.

Proof of Theorem 2.3. The existence theory of [**6**] (among others) implies the local existence of solutions and that the solutions are global if they are bounded uniformly on their interval of existence. We shall establish such bounds in the course of this proof. Since the ith nonlinearity is zero when $u_i=0$, it follows from standard invariant set theory (see [**51**]) that the set $\{\vec{u}\in\mathbb{R}^n : u_i \geqq 0,\ i=1,\ldots,n\}$ is positively invariant. It follows from the strong maximum principle that if $u_i \geqq 0$, $u_i \not\equiv 0$ at $t=0$, then $u_i>0$ on Ω for all $t>0$; also, under Dirichlet boundary conditions $\partial u_i/\partial v<0$ on $\partial\Omega$ and for Neumann or mixed boundary conditions $u_i>0$ on $\bar{\Omega}$. Suppose that we have a solution to (2.1) that exists on $[0,\tau)$. We have, by (2.4),

$$\begin{aligned} u_{n_t} &= L_n u_n + f_n(x,t,\vec{u})u_n \\ &\leqq L_n u_n + (R_n(x,t) - C_n(x,t)u_n)u_n, \end{aligned}$$

so that $u_n \leqq v_n$ with v_n satisfying $v_n(x,0)=u_n(x,0)$ and

$$\begin{aligned} v_{n_t} &= L_n v_n + (R_n(x,t) - C_n(x,t)v_n)v_n, \\ B_n v_n &= 0, \end{aligned} \tag{2.10}$$

because u_n is a subsolution of (2.10). Since $C_n(x,t) \geqq C_{n_0} > 0$, any sufficiently large constant is a supersolution to (2.10), so v_n exists globally and $v_n(x,t) \leqq V_n$ on $[0,\tau)$ for some constant V_n depending on $u_n(x,0)$. Thus $0 \leqq u_n \leqq V_n$ on $[0,\tau)$. By (2.4) we then have

$$\begin{aligned} u_{n-1_t} &= L_{n-1}u_{n-1} + f_{n-1}(x,t,\vec{u})u_{n-1} \\ &\leqq L_{n-1}u_{n-1} + (R_{n-1}(x,t,V_n) - C_{n-1}(x,t)u_{n-1})u_{n-1} \end{aligned}$$

on $[0,\tau)$, so we have $0 \leqq u_{n-1} \leqq v_{n-1}$ on $[0,\tau)$ where v_{n-1} satisfies $v_{n-1}(x,0)=u_{n-1}(x,0)$, and

$$\begin{aligned} v_{n-1_t} &= L_{n-1}v_{n-1} + (R_{n-1} - C_{n-1}v_{n-1})v_{n-1}, \\ B_{n-1}v_{n-1} &= 0. \end{aligned}$$

As in the case of v_n, we have $v_{n-1} \leqq V_{n-1}$ where V_{n-1} depends on V_n and $u_{n-1}(x,0)$, so $0 \leqq u_{n-1} \leqq V_{n-1}$ on $[0,\tau)$. Continuing in this way, we find that $u_k \leqq V_k$ on $[0,\tau)$ for $k=1,\ldots,n$ so that in fact $[0,\tau)$ cannot be the maximal interval of existence since $\sup|\vec{u}| \not\to \infty$ as $t\uparrow\tau$. Since $\tau>0$ was arbitrary, we have global existence of solutions.

The process of obtaining upper bounds on the variables u_k as $t \to \infty$ is a refinement of that used above to show global existence. Again, we start with the observation that u_n is a subsolution to (2.10). By Lemma 2.1, we have $v_n \to \bar{\theta}_n \equiv \theta(L_n, R_n, C_n)$ as $t \to \infty$, with convergence in $C^{1+\alpha,\alpha/2}(\Omega, (0, \infty))$ so that, for any $\varepsilon > 0$, we have $u_n \leqq v_n \leqq (1+\varepsilon)\theta(L_n, R_n, C_n)$ for sufficiently large t. It follows that, for t sufficiently large,

$$u_{n-1_t} \leqq L_{n-1}u_{n-1} + [R_{n-1}(x, t, (1+\varepsilon)\bar{\theta}_n) - C_{n-1}u_{n-1}]u_{n-1}$$

under boundary condition B_{n-1}, so that u_{n-1} is a subsolution for

$$v_{n-1} = L_{n-1}u_{n-1} + [R_{n-1}(x, t, (1+\varepsilon)\bar{\theta}_n) - C_{n-1}v_{n-1}]v_{n-1}.$$

We may assume that the principal eigenvalue σ_1 of

$$\varphi_t - L_{n-1}\varphi - R_{n-1}(x, t, (1+\varepsilon)\bar{\theta}_n)\varphi = \sigma\varphi,$$
$$B_{n-1}\varphi = 0,$$

is negative, so that $v_{n-1} \to \bar{\theta}_{n-1} \equiv \theta(L_{n-1}, R_{n-1}(x, t, (1+\varepsilon)\theta_n))$ as $t \to \infty$, and hence for t large we have $u_{n-1} \leqq v_{n-1} \leqq (1+\varepsilon)\bar{\theta}_{n-1}$. We may continue this process to conclude that, for t large enough, we have $u_k \leqq (1+\varepsilon)\bar{\theta}_k$ for $k = 1, \ldots, n$, where $\bar{\theta}_k$ is the unique positive globally attracting steady-state for

$$v_t = L_k v + [R_k(x, t, (1+\varepsilon)\bar{\theta}_{k+1}, \ldots, (1+\varepsilon)\bar{\theta}_n) - C_k v]v,$$
$$B_k v = 0.$$

This completes the proof of part (i).

Once we have obtained upper bounds on $u_1, \ldots, u_n$ for sufficiently large t, we can in principle obtain lower bounds, again starting with u_n and working up to u_1. By hypothesis (2.7) and the conclusion of part (i), we see that u_n is a supersolution to the problem

$$v_t = L_n v + [r_n(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-1}) - c_n v]v, \qquad B_n v = 0, \tag{2.11}$$

for $t \geqq t_0$ with t_0 sufficiently large. Also, u_n is positive on $\bar{\Omega}$ under Neumann or Robin boundary conditions and positive on Ω with $\partial u/\partial \nu < 0$ on $\partial\Omega$ under Dirichlet conditions. Choose v to satisfy (2.11) with $v(x, t_0) = u_n(x, t_0)$. By hypothesis, the principal eigenvalue σ_1 of (2.8) is negative, so $\underline{\theta}_n \equiv \theta(L_n, r_n(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-1}), c_n)$ is a global attractor for nontrivial non-negative solutions. Thus $v \to \underline{\theta}_n$ as $t \to \infty$, so for $t > t_1$ sufficiently large we have $u_n \geqq (1-\varepsilon)\underline{\theta}_n$. Next we observe that u_{n-1} is a supersolution to

$$v_t = L_{n-1}v + (r_{n-1}(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-2}, (1+\varepsilon)\bar{\theta}_n) - c_{n-1}v)v,$$
$$B_{n-1}v = 0,$$

if $k(n-1) = n$ and to

$$v_t = L_{n-1}v + (r_{n-1}(x, t, (1+\varepsilon)\bar{\theta}_1, \ldots, (1+\varepsilon)\bar{\theta}_{n-2}, (1-\varepsilon)\underline{\theta}_n) - c_{n-1}v)v,$$

if $k(n-1) = n-1$. In either case, hypothesis (2.9) and Lemma 2.1 imply that, if $v(x, t_1) = u_{n-1}(x, t_1)$, then v is positive inside Ω (at least) and so $v \to \underline{\theta}_{n-1}$ as $t \to \infty$.

Since $u_{n-1}=v$ at $t=t_1$ we have $u_{n-1} \geq (1-\varepsilon)\underline{\theta}_{n-1}$ for t sufficiently large. We may continue in this way to obtain the corresponding asymptotic lower bounds on $u_{n-2}, \ldots, u_1$, where the different possible estimates depending on the value of $k(i)$ for each i are taken into account by the definition of $\underline{\theta}_i$. □

Because the upper bounds in part (i) of Theorem 2.3 are used to define the lower bounds in part (ii), it is sometimes convenient to replace the upper bounds with constant bounds that are less sharp but simpler.

THEOREM 2.5. (i) *Suppose that the hypotheses of Theorem* 2.3(i) *up to* (2.5) *are satisfied. Define* $\bar{\theta}_n$ *as in Theorem* 2.3 *and let* M_n *be a constant such that* $M_n > \bar{\theta}_n$ *(for which it suffices to have* $M_n > \sup (R_n/C_n)$ *by the maximum principle). Define* M_i *inductively to be a constant such that* $M_i > \theta(L_i, R_i(x, t, M_{i+1}, \ldots, M_n), C_i)$, *where we assume in place of* (2.6) *that the principle eigenvalue for*

$$\begin{aligned} \varphi_t - L_i\varphi - R_i(x, t, M_{i+1}, \ldots, M_n)\varphi &= \sigma\varphi, \\ B_i\varphi &= 0, \end{aligned} \tag{2.12}$$

is negative for $i = 1, \ldots, n$. *In that case, we have* $u_i \leqq M_i$ *for all* i *when* t *is sufficiently large.*

(ii) *Suppose that the hypotheses of Theorem* 2.3(ii) *up to* (2.7) *are satisfied and that the principal eigenvalue in* (2.8) *remains negative if* $(1+\varepsilon)\bar{\theta}_i$ *is replaced with* M_i. *Define* $\underline{\theta}_n^* \equiv \theta(L_n, r_n(x, t, M_1, \ldots, M_{n-1}), c_n)$, *then define inductively*

$$\underline{\theta}_i^* \equiv \theta(L_i, r_i(x, t, M_1, \ldots, M_{k(i)}, (1-\varepsilon)\underline{\theta}_{k(i)+1}^*, \ldots, (1-\varepsilon)\underline{\theta}_n^*), c_i),$$

where we suppose that for $\varepsilon > 0$ *sufficiently small the principal eigenvalue of*

$$\begin{aligned} \varphi_t - L_i\varphi - r_i(x, t, M_1, \ldots, M_{k(i)}, (1-\varepsilon)\underline{\theta}_{k(i)+1}^*, \ldots, (1-\varepsilon)\underline{\theta}_n^*)\varphi &= \sigma\varphi, \\ B_i\varphi &= 0, \end{aligned} \tag{2.13}$$

is negative for $\varepsilon > 0$ *sufficiently small. Then for any sufficiently small* $\varepsilon > 0$ *we have* $u_i \geqq (1-\varepsilon)\underline{\theta}_i^*$ *for all* i, *provided* t *is sufficiently large.*

The proof is identical to that of Theorem 2.3, except that M_i replaces $(1+\varepsilon)\bar{\theta}_i$ throughout, so we omit it.

3. Some examples

In this section we shall apply the results and methods of the previous section in some specific examples. First we should note that there are a number of specific systems (mostly with Lotka–Volterra dynamics and constant or periodic coefficients) that have been treated using related methods; see for example [**1, 2, 4, 15, 18, 25, 26, 30, 49, 57**]. A typical case is that of n competitors, discussed in the comments in [**4**]. Suppose that for $i = 1, \ldots, n$,

$$\begin{aligned} &u_{i_t} = D_i \Delta u + \left(a_i - \sum_{j=1}^{n} b_{ij} u_j \right) u_i \qquad \text{in } \Omega \times (0, \infty), \\ &u_i = 0 \qquad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{3.1}$$

where all coefficients are positive constants. We may apply Theorems 2.3 and

2.5 with $R_i = a_i$, $C_i = c_i = b_{ii}$, and $r_i = a_i - \Sigma_{j \neq i} b_{ij} u_j$. Since everyone competes, $k(i) = n$ for all i. We immediately have the asymptotic upper bounds $u_i \leqq (1+\varepsilon)\theta(D_i\Delta, a_i, b_{ii}) \leqq a_i/b_{ii}$ for small $\varepsilon > 0$ and sufficiently large t, provided that $a_i > D_i\lambda_0$, where λ_0 is the principal eigenvalue of $-\Delta$ on Ω with Dirichlet boundary conditions. (The last assumption is needed for (2.6) and (2.12).) Using Theorem 2.5 with $M_i = a_i/b_{ii}$ yields the asymptotic lower bounds.

$$u_i \geqq (1-\varepsilon)\theta\left(D_i\Delta, a_i - \sum_{j \neq i} (b_{ij}a_j/b_{jj}), b_{ii}\right) \tag{3.2}$$

for $\varepsilon > 0$ and t sufficiently large, provided that

$$a_i - \sum_{j \neq i} (b_{ij}a_j/b_{jj}) > D_i\lambda_0, \quad i = 1, \ldots, n, \tag{3.3}$$

so that (2.13) is satisfied. Sharper but more complicated lower bounds can be obtained from Theorem 2.3, namely

$$u_i \geqq (1-\varepsilon)\theta\left(D_i\Delta, a_i - \sum_{j \neq i} b_{ij}(1+\varepsilon)\theta(D_j\Delta, a_j, b_{jj}), b_{ii}\right)$$

for $\varepsilon > 0$ small and t sufficiently large. (If ε is small enough that $(1+\varepsilon)\theta(D_i\Delta, a_i, b_{ii}) \leqq a_i/b_{ii}$ for all i, then (3.3) implies (2.9).) Finally, if we denote by $\varphi_0(x)$ the eigenfunction for λ_0 in

$$-\Delta\varphi = \lambda\varphi \qquad \text{on } \Omega,$$
$$\varphi = 0 \qquad \text{on } \partial\Omega,$$

with normalisation $\sup \varphi_0 = 1$, then we have

$$\theta(D\Delta, a, b) \geqq [(a - D\lambda_0)/b]\varphi_0, \tag{3.4}$$

which can easily be obtained via the method of upper and lower solutions, as in [**23, 30, 44**]. (The analogous estimate is valid under boundary conditions $B_i\varphi = 0$.) This last estimate combined with (3.2) yields the asymptotic lower bound

$$u_i \geqq (1-\varepsilon)\left[\left(a_i - \sum_{j \neq i} (b_{ij}a_j/b_{jj}) - D_i\lambda_0\right) \Big/ b_{ii}\right]\varphi_0(x) \tag{3.5}$$

for $\varepsilon > 0$ provided t is large. Since λ_0 and φ_0 can be explicitly computed for simple geometries and there are good numerical methods for computing them in general situations, the bound (3.5) is indeed 'practical'.

What if the coefficients depend on x, t or $\vec{u}$? Suppose that $\underline{a}_i \leqq a_i(x, t, \vec{u}) \leqq \bar{a}_i$ and that $\underline{b}_{ij} \leqq b_{ij}(x, t, \vec{u}) \leqq \bar{b}_{ij}$, with all constants positive. We may still use Theorem 2.5; now we take $R_i = \bar{a}_i$, $C_i = \underline{b}_{ii}$, $r_i = \underline{a}_i - \Sigma_{j \neq i} \bar{b}_{ij}u_j$, $c_i = \bar{b}_{ii}$. As before, we find that, for large t, $u_i \leqq M_i = \bar{a}_i/\underline{b}_{ii}$. If (3.3) is replaced with the condition

$$\underline{a}_i - \sum_{j \neq i} (\bar{b}_{ij}\bar{a}_j/\underline{b}_{jj}) > D_i\lambda_0, \quad i = 1, \ldots, n, \tag{3.6}$$

then we have the asymptotic lower bounds as $t \to \infty$

$$u_i \geqq (1-\varepsilon)\theta\left(D_i\Delta, \underline{a}_i - \sum_{j \neq i} (\bar{b}_{ij}\bar{a}_j/\underline{b}_{jj}), \bar{b}_{ii}\right) \tag{3.7}$$

$$\geqq (1-\varepsilon)\left[\left(\underline{a}_i - \sum_{j\neq i} (\bar{b}_{ij}\bar{a}_j/\underline{b}_{jj}) - D_i\lambda_0\right)\Big/\bar{b}_{ii}\right]\varphi_0(x).$$

Combining the above results, we have the following corollary.

COROLLARY 3.1. *Suppose that $\vec{u}$ satisfies (3.1) with $\underline{a}_i \leqq a_i(x, t, \vec{u}) \leqq \bar{a}_i$ and $\underline{b}_{ij} \leqq b_{ij}(x, t, \vec{u}) \leqq \bar{b}_{ij}$ with $\underline{b}_{ij} \geqq 0$, $\underline{b}_{ii} > 0$ for all i, j and with (3.6) satisfied. (That forces $\underline{a}_i > 0$.) Then for any $\varepsilon > 0$ and t sufficiently large, we have (3.7) for $i = 1, \ldots, n$, with corresponding asymptotic upper bounds $u_i \leqq \bar{a}_i/\underline{b}_{ii}$. (Note that only boundedness and regularity of the coefficients are needed for the bounds in (3.7); no monotonicity or periodicity are required.)*

The case of n competitors is somewhat special, since only upper bounds are used to obtain lower bounds. Cases where there are predator–prey interactions typically require more involved lower bounds on the predators which involve lower bounds on some of the prey and thus in many cases preclude the use of the simple estimate (3.4). To examine that case, let us suppose that u_1 represents a predator preying on competitors u_2 and u_3, and consider the simple model

$$\left.\begin{aligned} u_{1_t} &= D_1\Delta u_1 + (a_1 - b_{11}u_1 + b_{12}u_2 + b_{13}u_3)u_1 \\ u_{2_t} &= D_2\Delta u_2 + (a_2 - b_{21}u_1 - b_{22}u_2 - b_{23}u_3)u_2 \\ u_{3_t} &= D_3\Delta u_3 + (a_3 - b_{31}u_1 - b_{32}u_2 - b_{33}u_3)u_3, \\ u_1 &= u_2 = u_3 = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned}\right\} \tag{3.8}$$

The coefficients a_i, b_{ij} may depend on x, t, and $\vec{u}$. The Lotka–Volterra case (i.e. the case of constant coefficients) is treated in [**25**]. As in (3.1), suppose that there are constants $\underline{a}_i, \bar{a}_i, \underline{b}_{ij}, \bar{b}_{ij}$ with $\underline{a}_i \leqq a_i \leqq \bar{a}_i$ and $\underline{b}_{ij} \leqq b_{ij} \leqq \bar{b}_{ij}$, with $\underline{a}_2$, $\underline{a}_3$ and $\underline{b}_{ii}$, $i = 1, 2, 3$ strictly positive and $\underline{b}_{ij} \geqq 0$ for all i, j. To apply Theorem 2.5 to (3.8) we may use $R_1 = \bar{a}_1 + \bar{b}_{12}u_2 + \bar{b}_{13}u_3$, $R_2 = \bar{a}_2$, $R_3 = \bar{a}_3$, with $C_i = \underline{b}_{ii}$, and conclude that, for sufficiently large t, we have $u_2 \leqq M_2 = \bar{a}_2/\underline{b}_{22}$, $u_3 \leqq M_3 = \bar{a}_3/\underline{b}_{33}$ and $u_1 \leqq M_1 = [\bar{a}_1 + (\bar{b}_{12}\bar{a}_2/\underline{b}_{22}) + (\bar{b}_{13}\bar{a}_3/\underline{b}_{33})]/\underline{b}_{11}$, provided $M_1 > 0$, where the bounds on u_2 and u_3 are used to obtain the bound on u_1. (If we allow $a_1 < 0$, it may be the case that $M_1 < 0$ also; if so, the eigenvalue condition (2.12) fails. Since R_1 is increasing in u_2, u_3 and we have $u_i \leqq (1+\varepsilon)\theta(D_i\Delta, \bar{a}_i, \underline{b}_{ii}) < M_i$ for $\varepsilon > 0$ small and t large, $i = 2, 3$, it follows by the monotonicity of the principal eigenvalue with respect to the weight function that (2.6) also fails. The conclusion is that $u_1 \to 0$ as $t \to \infty$; see Remark 2.4. A related example for which a different prediction of extinction is discussed in more detail is given at the beginning of Section 4.) To get lower bounds, we take $k(2) = k(3) = 3$ since u_2 and u_3 compete, but $k(1) = 1$ since u_1 preys on u_2 and u_3. Hence, the lower bounds on u_2 and u_3 will depend only on the upper bounds already obtained for u_1, u_2 and u_3, while the lower bounds on u_1 depends on the lower bounds on u_2 and u_3. Thus, $r_1 = \underline{a}_1 + \underline{b}_{12}u_2 + \underline{b}_{13}u_3$, $r_2 = \underline{a}_2 - \bar{b}_{21}u_1 - \bar{b}_{23}u_3$, $r_3 = \underline{a}_3 - \bar{b}_{31}u_1 - \bar{b}_{32}u_2$. For u_2 and u_3 we can proceed as in the case of (3.1) provided that

$$\begin{aligned} \underline{a}_2 - \bar{b}_{21}M_1 - \bar{b}_{23}M_3 &> D_2\lambda_0, \\ \underline{a}_3 - \bar{b}_{31}M_1 - \bar{b}_{32}M_2 &> D_3\lambda_0, \end{aligned} \tag{3.9}$$

so that (2.13) holds. In that case, we find that, for any $\varepsilon>0$ and t sufficiently large, we have

$$\begin{aligned} u_2 &\geqq (1-\varepsilon)\theta(D_2\Delta, \underline{a}_2-\bar{b}_{21}M_1-\bar{b}_{23}M_3, \bar{b}_{22}) \equiv (1-\varepsilon)\underline{\theta}_2^*, \\ u_3 &\geqq (1-\varepsilon)\theta(D_3\Delta, \underline{a}_3-\bar{b}_{31}M_1-\bar{b}_{32}M_2, \bar{b}_{33}) \equiv (1-\varepsilon)\underline{\theta}_3^*, \end{aligned} \tag{3.10}$$

From (3.10) we can obtain the estimate

$$u_1 \geqq (1-\varepsilon)\theta(D_1\Delta, \underline{a}_1+\underline{b}_{12}(1-\varepsilon)\underline{\theta}_2^*+\underline{b}_{13}(1-\varepsilon)\underline{\theta}_3^*, \bar{b}_{11}) \tag{3.11}$$

for any $\varepsilon>0$ and t sufficiently large, provided that the principal eigenvalue for

$$\begin{aligned} -D_1\Delta\varphi-(\underline{a}_1+\underline{b}_{12}(1-\varepsilon)\underline{\theta}_2^*+\underline{b}_{13}(1-\varepsilon)\underline{\theta}_3^*)\varphi &= \sigma\varphi \qquad \text{in } \Omega, \\ \varphi &= 0 \qquad \text{on } \partial\Omega \end{aligned} \tag{3.12}$$

is negative. (Since there is no t-dependence in the coefficients, we will have $\varphi_t \equiv 0$ since φ must be periodic with arbitrary period in that case.) The estimates in (3.10) can be made less precise but more tractable via (3.4). It is fair to ask how practical the estimate (3.11) really is, since it involves $\underline{\theta}_2^*$ and $\underline{\theta}_3^*$, and even estimating $\underline{\theta}_2^*$, $\underline{\theta}_3^*$ in terms of φ_0 leaves (3.11) and (3.12) rather complicated. In fact, it is possible to obtain readily computable estimates that allow verification of (3.12) and interpretation of (3.11) provided that the geometry of the underlying domain Ω is simple. We shall consider the case where Ω is an interval, but rectangles could be treated in a very similar way and circles with a bit more work. The key point is to find tractable lower bounds on φ_0 that allow us to get a positive constant lower bound on the term $\underline{a}_1+\underline{b}_{12}(1-\varepsilon)\underline{\theta}_2^*+\underline{b}_{13}(1-\varepsilon)\underline{\theta}_3^*$ in (3.11), at least on some subdomain of Ω. In the case of Dirichlet boundary conditions, this is as much as can be asked since the densities u_i will be zero on $\partial\Omega$, as will φ_0 and $\theta(D\Delta, R, C)$. In general, we may still need to work on a subdomain of Ω since we may have $\underline{a}_1<0$ or even $\bar{a}_1<0$, indicating that the predator cannot survive in the absence of prey. For mixed boundary conditions, we will have $\varphi_0>0$ on $\bar{\Omega}$ but φ_0 will typically be larger near the centre of Ω than near $\partial\Omega$, so we may need to consider φ_0 on a subdomain to obtain sufficiently large lower bounds on $\underline{\theta}_2^*$ and $\underline{\theta}_3^*$ relative to $\underline{a}_1<0$. Only in the case of pure Neumann conditions can we expect φ_0 to be a constant. We shall examine the case of Dirichlet conditions in detail.

We want to use (3.4) together with the following observations about how eigenvalues for elliptic problems and the equibria for diffusive logistic equations on Ω are related to the corresponding quantities on subdomains of Ω.

LEMMA 3.2. *Suppose that $\tilde{\Omega} \subseteq \bar{\Omega}$ is a subdomain with $\partial\tilde{\Omega}$ smooth.*

(i) *Suppose that $Q(x)$ is defined on Ω, $q(x)$ on $\tilde{\Omega}$, with $Q(x) \geqq q(x)$ on $\tilde{\Omega}$ and both Q and q Hölder-continuous. The (respective) principal eigenvalues $\sigma_0(Q)$, $\tilde{\sigma}_0(q)$ for the problems*

$$\begin{aligned} -D\Delta\varphi-Q(x)\varphi &= \sigma\varphi \qquad \textit{in } \Omega, \\ \varphi &= 0 \qquad \textit{on } \partial\Omega, \end{aligned}$$

If (3.9) *holds with* $\lambda_0=\pi^2$ *and* (3.15) *holds then* (*for* $\varepsilon>0$ *sufficiently small, so that the lower bounds are nontrivial*) *the estimates* (3.13), (3.16) *hold for sufficiently large t.*

REMARK 3.4. The algebraic conditions of Corollary 3.3 are somewhat complicated but can be readily evaluated for specific values of the bounds on the coefficients. We can always obtain the upper bounds $u_i \leqq M_i$ for t large; the complications are in verifying (3.9) and (3.15). One obvious condition is that $\underline{a}_i$ be large for all i and $\bar{b}_{ij}$ be small for $i\neq j$, but others are also possible. Specifically, we could have $\underline{a}_1 \leqq \bar{a}_1 < 0$ provided that $\underline{a}_i>0$ for $i=2, 3$, $\underline{b}_{12}(\underline{a}_2/2\bar{b}_{22})+\underline{b}_{13}(\underline{a}_3/2\bar{b}_{33})+\underline{a}_1>0$, $\bar{b}_{ij}$ is small for $i=2, 3$ and $j\neq i$, and D_i is small for all i. That can be seen by noting that if $\bar{b}_{ij}\to 0$ for $i=2, 3$ and $j\neq i$, then the M_i terms in (3.9) disappear and $m_i\to \underline{a}_i/2\bar{b}_{ii}$ in (3.15) so that the inequalities will be satisfied for small ε if D_i is small for each i. This last case is interesting from the applied viewpoint, since it models a situation in which the predator will become extinct in the absence of prey, which is often a biologically realistic assumption.

So far we have focused our attention on problems where we generally could avoid detailed consideration of the time and space dependence of the coefficients and where the nonlinearities could be compared readily with those appearing in Lotka–Volterra models. In the next examples, we shall consider a case where the time and space dependence is treated more explicitly and another case where the nonlinearities are not so close to those in Lotka–Volterra systems.

Consider a predator–prey model of the form

$$\begin{aligned} u_{1_t} &= \nabla\cdot D_1(x)\nabla u_1 + (a_1(x,t,\vec{u}) - b_{11}(x,t,\vec{u})u_1 + b_{12}(x,t,\vec{u})u_2)u_1, \\ u_{2_t} &= \nabla\cdot D_2(x)\nabla u_2 + (a_2(x,t,\vec{u}) - b_{12}(x,t,\vec{u})u_1 - b_{22}(x,t,\vec{u})u_2)u_2, \\ u_1 &= 0, \qquad \frac{\partial u_2}{\partial \nu} = 0 \quad \text{on } \partial\Omega\times(0,\infty), \end{aligned} \tag{3.17}$$

where $D_1, D_2 \geqq D_0>0$ on $\bar{\Omega}$, the coefficients b_{ij} are all positive, and all coefficients are (perhaps trivially) T-periodic in t and bounded in $\vec{u}$. As before, let $\underline{a}_i$, $\bar{a}_i$, $\underline{b}_{ij}$ and $\bar{b}_{ij}$ denote respectively lower and upper bounds on the coefficients. We will want to allow some of these to be time dependent with period T, specifically $\underline{a}_1(t)$, $\underline{a}_2(t)$, $\underline{b}_{12}(t)$, $\bar{b}_{21}(t)$ and $\bar{b}_{22}(t)$; the others will be constants. For sharpness we would typically choose for example $\underline{a}_i(t)=\inf\{a_i(x,t,\vec{u}): x\in\bar{\Omega}, u_1, u_2\geqq 0\}$, but in some cases simpler but less sharp estimates might be useful. We may take $R_1=\bar{a}_1+\bar{b}_{12}U_2$, $R_2=\bar{a}_2$, $C_1=\underline{b}_{11}$, $C_2=\underline{b}_{22}$ and obtain the asymptotic upper bounds $u_2\leqq \bar{a}_2/\underline{b}_{22}\equiv M_2$, $u_1\leqq[\bar{a}_1+(\bar{b}_{12}\bar{a}_2/\underline{b}_{22})]/\underline{b}_{11}\equiv M_1$ for t sufficiently large. (We assume that $\bar{a}_2$ and $\bar{a}_1+(\bar{b}_{12}\bar{a}_2/\underline{b}_{22})$ are large enough that (2.12) is satisfied.) Next, with $k(1)=1$, $k(2)=2$, let $r_1=\underline{a}_1(t)+\underline{b}_{12}(t)U_2$, $r_2=\underline{a}_2(t)-\bar{b}_{21}(t)U_1$, $c_1=\bar{b}_{11}$, $c_2=\bar{b}_{22}(t)$. We obtain a positive T-periodic asymptotic lower bound on u_2 from the steady-state solution $\underline{\theta}_2^*$ of the problem

$$\begin{aligned} u_t &= \nabla\cdot D_2(x)\nabla u + (\underline{a}_2(t) - \bar{b}_{21}(t)M_1 - \bar{b}_{22}(t)u)u, \\ \frac{\partial u}{\partial \nu} &= 0 \quad \text{on } \partial\Omega\times(0,\infty), \end{aligned} \tag{3.18}$$

provided that (3.18) satisfies the eigenvalue condition (2.13). However, the eigenvalue problem has the form

$$\varphi_t - \nabla \cdot D_2(x)\nabla\varphi - (\underline{a}_2(t) - \bar{b}_{21}(t)M_1)\varphi = \sigma\varphi,$$
$$\frac{\partial\varphi}{\partial\nu} = 0 \quad \text{on } \partial\Omega \times (0, \infty), \qquad \varphi \quad T\text{-periodic in } t,$$

where $\underline{a}_2(t) - \bar{b}_{21}(t)M_1$ is T-periodic; so by [**30**, Lemma 15.3] the principal eigenvalue is given by $\sigma_2^* = \mu_2 - p_2/T$, where μ_2 is the principal eigenvalue of the problem

$$\begin{gathered}\varphi_t - \nabla \cdot D_2(x)\nabla\varphi = \mu\varphi,\\ \frac{\partial\varphi}{\partial\nu} = 0, \qquad \varphi \quad T\text{-periodic in } t,\end{gathered} \tag{3.19}$$

and

$$p_2 = \int_0^T (\underline{a}_2(t) - \bar{b}_{21}(t)M_1)\, dt. \tag{3.20}$$

Since there is no explicit t-dependence in (3.19) and the boundary condition is of Neumann type, the principal eigenvalue μ_2 in (3.19) is zero, so $\sigma_2^* < 0$ if $p_2 > 0$ in (3.20). Assuming that to be the case, let $\theta_2^*(t)$ denote the unique positive T-periodic steady-state for (3.18). It is easy to see that the positive T-periodic solution to the ordinary differential equation

$$\dot{v} = (\underline{a}_2(t) - \bar{b}_{21}(t)M_1 - \bar{b}_{22}(t)v)v \tag{3.21}$$

is a steady-state for (3.18), so by uniqueness $\underline{\theta}_2^*(t) = v$. (The periodic solutions to periodic logistic equations of the form (3.21) can be explicitly computed from the coefficients, so that $\underline{\theta}_2^*(t)$ is in principle a known function; see [**22**].). We assume $p_2 > 0$ in (3.20) and may then conclude that for arbitrary $\varepsilon > 0$ and large t, $u_2 \geqq (1-\varepsilon)\underline{\theta}_2^*(t) > 0$. Substituting that lower bound into r_1 yields

$$\begin{gathered}u_t = \nabla \cdot D_1(x)\nabla u + [\underline{a}_1(t) + \underline{b}_{12}(t)(1-\varepsilon)\underline{\theta}_2^*(t) - \bar{b}_{11}u]u\\ u = 0 \quad \text{on } \partial\Omega, \qquad u \quad T\text{-periodic.}\end{gathered} \tag{3.22}$$

Again, we need to verify (2.13). The assumptions required for that will also enable us to give an explicit asymptotic lower bound $(1-\varepsilon)\underline{\theta}_1^*(x, t)$ on u_1. We shall again use [**30**, Lemma 15.3], which states that the principal eigenvalue σ_1^* for

$$\begin{gathered}\varphi_t - \nabla \cdot D_1(x)\nabla\varphi - [\underline{a}_1(t) - \underline{b}_{12}(t)(1-\varepsilon)\underline{\theta}_2^*(t)]\varphi = \sigma\varphi,\\ \varphi = 0 \quad \text{on } \partial\Omega, \qquad \varphi \quad T\text{-periodic}\end{gathered} \tag{3.23}$$

is given by $\sigma_1^* = \mu_1 - p_1/T$, where

$$p_1 = \int_0^T [\underline{a}_1(t) + \underline{b}_{12}(t)(1-\varepsilon)\underline{\theta}_2^*(t)]\, dt \tag{3.24}$$

and μ_1 is the principal eigenvalue for

$$\begin{gathered}\varphi_t - \nabla \cdot D_1(x)\nabla\varphi = \mu\varphi,\\ \varphi = 0 \quad \text{on } \partial\Omega \times \mathbb{R}, \qquad \varphi \quad T\text{-periodic.}\end{gathered} \tag{3.25}$$

Since (3.25) has no explicit t-dependence, the eigenvalue μ_1 is simply the principal eigenvalue for the elliptic problem

$$\begin{aligned} -\nabla \cdot D_1(x)\nabla\psi &= \mu\psi, \\ \psi &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.26}$$

If $\sigma_1^* < 0$ we have the asymptotic lower bound $u_1 \geqq (1-\varepsilon)\underline{\theta}_1^*(x, t)$, where $\underline{\theta}_1^*(x, t)$ is the unique positive T-periodic steady-state for (3.22). We can make the lower bound more explicit by noting that $\underline{\theta}_1^*(x, t)$ is bounded below by the subsolution $\gamma q(t)\psi_1(x)$, where $\psi_1(x)$ is the eigenfunction of (3.26), corresponding to μ_1 normalised with $\sup \psi_1 = 1$, $q(t)$ is defined as

$$q(t) = \exp\left\{\int_0^t (\underline{a}_1(s) - \underline{b}_{12}(s)(1-\varepsilon)\underline{\theta}_2^*(s))\, ds - tp_1/T\right\} \tag{3.27}$$

and γ satisfies $-\sigma_1^* - \gamma\bar{b}_{11} \sup q \geqq 0$, that is, we have $\gamma \leqq -\sigma_1^*/\bar{b}_{11} \sup q$. (See [**30**], specifically the proof of Lemma 15.3 and Example 28.4.) We have

COROLLARY 3.5. *Suppose that $\vec{u}$ is a solution to* (3.17) *with u_1, u_2 initially non-negative and not identically zero. Define $M_2 = \bar{a}_2/\underline{b}_{22}$, $M_1 = [\bar{a}_1 + (\bar{b}_{12}\bar{a}_2/\underline{b}_{22})]/\underline{b}_{11}$ in terms of the bounds on the coefficients of* (3.17). *Suppose that $p_2 > 0$, where p_2 is defined in* (3.20), *and let $\underline{\theta}_2^*(t)$ be the unique positive periodic steady-state of* (3.21). *Suppose that $p_1 > \mu_1 T$, where p_1, μ_1 are defined in* (3.24), (3.25) *respectively. Then for any $\varepsilon > 0$ and t sufficiently large, $u_2 \geqq (1-\varepsilon)\underline{\theta}_2^*(t)$ and $u_1 \geqq (1-\varepsilon)(-\mu_1 + p_1/T)\psi_1(x)q(t)/\sup q(\bar{b}_{11})$, where $\psi_1(x)$ is the principal eigenfunction for* (3.26) *and hence* (3.25) *with $\sup \psi_1 = 1$ and where $q(t)$ is the T-periodic function defined in* (3.27).

REMARK 3.6. In view of [**22**], $\underline{\theta}_2^*(t)$ in principle can be computed explicitly in terms of integrals involving the coefficients in the periodic logistic equation (3.21), so that p_1 and $q(t)$ can also be explicitly computed. The eigenvalue and eigenfunction μ_1, ψ_1 may or may not be explicitly computable depending on $D_1(x)$ and the geometry of Ω; in any case, there are good numerical approximations and theoretical estimates available; see [**54**] or some of the articles in [**50**]. Again, the lower bounds are at least reasonably practical.

There are many reasons to consider periodic lower bounds of the type obtained in Corollary 3.5. Seasonal variations are often of biological interest, and in some cases either both species may experience a negative population growth rate for part of the year. The use of coefficient bounds that are T-periodic is appropriate since there will generally be random variations in weather but those are often limited deviations from an expected seasonal pattern. The eigenvalue μ_1 in (3.25) and (3.26) carries information on the geometry of Ω and the effects of variable diffusion. The sort of process used to obtain the estimates in Corollary 3.5 could also be used with different choices of which coefficients to bound in terms of constants and which to bound in terms of T-periodic functions, or functions of x alone, or functions of both x and t. The more complex the coefficient bounds, the more complicated the estimates. The bounds on coefficients can be chosen to include those spatial or temporal effects that are relevant to the system and to ignore others. The specific choices in Corollary 3.5 were rather arbitrary since the main point was simply to illustrate some of the flexibility of the method.

So far, all the examples we have considered could be viewed as Lotka–Volterra models with perturbed coefficients. As a final example of the general theory, we consider a more general form of predator–prey model, namely

$$\begin{aligned} u_{1_t} &= D_1 \Delta u_1 + (a_1 - b_{11} u_1 + b_{12} f(u_2) u_2) u_1, \\ u_{2_t} &= D_2 \Delta u_2 + (a_2 - b_{21} f(u_2) u_1 - b_{22} u_2) u_2, \\ u_1 &= u_2 = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{3.28}$$

where $f(u)$ is a positive function with $uf(u)$ monotone increasing in u. The function $f(u)$ is called the *predator's functional response to the prey*. It describes the rate at which predators consume the prey. In the Lotka–Volterra model, $f(u)$ is a positive constant. Some other typical forms are $f(u) = 1/(\alpha + \beta u)$ or $f(u) = u/(\alpha + \beta u^2)$; see for example [**46, 56**] for more discussion and biological background. Roughly speaking, these forms of functional response model situations were the rate at which as single predator consumes prey, described by the term $u_2 f(u_2)$, 'saturates' or levels off below some maximum value no matter how large the prey density might be. Since any given predator has finite capacity for consuming prey, models involving a functional response of the above type are in some ways more realistic than those where the predator's consumption rate is simply assumed to be proportional to prey density.

Since our main interest here is in how $f(u)$ may be included in our estimates, we shall assume that the coefficients in (3.28) are constants. It would certainly be possible to combine the functional response of (3.28) with the time and space dependence of (3.17) but we shall not do that here. Let $R_2 = a_2$, $R_1 = a_1 + b_{12} U_2 f(U_2)$, and $C_i = b_{ii}$ for $i = 1, 2$. Applying Theorem 2.5, we obtain the asymptotic upper bounds $u_2 \leqq a_2/b_{22} \equiv M_2$, $u_1 \leqq [a_1 + b_{12} M_2 f(M_2)]/b_1 \equiv M_1$ for t sufficiently large. Strictly speaking, we should require $a_2 - D_2\lambda_0 > 0$ and $a_1 + b_{12} M_2 (f(M_2)) - D_1 \lambda_0 > 0$ (where λ_0 is the principal eigenvalue of $-\Delta$ on Ω subject to Dirichlet boundary conditions) so that (2.12) is satisfied; however, if (2.12) fails for some value of i, the implication is that the ith species must decline toward extinction, so for that species we will have arbitrary small asymptotic upper bounds. The real point is that unless (2.12) is satisfied, there is no chance of obtaining lower bounds from the present methods. Since (3.28) is a predator–prey system, we take $k(i) = i$ for $i = 1, 2$ and use $r_2 = a_2 - b_{21} U_1 \bar{f}$, $r_1 = a_1 + b_{12} U_2 f(U_2)$, and $c_i = b_{ii}$, $i = 1, 2$, where $\bar{f} = \sup\{f(u) : 0 \leqq u \leqq M_2\}$. (Recall that the bounds (2.7) really need only hold when $0 \leqq U_i \leqq M_i$ since we require that t is large enough that the asymptotic upper bounds are all satisfied before deriving the lower bounds; see the remarks following Theorem 2.3.) To obtain a lower bound on u_2, we require

$$a_2 - b_{21} M_1 \bar{f} - D_2 \lambda_0 > 0 \tag{3.29}$$

so that (2.13) is satisfied. We then obtain the asymptotic lower bound

$$\begin{aligned} u_2 &\geqq (1-\varepsilon)\theta(D_2\Delta, a_2 - b_{21} M_1 \bar{f}, b_{22}) \equiv (1-\varepsilon)\underline{\theta}_2^*(x) \\ &\geqq (1-\varepsilon)[(a_2 - b_{21} M_1 \bar{f} - D_2 \lambda_0)/b_{22}]\varphi_0(x) \equiv (1-\varepsilon)\varphi^*(x) \end{aligned} \tag{3.30}$$

(where φ_0 is the principal eigenfunction of $-\Delta$ on Ω with Dirichlet boundary conditions normalised with $\sup \varphi_0 = 1$) for t sufficiently large and $\varepsilon > 0$ arbitrary. Using the estimates in (3.30), we must require that the principal eigenvalue for the that is the case, then all positive solutions to

$$u_t = D_2 \Delta u + (a_2 - b_{23}(1-\varepsilon)\underline{\theta}_3^* - b_{22} u)u, \quad u = 0 \quad \text{on } \partial\Omega \tag{4.4}$$

will tend to zero as $t \to \infty$, provided $\varepsilon > 0$ is sufficiently small. However, since $u_3 \geqq (1-\varepsilon)\underline{\theta}_3^*$ for large t, say $t \geqq t_0$, we see that eventually u_2 will be a subsolution of (4.4), so that u_2 will be less than or equal to the solution of (4.4) with 'initial' data $u(x, t_0) = u_2(x, t_0)$, and hence u_2 will tend to zero as $t \to \infty$. The principal eigenvalue in (4.3) will be less than the one in (4.2), so in some cases we can neither obtain extinction nor asymptotic lower bounds on u_2 without more (or different) analysis, as we could have a positive principal eigenvalue in (4.2) but a negative one in (4.3).

In Theorems 2.3 and 2.5, we obtained just one set each of upper and lower asymptotic estimates and then quit. In some cases it is possible to proceed further. Specifically, suppose we have a Lotka–Volterra system of the form

$$u_{i_t} = D\Delta u_i + \left(a + \sum_{j=1}^{n} b_{ij} u_j\right) u_i,$$

$$Bu_i = 0 \quad \text{on } \partial\Omega \times (0, \infty),$$

with constant coefficients where the diffusion rates, growth rates and boundary conditions are the same in each equation. In that case, all the functions $\underline{\theta}_i$ and $\bar{\theta}_i$ occurring in the lower and upper asymptotic estimates of Theorem 2.3 can be taken to be multiples of $\theta(D\Delta, a, 1)$. That will be possible because for any constant b, $\theta(D\Delta, a, b) = (1/b)\theta(D\Delta, a, 1)$, and also $\theta(D\Delta, a + c\theta(D\Delta, a, 1), 1) = (1+c)\theta(D\Delta, a, 1)$ for $c \geqq -1$, as can be seen by substitution and the uniqueness of the positive equilibrium for diffusive logistic equations. These observations permit iteration of the estimates; for example, in the system

$$\begin{aligned} u_{1_t} &= \Delta u_1 + (a - u_1 + b u_2) u_1, \\ u_{2_t} &= \Delta u_2 + (a - c u_1 - u_2) u_2, \\ u_1 &= u_2 = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{4.5}$$

we would compare the second equation to $u_t = \Delta u + (a-u)u$ and then the first to $u_t = \Delta u + (a + b\theta - u)u$ where we assume $a > \lambda_0$ and θ is the positive solution to $\Delta\theta + (a-\theta)\theta = 0$ on Ω, $\theta = 0$ on $\partial\Omega$. The asymptotic bounds are thus $u_2 \leqq (1+\varepsilon)\theta(\Delta, a, 1)$ and $u_1 \leqq (1+\varepsilon)(1+b)\theta(\Delta, a, 1)$; so now we would compare u_2 to the solution of

$$u_t = \Delta u + [a - c(1+b)(1+\varepsilon)\theta - u]u, \quad u = 0,$$

$$u = 0 \quad \text{on } \partial\Omega \times (0, \infty),$$

to obtain the asymptotic lower bound

$$\begin{aligned} u_2 &\geqq (1-\varepsilon)\theta(\Delta, a - c(1+b)(1+\varepsilon)\theta(\Delta, a, 1), 1) \\ &= (1-\varepsilon)(1 - c(1+b)(1+\varepsilon))\theta(\Delta, a, 1). \end{aligned}$$

(We assume here that b and c are small enough that $c(1+b)<1$, and make analogous assumptions as needed.) The asymptotic lower bound on u_1 is then taken from comparison with

$$u_t = \Delta u + [a + b(1-\varepsilon)(1 - c(1+b)(1+\varepsilon))\theta(\Delta, a, 1) - u]u,$$
$$u = 0 \quad \text{on } \partial\Omega,$$

which yields the lower estimate for large t

$$\begin{aligned} u_1 &\geqq (1-\varepsilon)\theta(\Delta, a + b(1-\varepsilon)(1-c(1+b)(1+\varepsilon))\theta(\Delta, a, 1), 1) \\ &= (1-\varepsilon)[1 + b(1-\varepsilon)(1-c(1+b)(1+\varepsilon))]\theta(\Delta, a, 1) \\ &\equiv k(\varepsilon)\theta(\Delta, a, 1). \end{aligned}$$

At this point in the proof of Theorem 2.3 we would quit; but here the facts that all the bounds are essentially multiples of $\theta(\Delta, a, 1)$ by algebraic combinations of coefficients and that such bounds lead to others in the same from allow us to continue. The last asymptotic lower bound on u_1 can be used to obtain a sharpened upper bound on u_2 via comparison with $u_t = \Delta u + (a - ck(\varepsilon)\theta(\Delta, a, 1) - u)u$, so that for large t we get

$$\begin{aligned} u_2 &\leqq (1+\varepsilon)\theta(\Delta, a - ck(\varepsilon)\theta(\Delta, a, 1), 1) \\ &= (1+\varepsilon)(1 - ck(\varepsilon))\theta(\Delta, a, 1). \end{aligned}$$

This process can be continued and the resulting algebraic dependence of the bounds on b and c can be analysed; this sort of process is carried to its conclusion in some of the estimates in [**18**], and some related ideas are used in [**12, 23, 44**] among other places.

A different sort of special case where the analysis can be simplifed and/or sharpened is that of small diffusion. As $D \to 0$, we have by results in [**13**] that $\theta(D\Delta, a, b) \to a/b$ uniformly on compact subsets of Ω on which a/b is continuous if there is no t dependence. This fact has been used to simplify estimates and facilitate computation in various contexts; one such example is treated in [**17**], but there are many others in the literature.

Finally, we note that our estimates are valid for short times as well as very long ones if we can control initial data. Suppose u_1 and u_2 satisfy the predator–prey system

$$\begin{aligned} u_{1_t} &= D_1 \Delta u_1 + (a_1 - u_1 + b_{12} u_2) u_1, \\ u_{2_t} &= D_2 \Delta u_2 + (a_2 - b_{21} u_1 - u_2) u_2, \qquad (4.6) \\ u_1 &= u_2 = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned}$$

with all coefficients positive constants, that initially u_2 is at the equilibrium $\theta(D_2\Delta, a_2, 1)$ it would attain in the absence of the predator, and initially u_1 is small. This would correspond to a situation where a few predators have been introduced into an area where there previously were prey but no predators. Throughout this discussion, we shall assume that all the necessary eigenvalue conditions are satisfied. Since u_2 is a subsolution of the equation $u_t = D_2\Delta u + (a_2 - u)u$ for any non-negative u_1, we see that u_2 must remain less than $\theta(D_2\Delta, a_2, 1)$ since that is the solution of the diffusive logistic equation with the same initial data. It follows that u_1 will always be a subsolution of $u_t = D_1\Delta u + (a_1 + b_{12}a_2 - u)u$ since $\theta(D_2\Delta, a_2, 1) < a_2$, so if u_1 is initially small then $u_1 \leqq \theta(D_1\Delta, a_1 + b_{12}a_2, 1) \leqq a_1 + b_{12}a_2$ for all t. Using that bound in the second equation, we may compare u_2 with the solution to $u_t = D_2\Delta u + (a_2 - b_{21}(a_1 + b_{12}a_2) - u)u$ with the same initial data. However, our initial datum $u_2 = \theta(D_2\Delta, a_2, 1)$ can easily be seen to be a supersolution to this last logistic problem, so the solution starting there approaches $\theta(D_2\Delta, a_2 - b_{21}(a_1 + b_{12}a_2), 1)$ from above. Hence, we will have the lower bound $u_2 \geqq \theta(D_2\theta, a_2 - b_{21}(a_1 + b_{12}a_2), 1)$ for all t. Since u_1 is initially small, we cannot expect a useful time-independent lower bound; but since $u_2 \geqq \theta(D_2\Delta, a_2 - b_{21}(a_1 + b_{12}a_2), 1)$ for all $t > 0$, we can at least say that u_1 will stay above the solution to the equation

$$u_t = D_1\Delta u + (a_1 + b_{12}\theta(D_2\Delta, a_2 - b_{21}(a_1 + b_{12}a_2), 1) - u)u$$

with the same initial data. That lower bound could be made more explicit but less sharp in some cases by the methods used in deriving the explicit estimates in Corollary 3.3.

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