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On a Diffusive Prey–Predator Model Which Exhibits Patchiness

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Spatial heterogeneity (patchiness) in certain predator–prey situations has been observed even though their environment appears homogeneous. As a model mechanism to explain this patchiness phenomenon we propose a predator–prey interaction system with diffusive effects. We show that when the diffusion of the prey is small compared with that of the predator the non-linearity which we call a hump effect in the prey interaction, is a key mechanism for the system to exhibit, asymptotically in time, stable heterogeneity in a bounded domain with zero flux boundary conditions. The model can reasonably be applied to certain terrestrial plant–herbivore systems.

1. Introduction

In several predator–prey situations spatial heterogeneity, known as patchiness, has been observed even though the environment appears homogeneous. For example, Cassie (1963) reported that, depending on the circumstances, plankton display such patchiness. Various theoretical models have been proposed to explain this planktonic behaviour, for example, by Stavn (1971), Platt (1972), Plesset & Whipple (1974), Steele (1974) and Okubo (1976). The classic Lotka–Volterra model in which the prey and predator diffuse, namely

$$\left.\begin{aligned}\frac{\partial P}{\partial t} &= d_P\frac{\partial^2 P}{\partial x^2}+(a-kQ)P\\ \frac{\partial Q}{\partial t} &= d_Q\frac{\partial^2 Q}{\partial x^2}-(b-hP)Q\end{aligned}\right\}, \tag{1}$$

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was proposed by Steele (1974). Here P and Q represent the phytoplankton (prey) and the zooplankton (predator) respectively, a, k, b and h are positive constants and d_P and d_Q the respective diffusion coefficients. He suggested that in a finite one-dimensional (x) domain with $d_P = d_Q$ and zero flux conditions on the boundaries, that is $\partial P/\partial x = 0 = \partial Q/\partial x$, the system (1) could exhibit patchiness. However, Murray (1975) proved that in this situation the system (1) cannot exhibit steady spatially heterogeneous solutions: this is typical of such conservative systems. The apparent "patchiness" found by Dubois (1975) is actually a *transient* behaviour which comes from an initial disturbance.

Mimura (1978) considered the system (1) when a and b are functions of P and Q respectively, namely

$$\left.\begin{aligned}\frac{\partial P}{\partial t} &= d_P\frac{\partial^2 P}{\partial x^2}+[a(P)-kQ]P\\ \frac{\partial Q}{\partial t} &= d_Q\frac{\partial^2 Q}{\partial x^2}-[b(Q)-hP]Q\end{aligned}\right\}, \qquad (2)$$

where k and h are positive constants. He showed that if $a(P)$ and $b(Q)$ are monotonic non-increasing and non-decreasing functions of P and Q respectively then the population densities $P(x, t)$ and $Q(x, t)$ are spatially homogeneous, asymptotically for large time in a bounded domain with zero flux boundary conditions. His result holds for two- and three-dimensional domains as well.

Whatever the form of the interaction terms if the solutions are bounded Conway, Hoff & Smoller (1977) have proved that if the diffusion of both species is sufficiently large there can be no spatial structure in bounded domains with zero flux. Their results cover a wider class of systems than that studied here. This is as would be expected heuristically.

Within the framework of the system (2) Segel & Jackson (1972) and Levin & Segel (1976) proposed a predator–prey model for patchiness using Turing's (1952) idea, and said that an autocatalytic effect in the prey could give patchiness. Okubo (1976) also suggested that Turing's idea would be applicable to the modelling of patchiness.

In this paper we consider the model (2) where $a(P)$ exhibits an Allee effect, or what can be described as a hump effect, and show that patchiness exists when diffusivity of the prey d_P is small and in particular small compared with that of the predator d_Q. Such a situation is primarily motivated by the study of plant–herbivore systems with small plant diffusion d_P. There are rather crucial differences between the Segel & Jackson (1972) model and ours in this case. A major difference is that although for finite d_P both models exhibit similar heterogeneous behaviour, for small d_P this is not the case as described below: we also discuss this analytically in the mathematical appendix B. If $d_P \to 0$ the non-linear effects of the Segel & Jackson (1972) model will give rise to very large and progressively narrower spike-like structures for the prey with $P = 0$ almost everywhere in the domain. On the other hand with the model discussed here an Allee effect leads to two quite different broad subdomains where $P = 0$ and $P \neq 0$: these are shown in results given in Figs 5 and 6. The model we analyse in this paper is fairly robust in its patchiness behaviour but the existence of it depends on appropriate interplay between diffusion and the predator–prey interaction. As would be expected heuristically the relative magnitude of the diffusivities affects the detailed spatial structure. In the following section specific conditions are given for the existence of patchiness.

In section 2 the mathematical model is described from an ecological point of view and the relevance of the necessary conditions for heterogeneous solutions to exist is discussed. In section 3 numerical results for a typical case which clearly indicates various aspects of stable patchiness are given. The necessary conditions for patchiness in a model are derived in Appendix A while in Appendix B the mathematical problem is discussed analytically with some detailed analysis of the solution and particularly the transition layers, that is regions in the domain where the prey density changes rapidly: these appear when the ratio of the diffusivities of the prey to predator is small: see Figs 5 and 6.

2. Mathematical Model and Practical Relevance

The general model system for which we derive necessary conditions for patchiness to exist is, in place of (2),

$$\left.\begin{aligned}\frac{\partial P}{\partial t} &= d_P \frac{\partial^2 P}{\partial x^2} + f_0(P, Q)[f_1(P) - Q]P \\ \frac{\partial Q}{\partial t} &= d_Q \frac{\partial^2 Q}{\partial x^2} - g_0(P, Q)[g_1(Q) - P]Q\end{aligned}\right\}, \tag{3}$$

for time $t \geqslant 0$ and space dimension x in some finite domain $0 \leqslant x \leqslant L$. The functions f_0, g_0, f_1 and g_1 are described below. We are interested in non-negative solutions of (3) which satisfy initial conditions and zero flux boundary conditions

$$\frac{\partial P}{\partial x} = 0 = \frac{\partial Q}{\partial x} \quad \text{for } x = 0,\, L \text{ and } t \geqslant 0. \tag{4}$$

For example, the following model, which belongs to the class (3), was proposed by May (1973) from experiment:

$$f_0 = \frac{a}{P+b}, \quad f_1 = \frac{c}{a}(d-P)(P+b), \quad g_0 = \frac{e}{P}, \quad g_1 = fQ, \tag{5}$$

where a, b, c, d, e and f are all positive constants. We call the type of non-linearity in f_1 a *hump* effect if $d > b$: that is $Q = f(P)$ exhibits a similar behaviour to that shown by $v = f(u)$ in Fig. 1. Later we shall be associating v and u with Q and P respectively when considering for algebraic convenience a more restrictive class than (3) but which has the essential features for exhibiting patchiness.

We now make certain assumptions about the system (3) which we relate to practical plant–herbivore systems. The prey (plant) is denoted by P and the predator (herbivore) by Q.

Assumption 1

The diffusion coefficients satisfy $0 \leqslant d_P \leqslant d_Q$. This is certainly reasonable for many plant–herbivore systems. Certain planktonic populations also have this characteristic (Okubo, 1976).

Assumption 2

The functions $f_0 > 0$, $g_0 > 0$ for $P, Q \geqslant 0$ and f_1 and g_1 satisfy

$$g_1'(Q) \geqslant 0 \text{ for } Q \geqslant 0; f_1'(P) \begin{cases} > 0; 0 \leqslant P < P^* \\ = 0, P = P^* \\ < 0, P > P^* \end{cases}$$

for some positive value P^*, where primes denote differentiation with respect to the argument. These conditions reflect the general characteristics of May's (1975) model (5): see also Fig. 1 where $f(u)$ and $g(v)$ are associated with f_1 and g_1.

Assumption 3

There exists one positive steady state solution (P_0, Q_0) of the system (3). If $g_1'(Q) > 0$ for large Q assumption 2 implies that the system (3) is globally (weakly) stable in the sense that the solution $[P(x, t), Q(x, t)]$ is confined in some finite domain in (P, Q) space [see, for example, Conway & Smoller (1977)].

The property of the solution in the neighbourhood of (P_0, Q_0) is obtained from the usual analysis of the linearized form of (3), namely,

$$\left.\begin{aligned} \frac{\partial p}{\partial t} &= d_P\frac{\partial^2 p}{\partial x^2}+f_0(P_0, Q_0)P_0\{f_1'(P_0)p-q\}, \\ \frac{\partial q}{\partial t} &= d_Q\frac{\partial^2 q}{\partial x^2}+g_0(P_0, Q_0)Q_0\{p-g_1'(Q_0)q\}, \end{aligned}\right\} \tag{6}$$

subject to zero flux conditions, where here (p, q) is the perturbation in (P, Q) about the steady state (P_0, Q_0).

If the diffusivities d_P and d_Q are both large [compared with the maximum of P and Q in the solution domain of (P, Q)] then as mentioned in the introduction the solution tends, for large time, to the homogeneous solution, that is patchiness cannot exist. In view of this we consider the situation in which one of d_P and d_Q is not large. We make the further

Assumption 4

The system (6) has one positive eigenvalue which depends on the presence of the diffusion terms. In other words the steady state (P_0, Q_0) is, on a linear basis, *diffusionally unstable:* if $d_P \equiv 0 \equiv d_Q$ the steady state is stable.

It is shown in Appendix A that Assumption 4 can be given in terms of f_0, f_1, g_0 and g_1: specifically there must exist at least one integer n such that, with $\sigma = n^2\pi^2/L^2$,

$$d_P d_Q \sigma^2 - [f_0(P_0, Q_0)f_1'(P_0)P_0 d_Q - g_0(P_0, Q_0)g_1'(Q_0)Q_0 d_P]\sigma \\ -[f_1'(P_0)g_1'(Q_0)-1]f_0(P_0, Q_0)g_0(P_0, Q_0)P_0Q_0 < 0, \qquad (7)$$

or

$$f_0(P_0, Q_0)f_1'(P_0)P_0 - g_0(P_0, Q_0)g_1'(Q_0)Q_0 - (d_P+d_Q)\sigma > 0. \qquad (8)$$

The subsidiary conditions for stability when $d_P = 0 = d_Q$ are $g_0Q_0g_1'(Q_0) - f_0P_0f_1'(P_0) > 0$ and $1-f_1'(P_0)g_1'(Q_0) > 0$. These conditions are obtained (Appendix A) by a conventional Fourier analysis of (6) with zero flux boundary conditions at $x = 0, L$.

With the ecology of plant–herbivore systems in mind we make the further

Assumption 5

The diffusion coefficient of the predator Q (herbivore) is large compared with that of the prey (plant), that is $0 \leqslant d_P \ll d_Q$. In this case condition (7) is satisfied if the following holds:

Assumption 6

$$f_1'(P_0) > 0.$$

That is the steady state lies to the left of the maximum in the $Q = f_1(P)$ curve: compare with Fig. 1 for $v = f(u)$.

We now apply Assumptions 2–6 to the system (3). These assumed conditions do not change if f_0 and g_0 are replaced by positive constants and so, for algebraic convenience, we consider the simpler form of (3) with (u, v) for (P, Q), namely.

$$\frac{\partial u}{\partial t} = \beta\frac{\partial^2 u}{\partial x^2} + [f(u)-v]u, \quad \frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - a[g(v)-u]v, \qquad (9)$$

where $\beta(\ll 1)$ and a are positive constants. The constant β is in effect the ratio of the diffusion coefficients d_P/d_Q. The problem thus reduces to the study of (9) with zero flux boundary conditions. Conditions (7) and (8) as applied to (9) become

$$\left.\begin{aligned} &\beta\sigma^2-[f'(u_0)u_0-ag'(v_0)\beta v_0]\sigma-[f'(u_0)g'(v_0)-1]au_0v_0 < 0,\\ &f'(u_0)u_0-ag'(v_0)v_0-(1+\beta)\sigma > 0;\ \sigma = n^2\pi^2/L^2. \end{aligned}\right\} \tag{10}$$

3. Numerical Results and Examples of Patchiness

For simplicity only we considered a one-dimensional domain with spatial coordinate $0 \leqslant x \leqslant L$ and as a simple illustrative and typical example of (9) we chose a $f(u)$ and $g(v)$ which satisfied all of the required practical assumptions discussed in section 2. Typical functions $f(u)$ and $g(v)$ are like those in the phase Fig. 1. Solutions of (9) were found numerically using a finite difference procedure for the initial and boundary value problem. We first investigated the dependency of the parameter a in (9) on the solution when β is fixed. The linear stability diagram of the relation between the number of the Fourier modes n and a is given by (10) for the case in Fig. 1 and is shown in Fig. 2. Note that there are two critical points, denoted by a_0 and a_1: the former is in fact determined by the non-diffusion system and the latter by the diffusion system. For illustration we computed for the functions in Fig. 1 the case $a = 1$, that is $a_0 < a < a_1$, with $\beta = 0{\cdot}0125$ and Fig. 3 gives the initial and final large time spatial distributions of u and v.

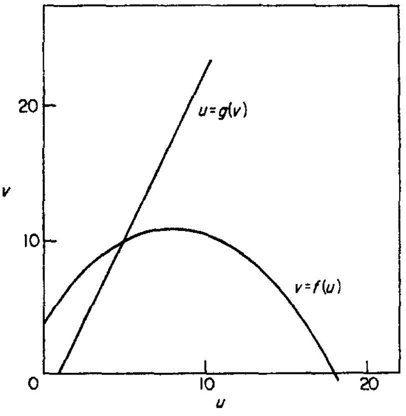

FIG. 1. Typical functions $f(u)$ and $g(v)$: those illustrated are $f(u) = (35+16u-u^2)/9$, $g(v) = 1+2v/5$. Note that the solution of $v = f(u)$ and $u = g(v)$, the positive steady state, lies to the left of the maximum of $v = f(u)$.

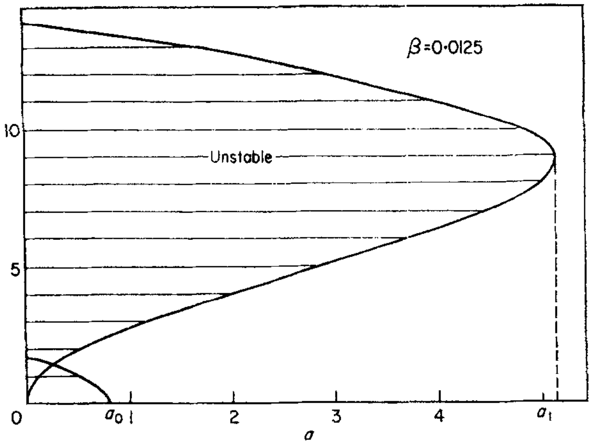

FIG. 2. Linear stability diagram: mode n as a function of a with a fixed $\beta = 0{\cdot}0125$. The shaded region gives the linearly unstable modes for a given a.

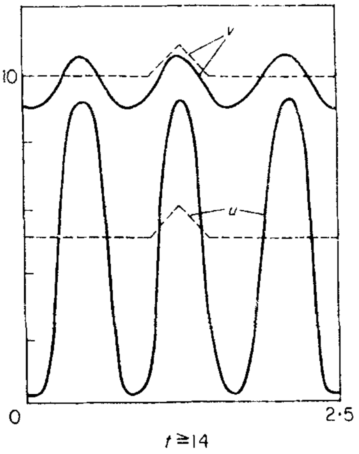

FIG. 3. Initial (– – –) and final spatial distributions for the equation system (9) with $a = 1$, $\beta = 0{\cdot}0125$ and $f(u)$, $g(v)$ as in Fig. 1: zero flux boundary conditions obtain at $x = 0, L(= 2{\cdot}5)$.

We next considered the dependency of the steady state on the parameter β when $a = 1$ and the linear stability diagram for the functions in Fig. 1 is illustrated in Fig. 4 where again we used (10): here there is one critical β. Figures 5 and 6 show the final spatial heterogeneity for $a = 0{\cdot}001$ with $\beta = 0{\cdot}0125$ and $\beta = 0$ as a special case.

One interesting aspect from an ecological point of view is that there are two very different regions for the prey density in the limiting situation

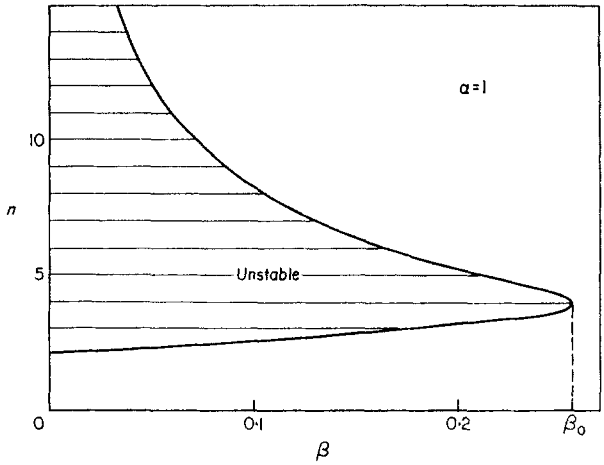

FIG. 4. Linear stability diagram: mode n as a function of β with fixed $a = 1$. The shaded region gives the linearly unstable modes for a given β.

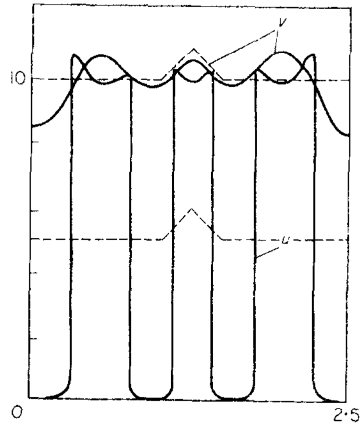

FIG. 5. Initial (– – –) and final spatial distributions for solutions of the equation system (9) with $a = 0{\cdot}001$, $\beta = 0{\cdot}0125$ and $f(u)$ and $g(v)$ as in Fig. 1: zero flux boundary conditions obtain at $x = 0$, $L(= 2{\cdot}5)$.

as its diffusion coefficient [β in (9)] tends to zero. The fact that these regions are of *finite* width is a consequence of the fact that the curve of $v = f(u)$ (see Fig. 1) has a definite positive maximum, that is it exhibits the hump effect. The model of Segel & Jackson (1972) in the situation of small β gives markedly different results as mentioned above. As $\beta \to 0$, that is the typical case illustrated in Figs 5 and 6, there are progressively narrower regions in the spatial

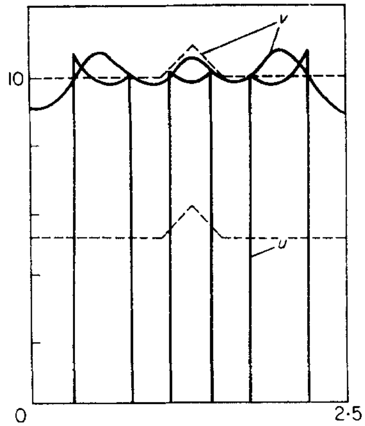

FIG. 6. Initial (– – –) and final spatial distributions for solutions of (9) with $a = 0{\cdot}001$, $\beta = 0$ and $f(u)$ and $g(v)$ as in Fig. 1 : zero flux boundary conditions obtain at $x = 0, L(= 2{\cdot}5)$.

domain where there are rapid changes in the prey density which gives sharp spike-like behaviour. Practically $\beta \neq 0$ although for plant–herbivore systems it is small. In this case the detailed structure of these interior transition layers can be treated using singular perturbation theory. On the basis that steady state patchiness exists for such systems (9) with $f(u)$ and $g(v)$ satisfying the appropriate conditions in section 2 we show mathematically in Appendix B that the spatial heterogeneity is due to the nonlinearity of the hump effect in $f(u)$. We believe that a hump effect is one of the important mechanisms which produces patchiness with a rather interesting heterogeneity when $\beta \ll 1$, that is small diffusivity of the prey as compared with that of the predators. The existence of patchiness is dependent on the interaction between the predator and prey and on their relative diffusivities.

One aspect of the interaction between the hump effect and diffusion which gives patchiness can be described as diffusive instability. That is there must exist at least one positive integer n which satisfies (7) and (8) or, for our system, (10). We conjecture that the number of finite amplitude structures is the same as the minimum n satisfying the linearized conditions (7) and (8) or (10).† In conclusion we suggest that if (i) f and g are typically as in Fig. 1, (ii) the positive steady state is only unstable as a consequence of diffusion, (iii) the solutions of the system (9) are globally stable, then patchiness will exist in a finite domain with zero flux conditions and will be independent of initial conditions.

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† In this one-dimensional situation the minimum n gives the maximum linearized growth so such a conjecture is not surprising.

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APPENDIX A

Conditions for Diffusive Instability

Here we derive the conditions necessary for the steady state of the prey–predator system (3), in which the interaction terms have certain properties, to be diffusionally unstable: these conditions are (7) and (8) used in Section 2 above.

The linearized form of the system (3) about the steady state (P_0, Q_0) is given by (5), namely

$$\left.\begin{aligned}\frac{\partial p}{\partial t} &= d_P\frac{\partial^2 p}{\partial x^2}+f_0(P_0, Q_0)P_0[f_1'(P_0)p-q],\\ \frac{\partial q}{\partial t} &= d_Q\frac{\partial^2 q}{\partial x^2}+g_0(P_0, Q_0)Q_0[p-g_1'(Q_0)q],\end{aligned}\right\} \tag{A1}$$

where p, q are the perturbations in P and Q about (P_0, Q_0). Since P, Q and hence p, q satisfy zero flux conditions solutions of (A1) satisfy

$$\frac{\partial p}{\partial x} = 0 = \frac{\partial q}{\partial x} \quad \text{on} \quad x = 0, L, \tag{A2}$$

which suggests that we look for general solutions of (A1) in the Fourier spectrum form

$$p(x, t) = \sum_{n=1}^{\infty} a_n \mathrm{e}^{\lambda t} \cos\frac{n\pi x}{L},\ q(x, t) = \sum_{n=1}^{\infty} b_n \mathrm{e}^{\lambda t} \cos\frac{n\pi x}{L}, \qquad \text{(A3)}$$

which automatically satisfy (A2). We are interested in conditions which make the eigen values λ have a positive real part due to the diffusive terms in (A1): these are then the necessary conditions for diffusive instability.

Substituting of (A3) into (A1) gives the following equation for the eigen values λ:

$$\begin{vmatrix} f_0P_0f_1'(P_0)-d_P\sigma-\lambda & -f_0P_0 \\ g_0Q_0 & -g_0Q_0g_1'(Q_0)-d_Q\sigma-\lambda \end{vmatrix} = 0,$$

where $\sigma = n^2\pi^2/L^2$, and so

$$\lambda^2+\lambda[g_0Q_0g_1'(Q_0)-f_0P_0f_1'(P_0)+\sigma(d_P+d_Q)]$$
$$+[\{d_Q\sigma+g_0Q_0g_1'(Q_0)\}\{d_P\sigma-f_0P_0f_1'(P_0)\}+f_0g_0P_0Q_0] = 0. \qquad \text{(A4)}$$

If we consider the spatially homogeneous case then the eigen values satisfy (A4) with $d_P = 0 = d_Q$ and in this situation (P_0, P_0) is to be linearly stable, that is, the real part of $\lambda < 0$. When $d_P \neq 0$, $d_Q \neq 0$ we require at least one solution λ of (A4) to have a positive real part λ in which case (P_0, Q_0) is then diffusionally unstable. If we write (A4) as $\lambda^2+A\lambda+B = 0$, with A and B defined accordingly, the condition for Rl $\lambda > 0$ is that $A < 0$, which is condition (8) above, *or* $B < 0$ which is condition (7) above. We further require Rl $\lambda < 0$ when $d_P = 0 = d_Q$ which by a similar analysis on the equivalent A and B require $A > 0$ and $B > 0$, that is

$$g_0Q_0g_1'(Q_0)-f_0P_0f_1'\,(P_0) > 0 \text{ and } 1-f_1'(P_0)g_1'(Q_0) > 0.$$

APPENDIX B

Analysis of Steady Heterogeneous Structures

Here we consider the heterogeneous steady state solution of (9), the existence of which is indicated by the numerical results in section 3. The method we use is in part based on the papers by Fife (1976,*ab*). The steady state solution $[U(x), V(x)]$ satisfies (9) with $\partial/\partial t \equiv 0$, that is the (elliptic) system

$$\left.\begin{aligned} &\beta\frac{\mathrm{d}^2U}{\mathrm{d}x^2}+[f(U)-V]U = 0 \\ &\frac{\mathrm{d}^2V}{\mathrm{d}x^2}-\alpha[g(V)-U]V = 0 \end{aligned}\right\}, \quad 0 < x < L, \qquad \text{(A5)}$$

with zero flux boundary conditions

$$\frac{dU}{dx} = 0 = \frac{dV}{dx}, \; x = 0, L. \tag{A6}$$

In this section we analyse the solutions of (A5), with (A6), asymptotically for β small: these correspond to solutions such as illustrated in Figs 5 and 6. In the following the position of the steady state solution as shown in Fig. 1 should be kept in mind; it is to the left of the maximum in $v - f(u)$.

As a first approximation to the solution $[U(x), V(x)]$ as $\beta \to 0$ we expect the limiting solution $[U^*(x), V^*(x)]$ to satisfy

$$\left.\begin{aligned} &[f(U^*)-V^*]U^* = 0, \\ &\frac{d^2V^*}{dx^2} - a[g(V^*)-U^*]V^* = 0, \end{aligned}\right\} \quad 0 < x < L \tag{A7}$$

and, from (A5).

$$\frac{dU^*}{dx} = 0 = \frac{dV^*}{dx}, \quad x = 0, L. \tag{A8}$$

The perturbation in β [that is in the first of (A5)] is unlikely to give rise to singular (rapidly changing) boundary regions since the zero flux boundary conditions are still satisfied by the reduced problem (A7) and (A8). From the first of (A7)

$$U^* = 0 \quad \text{or} \quad f(U^*) = V^*. \tag{A9}$$

Note that the inverse function $U^* = f^{-1}(V^*)$ is not a single-valued function of V^* for $f(0) \leqslant V^* \leqslant f(U^*_{\max}) = \bar{f}$, say, because we assume f to behave schematically as in Fig. 1, that is it exhibits a hump effect. Denoting the three possible solutions of (A9) by

$$U^* = h_1(V^*) \equiv 0, \quad U^* = h_2(V^*), \quad U^* = h_3(V^*) \tag{A10}$$

with, to be specific, $h_2 < h_3$, then (A7) becomes the single equation for V^*

$$\frac{d^2V_i^*}{dx^2} - a[g(V_i^*) - h_i(V_i^*)]V_i^* = 0 \tag{A11}$$

for the three cases $i = 1, 2, 3$ of (A10). For convenience we denote the x-region in which (A11) is satisfied by Ω_i. We can now make certain statements about the solutions.

For $i = 1$ and 3 the solution of (A11) and (A8) is $V_i^* \equiv 0$, that is in the regions Ω_1 and Ω_3 in $0 \leqslant x \leqslant L$ no heterogeneous solutions exist for the prey. We see this by referring to Fig. 1 where it can be seen that in these cases $g(V^*) - h_1(V^*) > 0$ and $g(V^*) - h_3(V^*) < 0$ and so the coefficient of V^* in (A11) is always of one sign and so the only solution satisfying (A8) is $V^* \equiv 0$.

Consider now the region Ω_2, that is $i = 2$ in (A11). Here solutions can exist since the coefficient of V^* changes sign in the domain.

From these results we infer that the whole domain $0 \leqslant x \leqslant L$ is divided in two of three subdomains. In other words the limiting solutions $[U^*(x), V^*(x)]$ may be constructed from $[U_i^*(x), V_i^*(x)]$ with $i = 1, 2, 3$. The prey density at the boundaries between any two domains Ω_i and Ω_j $(i, j = 1, 2, 3)$ is discontinuous. When $0 < \beta \ll 1$ these discontinuities become rapid transition layers: see Figs 5 and 6 for example. This property clearly differentiates between the Segel & Jackson (1972) model and that proposed here: their model has only two solutions, rather than the crucial three for (A9), since their equivalent form for $f(U^*)$ is linear. The hump effect is thus seen as being crucial.

The spatial structure of the solution $[U^*(x), V^*(x)]$ can now be made clear using a singular perturbation analysis. Suppose that x^* is the point of separation between Ω_i and Ω_j, in one of which, of course, $U^* \equiv 0$, then in the usual boundary layer manner for considering internal singular layers [see, for example, Murray (1968) or the pedagogical discussion in Murray (1977)] we introduce a transformation which stretches out the domain in the vicinity of x^*. If we write $y = (x-x^*)/\sqrt{\beta}$ then since $\beta \ll 1$ the vicinity of $x = x^*$ becomes large in the y-plane and we can then analyse the transition structure. With this transformation the first of (A5) becomes

$$U_{yy} + [f(U) - V(x^*)]U = 0. \tag{A12}$$

The boundary conditions in the stretched variable y for (A12) are

$$\lim_{y \to -\infty} U(y) = U_i^*(x^*), \quad \lim_{y \to \infty} U(y) = U_j^*(x^*). \tag{A13}$$

The reasoning for conditions (A13) is that when x is slightly greater than x^*, $y = (x-x^*)/\sqrt{\beta} \gg 1$ because β is very small. In the limit of $\beta \to 0$, $y \to \infty$ for $x = x^*+$ and similarly $y \to -\infty$ for $x = x^*-$. With this singular perturbation procedure the thin transition domain [it is $0(\sqrt{\beta})$] can be examined and the nature of the join between $U^* = 0$ and U^* finite can be seen. In this transition region U^* is continuous although rapidly changing while V^* is essentially constant over the transition domain: see for example, Fig. 5. This is why $V(x^*)$ is used in (A12).

The value of V at $x = x^*$ is determined by using (A11) and (A12) and integrating across the transition layer. This requires $V(x^*)$ to satisfy

$$\int_{U_i^*(x^*)}^{U_j^*(x^*)} [f(s) - V(x^*)]s \, ds = 0 \Rightarrow V = V_c^*, \text{ say} \tag{A14}$$

which also gives the value of V^* at all of the separation points as $\beta \to 0$. Consequently our problem for $V^*(x)$ throughout the complete domain

$0 \leqslant x \leqslant L$ reduces to

$$\frac{\mathrm{d}^2 V^*}{\mathrm{d}x^2} - G(V^*) = 0,\ 0 \leqslant x \leqslant L, \tag{A15}$$

with $\mathrm{d}V^*/\mathrm{d}x = 0$ at $x = 0, L$ and

$$G(V^*) = \begin{cases} a[g(V^*) - h_1(V^*)]V^* \text{ for } 0 \leqslant V^* < V_c^* \\ a[g(V^*) - h_3(V^*)]V^* \text{ for } V_c^* < V^* \leqslant \bar{f} \end{cases}, \tag{A16}$$

where $\bar{f} = f(u_{\mathrm{max}})$, that is the value for f at the top of the hump. By solving (A15) with (A16) we can get the heterogeneity in $V^*(x)$ and hence the crucial heterogeneity in $U^*(x)$ which is in good agreement with the numerical results given in section 3 (Fig. 5).