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Selecting a common direction

II. Peak-like solutions representing total alignment of cell clusters

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Abstract. The problem of alignment of cells (or other objects) that interact in an angle-dependent way was described in Mogilner and Edelstein-Keshet (1995). In this sequel we consider in detail a special limiting case of nearly complete alignment. This occurs when the rotational diffusion of individual objects becomes very slow. In this case, the motion of the objects is essentially deterministic, and the individuals or objects tend to gather in clusters at various orientations. (Numerical solutions show that the angular distribution develops sharp peaks at various discrete orientations.) To understand the behaviour of the deterministic models with analytic tools, we represent the distribution as a number of δ-like peaks. This approximation of a true solution by a set of (infinitely sharp) peaks will be referred to as the **peak ansatz**. For weak but nonzero angular diffusion, the peaks are smoothed out. The analysis of this case leads to a singular perturbation problem which we investigate. We briefly discuss other applications of similar techniques.

Key words: Orientation selection – Total alignment – Peak ansatz – Parallel cells

1 Introduction: the peak ansatz

In this paper we develop a method for investigating solutions to a system of equations that were proposed in Mogilner and Edelstein-Keshet (1995), further called MEK (1995). We are particularly interested in sharp peak-like solutions that develop when the effects of dispersal are very small. Such solutions are known to occur in a number of systems of physical and biological relevance. Examples include: peaks of cell density in chemotaxis equations (Grindrod et al., 1989) in cell-contact models (Edelstein-Keshet and Ermentrout, 1990), and in models for individual aggregation in population dynamics (Grindrod, 1988). Other applications include the analysis of models for the distribution of traits (for example, dominance) in animals (see Jaeger and Segel, 1992).

First, the technique, which we call the **peak ansatz**, will be illustrated on an explicitly solvable system from the literature, and then this method will be applied to studying behaviour of the models for angular distributions described in the previous chapter.

The following example comes from a model for the dispersal of a population of insects with density distribution $u(x, t)$ given in (Grindrod, 1991) :

$$u_t = \varepsilon u_{xx} - (uw)_x \tag{1.1}$$

where

$$w = \int_x^{\infty} u(y)\,dy - \int_{-\infty}^{x} u(y)\,dy \tag{1.2}$$

Here w is the swarming velocity, and is positive if the total density ahead of an individual is higher than the density behind it. (If the density ahead is lower, the velocity is negative.) The parameter ε is a measure of the random dispersal of the swarm. The model is somewhat unrealistic as it assumes an infinite viewing horizon to the front and back of an individual. However, it is attractive mathematically, as it is an explicitly solvable case. The steady state solution (given in Grindrod, 1991) is:

$$u(x) = \frac{M^2}{8\varepsilon}\,\mathrm{sech}^2\left(\frac{M}{4\varepsilon}(x - x_0)\right) \tag{1.3}$$

where

$$M = \int_{-\infty}^{\infty} u(y)\,dy \tag{1.4}$$

is the total number of insects in the population.

For us the most interesting case is the case of ε approaching zero, when the solution (1.3) represents a δ-like peak with width of order ε. In the limit $\varepsilon = 0$, the shape of the peak is formally a δ function itself. The location of the center of the peak, x_0 is arbitrary due to the fact that space is homogeneous. In this particular model, the unrealistic but simple nature of w, permits the above explicit solution to be computed. However, in many more realistic models, no such explicit solution can be found, and then the peak ansatz can reveal the behaviour of solutions for negligeable dispersal rates. Our approach to this problem would be as follows:

We start with the case $\varepsilon = 0$ and find that the solution of the truncated equation

$$u_t = -(uw)_x, \tag{1.5}$$

can be formally represented as a superposition of a few delta-like peaks, the heights of which are constant. The locations of the peaks change due to interaction between individuals. The only stationary stable configuration would be that of one peak. If one now wants to take diffusion into account, and this diffusion is slow, one can consider it as a small stochastic perturbation of the quasi-deterministic processes described above. Mathematically, because diffusion is described by a Laplacian, while the interaction terms are algebraic or integral, we have a singular perturbation problem. (The character of the problem changes if the small parameter ε is set equal to zero.) This situation is similar to the Fokker-Planck equation with a small diffusion term described in Gardiner (1985). As in his treatment, we introduce a scaled variable and try one or another perturbational expansion of the solution. One of the approaches to this type of problem is to assume solutions of the form

$$u(x) = \exp(-\phi(x)/\varepsilon) \tag{1.6}$$

where ε is a small parameter, and then look for an expansion of the form

$$\phi(x) = \sum \varepsilon^n \phi_n(x) \, . \tag{1.7}$$

Our approach is similar to this, but rather than dwell on the mathematical technicalities, we essentially consider only the first approximation in this expansion. The idea illustrated here will be applied to studying the behaviour of three angular-distribution models which were derived and introduced in MEK (1995). For convenience we briefly summarize the equations in Sect. 2.

The paper is organized as follows: in Sect. 3 we demonstrate the existence of δ-like peak solutions in Model I and consider the stability of these solutions. We investigate the shape of these peaks under the influence of small ε (i.e., weak random turning) in Sect. 4. The peak ansatz is applied to Models II and III in Sects. 5 and 7, respectively. We investigate the profile of the peak-like solutions of Model II at small random turning in Sect. 6. In Sect. 8 we describe the results of numerical experiments for Model I, and correspondence with our analytic results. As we will show, when the rotational diffusion of objects becomes very slow, the objects tend to gather in clusters at various orientations. We will describe in detail the case of objects turning in two dimensions, but the results can be generalized (as we will indicate briefly) to three dimensions.

2 Summary of the angular distribution models

In MEK (1995) we considered three models which describe the dynamics of angular distributions of interacting cells (or other kinds of individuals or objects). Two of these (Models I, III) describe the redistribution of the objects between different angles as the result of an instantaneous realignment, as if by a jump process. In Model II the individuals turn gradually under the influence of forces. For completeness, we summarize the three models (in dimensionless form) below:

Model I

$$\begin{cases} \dfrac{\partial P}{\partial t}(\theta, t) = CK * C + PK * C - aP \ , \\ \dfrac{\partial C}{\partial t}(\theta, t) = \varepsilon \Delta_\theta C - CK * C - CK * P + aP \ . \end{cases} \tag{2.1}$$

where

$$K * C(\theta) = \int_{-\pi}^{\pi} K(\theta - \theta')C(\theta', t)\, d\theta' \ . \tag{2.2}$$

In this model, $K(\theta, \theta') = K(\theta - \theta')$ is the probability of (instantaneous) contact-induced alignment from θ' to θ. We consider $K(\theta)$ strictly positive and even. We also assume that K attains an absolute maximum at $\theta = 0$. In this paper we concentrate on the 2D case, so $\Delta_\theta = \partial^2/\partial\theta^2$. The variables represent

$C(\theta, t) =$ density of free objects oriented at angle θ at time t,

$P(\theta, t) =$ density of bound objects oriented at angle θ at time t,

a, ε are dimensionless parameters ($a = \gamma/\beta$, $\varepsilon = \mu/\beta$ in the notation of MEK (1995)) governing the relative rates of fragmentation of clusters and random turning of free objects, respectively.

Model II

In this paper we also discuss a second model, **Model II** (in MEK (1995)) which for the sake of convenience we write in the form:

$$\frac{\partial C}{\partial t} = \varepsilon \Delta_\theta C - \frac{\partial}{\partial \theta} \cdot (C(W * C)) \ , \tag{2.3}$$

where

$$W * C \equiv \int W(\theta - \theta')C(\theta', t)\, d\theta' \ . \tag{2.4}$$

We assume that $W(\theta)$ is an odd function, and that $W(0) = W(\pi) = 0$, $W(\theta) < 0$ for $0 < \theta < \pi$, and $W(\theta) > 0$ if $-\pi < \theta < 0$. The single variable $C(\theta, t)$ is the density of objects of one type at orientation θ. This equation describes the convectional drift of the objects in angular space towards the points of highest concentration, causing alignment.

Model III

The third model which was introduced in MEK (1995) is

$$\frac{\partial C}{\partial t} = \varepsilon \Delta_\theta C + C(Q(C) * C) \ . \tag{2.5}$$

Here the integral term is defined as:

$$Q(C) * C = \int_S d\theta' \, L(C(\theta) - C(\theta'))G(\theta - \theta')C(\theta', t) \ . \tag{2.6}$$

The function $L(C(\theta) - C(\theta'))$ governs the tendency for a bigger cluster to grow at the expense of the smaller cluster. We assume that the function L is odd, monotonically increasing, and bounded. The function G describes the angle dependence and has the same meaning and form as K in Model I. This is a rough approximation of the process of fast turning of a small cluster of objects towards a more slowly moving big cluster, and their final merging.

In the above three models, there are two types of elementary processes leading to turning of the individuals: The first is random rotational diffusion, while the second is mean turning caused by direct interaction (the mean of a certain stochastic process). A special case occurs when rotational diffusion is very slow compared to the interaction-mediated turning. In this case, the random element of the models can be essentially neglected. Models I and III have the following important feature in common: When rotational diffusion is omitted ($\varepsilon = 0$), individuals can only "be attracted" to some angle by sticking to other individuals or clusters already oriented at that angle. Thus, if there are no individuals at some angle, none will appear there. This suggests applying the peak ansatz and reducing the system of integro-partial differential equations (IPDE's) of the models to ODE's.

In the limiting case of $\varepsilon = 0$ in Model II, if a number of cells are concentrated at the same angle, the velocity of each individual in the group is completely prescribed by deterministic terms in the model. Moreover, individuals at a given angle move collectively with the same velocity. This can be represented as convection of a number of δ-like peaks in the angular distribution. Contrary to the case of Models I and III, in Model II the location of the peaks changes but the heights remain constant. Each peak has a deterministic trajectory prescribed by a kinematic equation (which is Liouville-like). There are a number of stable static equilibria for the ensemble of δ-like peaks. In a way, this case reduces to a problem in nonlinear classical mechanics. Again this limiting case allows analytic treatment.

In MEK (1995) we distinguished between cases where parallel and antiparallel interactions were identical versus those in which only parallel interactions occur. This was depicted by **double humped** versus **single humped** kernels K. Here we will consider only one type of interaction kernel (the **one-humped** case), in which objects align only in parallel. This case usually leads to the existence of a single peak. We speculate that generalization to other kernels would also lead to the existence of a number of stable peaks.

3 Application of the peak ansatz to Model I

Let us start with equations (2.1) of Model I and explore the behaviour of these equations in the limit as the parameter ε gets small. This means that the angular "diffusion" of the population becomes insignificant compared to the rates of the other processes. Note that the absence of diffusion does not mean that there is no transfer of "mass" from one angle to another, since the convolution terms still represent reorientation of cells due to interactions.

(For small rotational diffusion individuals tend to maintain their directions of motion until they make contact with another individual.)

This suggests a solution in the form of a number of δ-like peaks in the angular distribution, the location of which is constant and the heights of which change due to exchange of individuals. The heights of the peaks are governed by a system of nonlinear ordinary differential equations (ODE's).

The stability properties of these peaks can be studied. It is convenient to rewrite the model in terms of the mass at a given angle θ, which is

$$M(\theta, t) = C(\theta, t) + P(\theta, t)\ . \tag{3.1}$$

(The total mass M defined as $M = \int M(\theta, t)\, d\theta$ is conserved and can be considered as a parameter of the model, see MEK (1995).) Plugging the expression $P = (M - C)$ into (2.1) and assuming $\varepsilon = 0$, the model can be reformulated in a more convenient form:

$$\begin{aligned} \frac{\partial M}{\partial t} &= M(K * C) - C(K * M)\ , \\ \frac{\partial C}{\partial t} &= -C(a + (K * M)) + aM\ . \end{aligned} \tag{3.2}$$

(Note that while not evident from this form of the model, the positivity of M and C is implied by the original model.) The second equation can be interpreted in the following way: the rate of change of the total mass of cells at a given orientation is the sum of effects of free cells attracted to that direction minus the mass of free cells that are attracted to other directions. The expression $K * M$ represents the **influence of the mass distribution on the direction** θ. Since it appears repeatedly in these equations and their analysis, it is convenient to use the notation

$$F(\theta) \equiv (K * M)(\theta)\ . \tag{3.3}$$

Setting the time derivatives to zero we arrive at the steady state equations:

$$\begin{cases} -C(a + (K * M)) + aM = 0\ , \\ M(K * C) = C(K * M)\ . \end{cases} \tag{3.4}$$

From equations (3.4) we can observe that

$$C = \frac{aM}{a + (K * M)} = \frac{aM}{a + F}\ . \tag{3.5}$$

Further, inserting this result into the equation for M we get

$$M\left(K * \frac{M}{a + F}\right) = M \frac{K * M}{a + F}\ . \tag{3.6}$$

The only possible solutions to this equation are those satisfying pointwise

$$M = 0\ , \tag{3.7}$$

or

$$K * \frac{M}{a+F} = \frac{K * M}{a+F} \ . \tag{3.8}$$

Here only the class of peak-like solutions will be explored:

$$M(\theta) = \begin{cases} 0, & \theta \notin \{\theta_1, \ldots, \theta_n\} \ , \\ \sum_{j=1}^{n} M_j \delta(\theta - \theta_j), & \theta \in \{\theta_1, \ldots, \theta_n\} \ . \end{cases} \tag{3.9}$$

The masses concentrated at these angles, namely $\{M_1, M_2, \ldots, M_n\}$ satisfy a set of n equations:

$$(K * M)(\theta_i) = \text{constant}, \quad \theta_i \in \{\theta_1, \theta_2, \ldots, \theta_n\} \ . \tag{3.10}$$

(See Appendix A.)

Note that we are not claiming that this solution is unique, as there may also be solutions in the form of functions with an absolutely or singularly continuous support. However, in the case of this model of a finite collection of objects, such solutions are of lesser interest. As will be shown by numerical simulations, these peak-like solutions evolve from a variety of initial data.

Biologically, this solution can be interpreted as the existence of a discrete set of directions $\{\theta_1, \theta_2, \ldots, \theta_n\}$, $n = 1, 2, \ldots$ along which cells are oriented.

3.1 Reduction of Model I to discrete equations governing the peaks

In this section the peak ansatz will be applied to reducing Model I from a set of integro-partial differential equations to a set of ordinary differential equations for the masses concentrated at a number of peaks. We will consider individually the cases of one, two, and more than two δ-like peaks. An eventual goal is to investigate the stability of such peaks. Note that understanding stability to an arbitrary perturbation is a challenging problem not here attempted. Rather, we formulate and study the equations governing interactions between these discrete peaks, and determine whether one or more peaks can persist. We develop here a short-hand notation for describing various special cases.

In the equations below the following short-hand notation is used for the probability that a cell at direction θ_i turns to direction θ_j:

$$K_{ij} \equiv K(\theta_i - \theta_j) \ . \tag{3.11}$$

Observe that since $K(\theta_i - \theta_j) = K(\theta_j - \theta_i)$ it follows that $K_{ij} = K_{ji}$. The convolution in equation (3.10) is now a finite sum, rather than an integral, but the interpretation is the same: the influence of the distribution is the same for each value of θ_i. Thus, the steady state satisfies

$$\sum_{j=1}^{n} K_{1j} M_j = \sum_{j=1}^{n} K_{2j} M_j = \cdots = \sum_{j=1}^{n} K_{nj} M_j \ . \tag{3.12}$$

The conservation of total mass must also be maintained, so that

$$\sum_{j=1}^{n} M_j = M . \tag{3.13}$$

These steady state equations have a unique solution in the set of real numbers, but clearly, for biological applications, only nonnegative values of the M_j's are acceptable. This system does not have a unique solution if the matrix $\{G_{ij}\}_{i,j=1\ldots n}$ is singular, where

$$\begin{aligned} &G_{ij} = K_{ij} - K_{nj}, \quad i = 1 \ldots n-1, \quad j = 1 \ldots n; \\ &G_{nj} = 1, \quad j = 1 \ldots n \end{aligned} \tag{3.14}$$

The elements of this matrix are defined on an $(n-1)$ dimensional parameter space of $(n-1)$ angles between the peaks. This matrix is singular on some manifold of co-dimension 1 in the parameter space (Arnold, 1978), so, in a generic case, the steady state equations (3.12–13) have a unique solution.

The amplitudes of the peaks, $\{M_1, M_2, \ldots, M_n\}$ are fully determined by the set of directions $\{\theta_1, \theta_2, \ldots, \theta_n\}$ given a particular choice of the kernel function $K(\theta)$, as the values of the coefficients K_{ij} are defined by this set of values. This means that not all sets $\{\theta_1, \theta_2, \ldots, \theta_n\}$ have meaningful solutions. It can happen that an arbitrary set of directions leads to a system of algebraic equations having one or more negative values of M_j in its solution. This set must then be rejected as unbiological.

Given a strictly positive solution, $\{M_1, M_2, \ldots, M_n\}$, the masses of the free cells, $\{C_1, C_2, \ldots, C_n\}$ are given by the expression

$$C_j = \frac{a}{a + F_0} M_j, \qquad F_0 = \sum_{j=1}^{n} K_{ij} M_j . \tag{3.15}$$

In order to understand stability of the steady state in the general case, in the sections below we will consider sequentially the behaviour of one, two, and three peaks. We shall restrict attention to a limited class of perturbations consisting of a finite number of peaks. (The analysis of the general case is considerably more challenging.)

3.2 Stability for the case of two competing peaks

In this case all material is concentrated in two peaks located at angles θ_1 and θ_2, and the amplitudes (M_1, C_1) and (M_2, C_2) define the distributions. According to the definition of K_{ij}, cells having the same orientation will be represented by interactions

$$K_{11} = K_{22} \equiv K_0 , \tag{3.16}$$

and the interaction of cells in distinct clusters is given by:

$$K_{12} = K_{21} \equiv K_1 . \tag{3.17}$$

Recall the assumption that $K(0)$ represents interactions that are stronger than at other relative orientations. This means that

$$K_0 > K_{ij} \quad i \neq j \, . \tag{3.18}$$

Then by equation (3.12) we have for the steady states:

$$K_0 \bar{M}_1 + K_1 \bar{M}_2 = K_1 \bar{M}_1 + K_0 \bar{M}_2 \, . \tag{3.19}$$

The above equation leads to the following steady state solutions:

$$\bar{M}_1 = \bar{M}_2 = \frac{M}{2}, \quad \bar{C}_1 = \bar{C}_2 = \frac{a}{a + \bar{K}M/2} \frac{M}{2} \, , \tag{3.20}$$

where $\bar{K} \equiv (K_0 + K_1)$, and M is the total mass.

Now time-dependent peaks at fixed angles are considered. We start with the properties of the stationary solution given in (3.20), namely the case of two peaks. Since mass is concentrated only at two discrete angles, we can consider the ordinary differential equations that describe these masses.

The total mass is conserved: $\dot{M} \equiv (\dot{M}_1 + \dot{M}_2) = 0$ (where the traditional dot notation is used here for time derivatives.) This can be put into a more convenient form by defining the difference of masses m, as follows:

$$m = \frac{M_1 - M_2}{2} \, . \tag{3.21}$$

The dynamics of the variables, m, C_1, C_2 is given by the system

$$\begin{cases} \dot{m} = K_1 \left[\dfrac{M}{2}(C_2 - C_1) + m(C_1 + C_2) \right], \\ \dot{C}_1 = C_1 \left(-\left(a + \dfrac{\bar{K}M}{2} \right) + (K_1 - K_0)m \right) + \dfrac{aM}{2} + am \, , \\ \dot{C}_2 = C_2 \left(-\left(a + \dfrac{\bar{K}M}{2} \right) + (K_0 - K_1)m \right) + \dfrac{aM}{2} - am \, , \end{cases} \tag{3.22}$$

We look for the solutions of this system in the form $C_1 = \bar{C}_1 + c_1$, $C_2 = \bar{C}_2 + c_2, m$, where m, c_1, c_2 are small perturbations from the steady state. In Appendix B the linearized system of equations for the variables m, c_1, c_2 will be derived, and linear stability will be investigated. It is shown there that small deviations from the stationary steady state grow exponentially and that therefore two peaks are unstable.

3.3 Stability for the case of a single peak

Here we formally consider two directions in order to then investigate the stability of one peak. In the stationary state, we consider all cells concentrated along the first direction and none of them along the second direction. Then,

$$\bar{M}_1 = M, \qquad \bar{M}_2 = 0, \qquad \bar{C}_1 = \frac{aM}{a + K_0 M}, \qquad \bar{C}_2 = 0 \, . \tag{3.23}$$

The stability of one peak is to be considered. As a result of small perturbation, a small peak may appear in the second direction. We look for solutions of the system (3.22) in the form $C_1 = \bar{C}_1 + c_1$, $C_2 = \bar{C}_2 + c_2$, $m = \bar{m} + \tilde{m}$, where $\tilde{m}$, c_1, c_2 are small perturbations of the steady state (3.23) (in this case the steady state value of $\bar{m} = M/2$). In Appendix C the linearized system of equations for the variables $\tilde{m}$, c_1, c_2 is considered in order to investigate linear stability. The conclusion reached there is that one peak is stable to a perturbation consisting of one other small competing peak.

3.4 *The case of three interacting peaks*

Two possible cases are considered, one in which the three peaks are equally separated from each other by angles of $2\pi/3$, and a second case in which there are three uneven peaks.

(a) Equally spaced peaks
In this case, $\theta_2 - \theta_1 = \theta_3 - \theta_2 = \theta_1 - \theta_3 = 2\pi/3$. We will denote the values of the kernel as $K(0) = K_0$, $K(\pm 2\pi/3) = K_1$. Then it follows from (3.12–13) that a steady solution exists provided

$$K_0 M_1 + K_1(M_2 + M_3) = K_0 M_2 + K_1(M_1 + M_3) = K_0 M_3 + K_1(M_1 + M_2)\,. \tag{3.24}$$

As $K_0 > K_1$, the stationary solution is

$$M_1 = M_2 = M_3 = M/3\,. \tag{3.25}$$

We are not interested here in solutions having some of the M_i's zero, since these cases have already been covered under the previous analysis of two and one peaks. Then the masses at the three peaks satisfy a system of six equations which are shown in Appendix C. The stability calculation there demonstrates that three equally spaced peaks are unstable. As expected, the analysis of this problem is more taxing than those of the previous cases of one and two peaks.

(b) Unequally spaced peaks
In this case $\theta_2 - \theta_1 \neq \theta_3 - \theta_2 \neq \theta_1 - \theta_3$. Then there are three peaks located at some angles which are not equally spaced. The sizes of the peaks may also be different. This case in which the peaks are unequal and/or are located at three arbitrary angles is analytically forbidding, and will be explored with a limited numerical experiment.

The problem of investigating the stability of three or more peaks in this model appears to be extremely difficult and may or may not be analytically tractable. This problem has a full analytic solution in the case of Models II and III. But from previous discussion it would appear that the only stable situation is a single peak, i.e. a stationary solution in which all cells are lined up along a single direction.

The equations of this system are analogous to those of case (a), but allowing for differences in the values of $K(0), K(\theta_1 - \theta_2), K(\theta_1 - \theta_3), K(\theta_2 - \theta_3)$, since the angles need not be equally spaced. As a specific example, the software program Mathematica for certain parameter values was used to investigate the stability matrix. The exact values and the resulting stability matrix and eigenvalues in that example case are shown in Appendix C. Two of these eigenvalues are positive, so that this situation of three uneven peaks is unstable. One of the eigenvalues is zero since $M = M_1 + M_2 + M_3 = \text{const}$.

4 The form of the peaks in Model I (weak angular diffusion)

To find out more about the form of peaks in Model I before they become infinitely sharp (when ε attains the limit $\varepsilon = 0$) consider the influence of a small but non-zero value for the random turning rate, $\varepsilon \neq 0$, in equations (2.1) for the distribution of free cells.

We look only for the time-independent solutions. In this case we deduce from equations (2.1) that

$$P = \frac{C(K * C)}{a - (K * C)}, \tag{4.1}$$

$$\varepsilon \Delta_\theta C + V(C) \cdot C = 0, \tag{4.2}$$

$$V(C) = \frac{(K * C)^2}{a - (K * C)} - K * \left(\frac{C(K * C)}{a - (K * C)} \right). \tag{4.3}$$

The presence of a small parameter as a coefficient of the second derivative term leads to a singular perturbation problem. (See, for example, Chang and Howes, 1984; Smith, 1987; O'Malley, 1974.) Clearly, the presence of the Laplacian operator will cause the sharpness of the peaks to be smoothed somewhat, depending on the value of ε. The distribution of bound cells can also be easily found with the help of expression (4.1). (In particular, it is found that the width of the peak of P is of the same order of magnitude as the one for the free cells.)

The unperturbed solution is taken to be a δ-like peak which is non-vanishing in the limit $\varepsilon \to 0$. The solutions are asymptotically zero except at regularly spaced points (one point in our case). In the neighborhood of such a point the solution has a spike of finite height.

Without loss of generality, assume a peak at $\theta = 0$ and $\bar{C} = 1$. (It will be seen that the shape of the peak can be approximated by the form $A(\varepsilon) exp(-\theta^2/\sigma^2(\varepsilon))$.) Then σ represents the width of the peak. We are interested in how σ depends on ε). Since $C(\theta)$ is asymptotically zero away from $\theta = 0$, the behaviour of the function $V(C)$ is of interest in the vicinity of $\theta = 0$.

Rescale the angular variable $x = \theta/\varepsilon^{1/4}$, and look for the solution of equation (4.2–3) in the form $S(x) = \varepsilon^{1/4}C$ where S obeys the following equation:

$$\varepsilon^{1/2}\frac{\partial^2 S}{\partial x^2} + V(\varepsilon^{1/4}x)S = 0\,. \tag{4.4}$$

Assume that S is expanded in the following asymptotic series:

$$S(x) = \sum_{n=0}^{\infty} \varepsilon^{n/4} S_n(x)\,. \tag{4.5}$$

and that

$$V(\varepsilon^{1/4}x) = \sum_{n=2}^{\infty} \varepsilon^{n/4} V_n(x)\,. \tag{4.6}$$

We find only the first terms in the asymptotic series for S and V. (Finding the next term presents serious mathematical difficulties.) The equation for the first approximation has the form

$$\begin{gathered}\frac{\partial^2 S_0}{\partial x^2} + V_2(x)S_0 = 0\,,\\ V_2(x) = \alpha_1 - \alpha_2 x^2, \quad \varepsilon^{1/4}x \ll 1\,,\\ \alpha_1 = bA_2, \qquad \alpha_2 = \frac{b}{2}, \qquad b = -\,a\frac{K(0)K''(0)}{(a-K(0))^2} > 0\,,\\ A_2 = \int_{-\infty}^{\infty} x^2 S_0(x)dx\,.\end{gathered} \tag{4.7}$$

The form of the function $V_2(x)$ was obtained from plugging the expansion (4.5) into the expression (4.3). Then the kernel $K(\varepsilon^{1/4}(x - x'))$ was expanded in a Taylor series. After cumbersome calculations two first terms of order $\varepsilon^{1/2}$ were obtained. For given coefficients, equation (4.7) is the well-known linear equation for the harmonic oscillator in quantum mechanics, see Morse and Feshbach (1953). There is a unique strictly positive solution to this equation which decreases at infinity. This solution occurs under the condition $\alpha_1 = \sqrt{\alpha_2}$.

This condition is equivalent to the expression $A_2 = 1/\sqrt{2b}$. Under this condition, the normalized solution of the nonlinear equation (4.7) is

$$S_0 = \left(\frac{b}{8\pi^2}\right)^{1/4} \exp\left(-\sqrt{\frac{b}{8}}\,x^2\right). \tag{4.8}$$

Calculating A_2 using the definition (4.7), and the form of the solution (4.8), we find that

$$A_2 = \frac{1}{2}\sqrt{\frac{2}{b}} = \frac{1}{\sqrt{2b}}.$$

Thus the condition $\alpha_1 = \sqrt{\alpha_2}$ is fulfilled, and so the solution is valid. The corresponding form of the peak in the first approximation has the form:

$$C_0 = \frac{1}{\varepsilon^{1/4}}\left(\frac{b}{8\pi^2}\right)^{1/4} \exp(-\theta^2/\sigma^2), \qquad \sigma = (8\varepsilon/b)^{1/4} \tag{4.9}$$

where b is given in (4.9).

This means that the width of the peak $\sigma(\varepsilon)$ in the limit of slow diffusion in Model I is small, of order $\varepsilon^{1/4}$.

5 Application of the peak ansatz to Model II

In this section we consider Model II in the limiting case of zero rotational diffusion. The equation for the dynamics of the continuous angular distribution has the form

$$\frac{\partial C}{\partial t} = -\frac{\partial (Cv)}{\partial \theta}, \tag{5.1}$$

where

$$v = W * C. \tag{5.2}$$

From these equations it can be seen that the angular dynamics become purely deterministic in this case. This fact suggests that the motion of each individual object can be followed. This is the so-called Lagrangian approach, in the traditional terminology of theoretical mechanics in contrast to the Eulerian approach of following behavior at a given point. Mathematically, the nonlinear equation (5.1) is hyperbolic, and the trajectories of individual objects are given by the equations of the characteristic curves. If the equations of these characteristics are solved, a link can be made between the two approaches. Unfortunately, in general, nonlinear equations for characteristics cannot be solved in closed form (Logan, 1994). For this reason, we restrict attention to a special case whose qualitative nature can be fully described.

Let the vector describing the state of the system at a given time, t, be

$$\Omega(t) = \{\theta_1, \ldots, \theta_n\}.$$

Here, $\theta_i(t)$ is the orientation of the ith object at time t. The number n of objects in the system is conserved in time. ($n \gg 1$). The dynamics of the i'th object is given by the definition of its angular velocity:

$$\frac{d\theta_i}{dt} = v(\theta_i(t)). \tag{5.3}$$

To ensure that the former Eulerian definition of density reduces to the Lagrangian definition, it is necessary to define the angular velocity as follows:

$$v(\theta) = \int_{-\pi}^{\pi} W(\theta - \theta')C(\theta')d\theta',$$

where $C(\theta)$ is formally defined as:

$$C(\theta) = \sum_{j=1}^{n} \delta(\theta - \theta_j)\,.$$

Then the angular velocity can be written in the form:

$$v(\theta) = \sum_{j=1}^{n} W(\theta - \theta_j)\,. \tag{5.4}$$

We introduce the "potential function" $V(\theta)$,

$$V(\theta) = -\int W(\theta)\,d\theta\,. \tag{5.5}$$

(The constant of integration is irrelevant, as potentials are always defined up to some additive constant.) We also define the Lyapunov function $\bar{V}(\Omega)$:

$$\bar{V}(\Omega) = \sum_{(ij)} V(\theta_i - \theta_j)\,. \tag{5.6}$$

(Here the summation is taken over all pairs of objects.) Now the dynamics of the objects is governed by the following equations:

$$\frac{d\theta_i}{dt} = -\frac{\partial \bar{V}(\Omega)}{\partial \theta_i}\,.$$

(Recall, that $d\theta_i/dt$ is the angular velocity proportional to the "force" (5.4) which is the gradient of the Lyapunov function (5.6).) These equations can be written in the vector form:

$$\frac{d\Omega}{dt} = -\frac{\partial \bar{V}(\Omega)}{\partial \Omega}\,. \tag{5.7}$$

The advantage of this approach is clear from the form of the last equation. This is now a gradient system (Gross, Hohenberg, 1993). The behavior of such systems is much simpler than that of general non-linear dynamics. If an attractor Ω_0 can be found such that the Lyapunov function $\bar{V}$ has a global minimum at $\Omega = \Omega_0$, then the dynamics of the system is just relaxation towards this attractor.

With the definition of the interaction kernel $W(\theta)$ (see Sect. 2), the corresponding potential function $V(\theta)$, (5.5) has a global minimum at $\theta = 0$. Note the analogy with the following physical description: the interaction kernel W corresponds to the forces between two objects. According to the definition of the kernel, these forces are attractive. The potential V thus has a global minimum when the distance between two objects is zero. The Lyapunov function $\bar{V}$ is the total potential energy of the system. Obviously, in the present case this total energy has a global minimum when all objects have the same orientation.

The global attractor for our definition of the Lyapunov function $\Omega_0 = \{\theta, \theta, \ldots, \theta\}$ where θ is an orientation of complete alignment (arbitrary due to rotational invariance of the system).

The above argument proves the assertion that after large enough perturbation the objects converge to a unique globally stable state of complete alignment. Note that another locally stable stationary angular configuration may exist. The biological meaning of this fact is that in nature there may be quasi-stationary angular patterns different from total alignment.

6 The shape of peaks in Model II (weak angular diffusion)

Consider now the situation when one globally stable peak is present and angular diffusion is weak, but not absent. As in the case of the first model, we look for a steady state solution in the form of a single sharp peak at $\theta = 0$.

Integrating equation (2.3) once with respect to θ leads to the first order ODE:

$$\varepsilon \frac{\partial C}{\partial \theta} = vC, \qquad v = W * C. \tag{6.1}$$

(The constant of integration has the meaning of flux, and is equal to zero for periodic solutions on the circle.) Rescale the angular variable: $x = \theta/\sqrt{\varepsilon}$ and look for a solution in the form $S = \sqrt{\varepsilon}C$, where S obeys the equation

$$\frac{\partial S}{\partial x} = \frac{v(\sqrt{\varepsilon}x)}{\sqrt{\varepsilon}} S\,. \tag{6.2}$$

We assume that the functions v and S have the following asymptotic expansions:

$$v(\sqrt{\varepsilon}x) = -\sum_{n=1}^{\infty} v_n \varepsilon^{n/2} x^n, \qquad S = \sum_{n=0}^{\infty} \varepsilon^{n/2} S_n\,.$$

Here we find the first approximation S_0. Finding the higher approximations is a very serious mathematical problem (Gardiner, 1985) and is beyond the scope of the present work. S_0 obeys the equation

$$S_0' = -v_1 x S_0\,, \tag{6.3}$$

with the solution

$$S_0 \sim \exp\left(\frac{-v_1 x^2}{2}\right). \tag{6.4}$$

The first term in the expansion for the function v can be found as follows:

$$\begin{aligned}
\frac{v(\sqrt{\varepsilon}x)}{\sqrt{\varepsilon}} &= \frac{1}{\varepsilon}\int_{-\infty}^{\infty} W(\sqrt{\varepsilon}(x - x'))S(\sqrt{\varepsilon}x')\,dx' \\
&= \frac{1}{\varepsilon}\int_{-\infty}^{\infty} W(\sqrt{\varepsilon}(x - x'))S_0(x')\,dx' + O(\sqrt{\varepsilon}) \\
&= \frac{1}{\sqrt{\varepsilon}} W'(0)\int_{-\infty}^{\infty} (x - x')S_0(x')\,dx' + O(\sqrt{\varepsilon}) = W'(0)\bar{C}x\,.
\end{aligned}$$

Here we used the facts that $W(0) = 0$, that $\int xS_0(x)\,dx = 0$ and the definition of $\bar{C}$: $\bar{C} = \int C(x)dx$. Thus,

$$v_1 = -W'(0)\bar{C} > 0\,. \tag{6.5}$$

(Recall that $W'(0) < 0$.) The peak solution has the asymptotic form:

$$C(\theta) = \bar{C}^{3/2}\sqrt{\frac{-W'(0)}{\pi\varepsilon}}\exp(-\theta^2/\sigma^2), \qquad \sigma = \sqrt{\varepsilon/(-W'(0))\bar{C}}\,. \tag{6.6}$$

We have shown that in the limit of slow diffusion, the width of the peak σ is small, of order $\varepsilon^{1/2}$.

7 Application of the peak ansatz to Model III

We discuss Model III when angular diffusion is absent ($\varepsilon = 0$). If there are initially n infinitely narrow peaks in the angular distribution, then the redistribution of individuals over various angles (i.e. the transitions of the individuals from one peak to another) is due to the integral term in the equation

$$\frac{\partial C}{\partial t} = C(Q(C) * C)\,. \tag{7.1}$$

This equation describes a set of discrete peaks (say n peaks) at constant angles, $\{\theta_1, \ldots, \theta_n\}$ with $\{c_1(t), \ldots, c_n(t)\}$ individuals in each peak. None can appear in other directions due to the form of the equations. The continuous convolution in (7.1) will be represented by a discrete sum, leading to an equation of the form

$$\frac{\partial c_i}{\partial t} = c_i \sum_{j=1}^{n} L(c_i - c_j) G_{ij} c_j\,. \tag{7.2}$$

Equations (7.2) (one equation for each peak) state that the growth and decay rates of a peak c_i are proportional to its size. Whether this peak actually grows or decays depends on competition with all other peaks. The growth or decay rate of c_i depends on the net balance of power between the i'th peak and all other peaks.

This model has the following properties:

1. **Any steady state of (7.2) is an equal subdivision of objects among *n* peaks.** By this we mean that $c_i = 0$ or $c_i = M/n$. This observation is a consequence of the fact that G is positive and follows directly from the steady state equation corresponding to (7.2). If the peaks are not equally sized, they continue to "pull" individuals away from one another, contradicting the steady state assumption.

   Note that $G > 0$ and consider the steady state equation.

$$0 = c_i \sum_{j=1}^{n} L(c_i - c_j) G(\theta_i - \theta_j) c_j\,. \tag{7.3}$$

The equation is clearly satisfied if $c_i = 0$ or if $c_i = c_j = M/n$ for every i, j, since then $L(c_i - c_j) = L(0) = 0$. (Without loss of generality we consider all n peaks non-zero.) This implies that equal subdivision of objects among n groups is indeed a steady state. To show that no other kind of steady states exist, we use an argument by contradiction. Suppose some peaks are bigger than others. Then we can order them according to size.

$$c_1 \geqq c_2 \geqq \cdots \geqq c_n > 0 . \tag{7.4}$$

Then in the steady state equation for c_1

$$0 = \sum_{j=1}^{n} L(c_1 - c_j) G_{ij} c_j , \tag{7.5}$$

$L(c_1 - c_j) \geqq 0$ (since c_1 is maximal). Then (7.5) can only be satisfied if $L = 0$, i.e. $c_1 = c_j$ for every j. Thus the presence of peaks of different sizes is not possible at steady state, verifying our claim.

2. **The steady state of (7.2) in which the population is concentrated in one peak is locally stable.** By rotational symmetry we can take $i = 1$ to be the direction of the single peak without loss of generality. Then $c_1 = M$ and $c_j = 0$ for all $j \neq 1$. Stability of the peaks c_j, $j \neq 1$, is governed by the linearized equation (7.2) reproduced here:

$$\frac{ds_j}{dt} = s_j L(-M) G_{1j} M \tag{7.6}$$

where s_j is a small positive density (a perturbation from $c_j = 0$). But $M > 0$, $G_{ij} > 0$, $L(-M) < 0$, so all perturbations decay exponentially to zero meaning that peaks whose initial masses are quite small will not get bigger. For the initial peak in which most of the mass is concentrated, c_1, local stability is governed by

$$\frac{dc_1}{dt} = M \sum_{j=2}^{n} L(M) G_{1j} s_j . \tag{7.7}$$

Since all $s_j \, j \neq 1$ decay exponentially to zero, this problem has a single zero eigenvalue, indicating that $c_1 = M$ is a locally stable solution for *any* value of the total mass M, verifying the assertion.

3. **All other steady states are unstable.** Consider the case of n directions each having mass M/n for which one obtains the linearized equation

$$\frac{ds_i}{dt} = \left(\frac{M}{n}\right)^2 \eta \sum_{j=1}^{n} G_{ij}(s_i - s_j) , \tag{7.8}$$

where $\eta = L'(0) > 0$. Directions not represented by any peak, k such that $c_k = 0$, would satisfy the linearized equations

$$\frac{ds_k}{dt} = -s_k \frac{M}{n} L\left(\frac{M}{n}\right) \sum_{j=1}^{n} G_{kj} . \tag{7.9}$$

Clearly, each of these decays to zero since $G_{kj} > 0$. Thus stability of these steady states hinges on the behavior of equations (7.8). The matrix of coefficients of this system is symmetric and $G_{ij} > 0$. The Gerschgorin circle theorem (see, for example, Gantmakher, 1966; Marcus and Ming, 1964) then states that all eigenvalues lie in the interval

$$0 \leqq \lambda \leqq 2(M/n)^2 \eta \sum_{j=1}^{n} G_{ij} . \tag{7.10}$$

Since $n > 1$, the rank of the matrix of coefficients in equation (7.8) is at least 1, and since the matrix is symmetric, not all n eigenvalues are zero. Thus there is at least one positive eigenvalue and the equilibrium is unstable.

Thus, in this third model, in the case of no angular diffusion, the only distribution which is stable is one in which all individuals are in a single cluster, having the same orientation. The problem of the form of the peak in Model III in the case of weak angular diffusion leads to an inherently nonlinear singular perturbation problem. The treatment of this case is beyond the scope of this work.

Whether the peak actually grows or decays depends on competition with all other peaks. It is interesting to observe this in numerical solutions of this discrete model. We simulated the equation (7.2) numerically with four orientations, $\theta_1 = 0, \theta_2 = \pi/2, \theta_3 = \pi, \theta_4 = -\pi/2$. We chose the specific values $G(\pi/2) = G(-\pi/2) = 1.0$, $G(\pi) = G(-\pi) = 0.05$, the function $L(c) = c$, and the initial heights of the peaks, 1.0, 0.9, 0.5, respectively. The time behavior of this system is shown in Fig. 1. Observe that peaks 2 and 3 decay in size quite rapidly, while 1 and 4 have a more lengthy competition. Also note that even

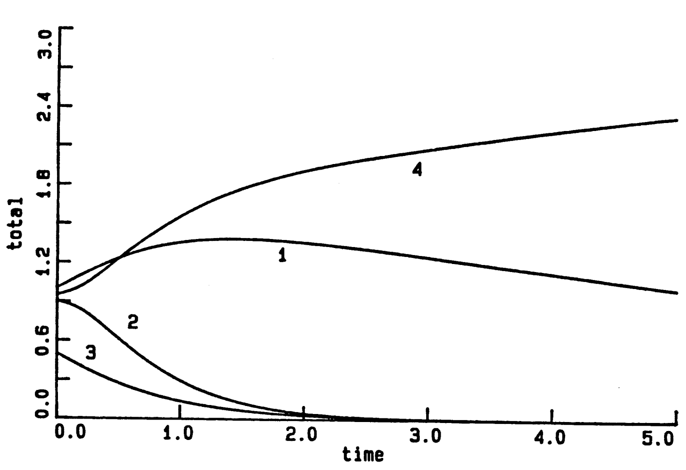


Fig. 1. The evolution of four interacting peaks in Model III. The fourth peak overtakes the others which decay monotonously

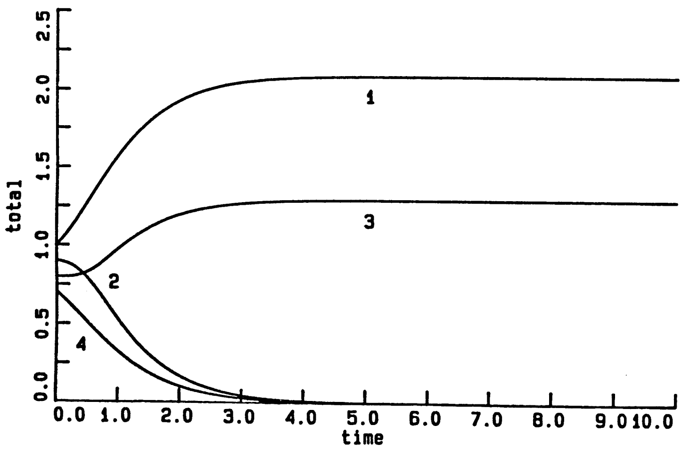


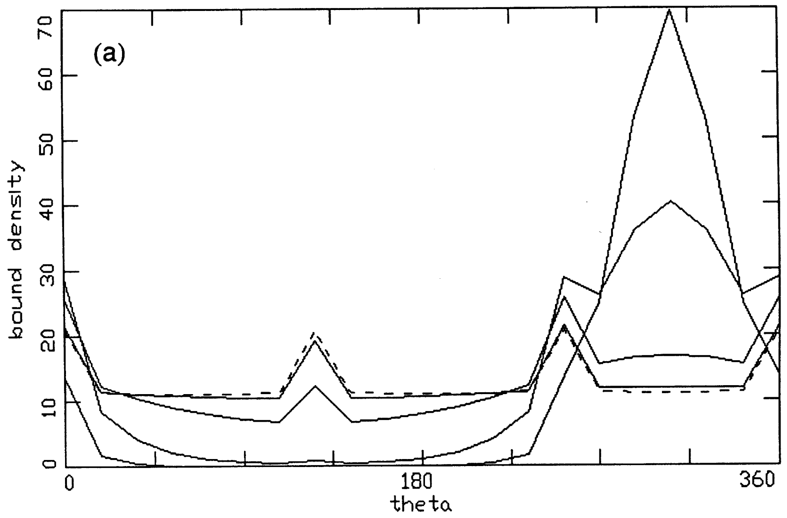
Fig. 2. The evolution of four peaks in Model III. The first peak does not interact with the third one. Similarly the second and fourth peaks do not interact. The first and third peaks persist while the second and the fourth ones decay

though the first peak is higher than the fourth, initially, after some time, the fourth peak overtakes all the others and becomes the nonzero equilibrium, while all others decay. We have assumed in this model that all peaks interact with each other. If, on the other hand the peaks do not interact at some angles, then the prediction of a single equilibrium direction no longer holds. Fig. 2 illustrates a typical case of this sort in which $G(\pi/2) = G(-\pi/2) = 1.0$, $G(\pi) = G(-\pi) = 0$. We find that peaks 1 and 3 both persist.

8 Numerical experiments for Model I

In this section we compare the predictions of the analysis of Sections 2–4 with a few numerical experiments, in which equations (2.1) were simulated, starting from an initial situation in which a number of peaks were present. (A set of three roughly equally spaced peaks, shown dashed in Fig. 3, was used.) Simulations were carried out by methods described in (Edelstein-Keshet and Ermentrout, 1990). Angular space $0 < \theta < 2\pi$ was discretised into 20 grid points, and a time increment of $\Delta t = 0.05$ was used. The equations were discretized and convolutions as well as the Laplacian were formulated in explicit (forward differencing) scheme. The results give a good qualitative description of the model.

We started with a kernel which had a single hump and was strictly positive for all θ, $K(\theta) = 1.5 + \cos\theta$. This means that there are interactions between cells at all angles. Figure 3 shows how at weak diffusion, a single narrow peak evolves from a set of three small peaks.



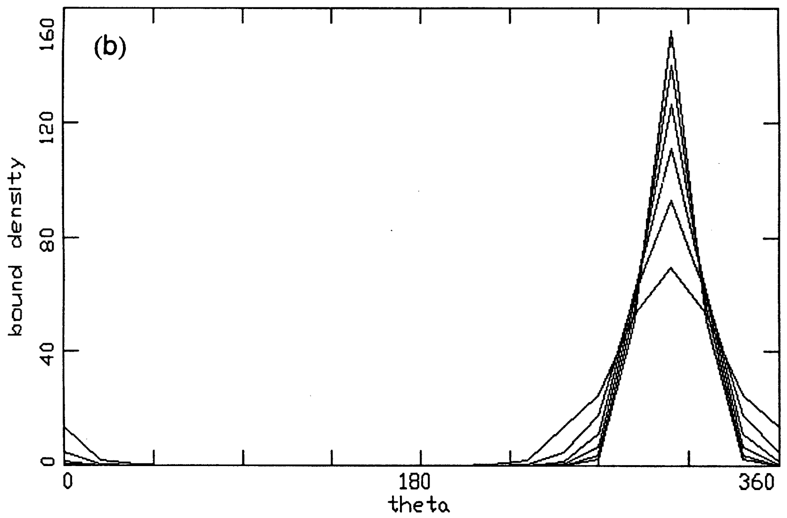


Fig. 3a, b. We simulate the evolution of peaks for Model I. Development of an initial distribution (dashed lines) consisting of three small peaks under the dynamics predicted by the model (2.1). Shown is the density of bound cells only. (The density of free cells is quite similar, but of different magnitude.) The turning due to cell contact is here based on a strictly positive, single humped kernel $K(\theta) = 1.5 + \cos\theta$. The discretised equations were simulated for $\beta = \gamma = 0.3$, $\varepsilon = 0.001$, $\Delta t = 0.05$ for **a** the first 150 time units, **b** the next 150 time units. A single peak forms, and stabilizes

Next, in Fig. 4, the results of a simulation using a kernel with one hump which is nonzero for a finite range, smaller than 2π are shown. The form of the kernel is

$$K(\theta) = \begin{cases} \cos\frac{\theta}{1.11}, & \text{if } -1.74 < \theta < 1.74 \ , \\ 0, & \text{otherwise} \ . \end{cases} \tag{8.1}$$

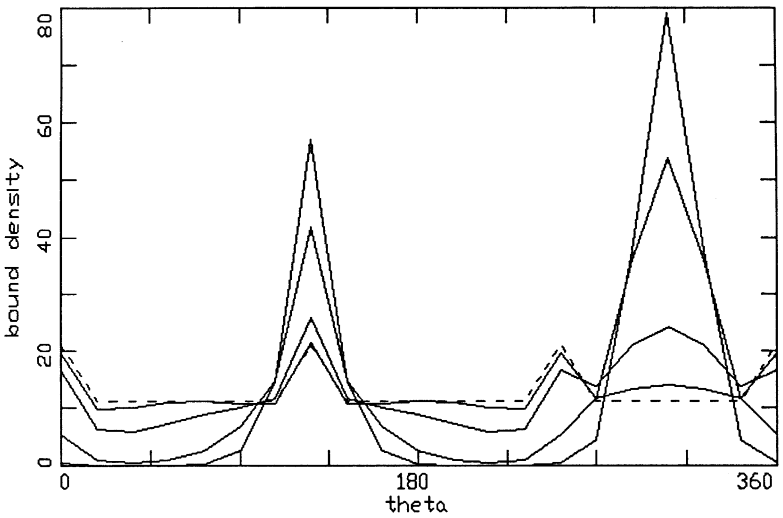


Fig. 4. As in Fig. 3 but with a single-humped kernel of the form (8.1) which is nonzero only on a compact set. Two peaks persist. All parameters and conditions were the same as in Fig. 3

(The range of influence was taken to be 100°.) It can be seen that two out of the initial three small peaks are absorbed into one large peak, and the remaining small peak separately grows into a smaller final peak. In this degenerate situation though two unequal peaks are not stationary (see Sect. 3), their rate of equalization becomes small. Therefore, in practice, two peaks of unequal size can become meta-stable (non-stationary but long-lasting).

In Fig. 5, the range of the kernel was decreased to 55°. The form of the kernel in this case was:

$$K(\theta) = \begin{cases} \cos\frac{\theta}{0.61}, & \text{if } -0.96 < \theta < 0.96, \\ 0, & \text{otherwise}. \end{cases} \tag{8.2}$$

In this case, three meta-stable peaks grow in positions identical to those of the three small peaks. The explanation for this phenomenon is that due to the narrow kernel, the peaks have a minimal interaction with one another. This was not true in the previous simulation, where the tails of the peaks were separated by an angle smaller than the effective range of interaction. Note that the peaks are not of the same height.

In Fig. 6, we explore the same situation as in Fig. 5, but with a larger diffusion coefficient ($\varepsilon = 1$). The initial peaks apparently start to communicate as a result of increased diffusion and, finally, a single peak evolves.

In Fig. 7 a double-humped kernel $K(\theta) = 1.5 + \cos(2\theta)$ is used. In the case of small diffusion two unequal meta-stable peaks evolve at a relative angle π. Though these peaks are non-stationary (as it was shown analytically in Sect. 3), the diffusion is so small that exponentially small growth rate does not

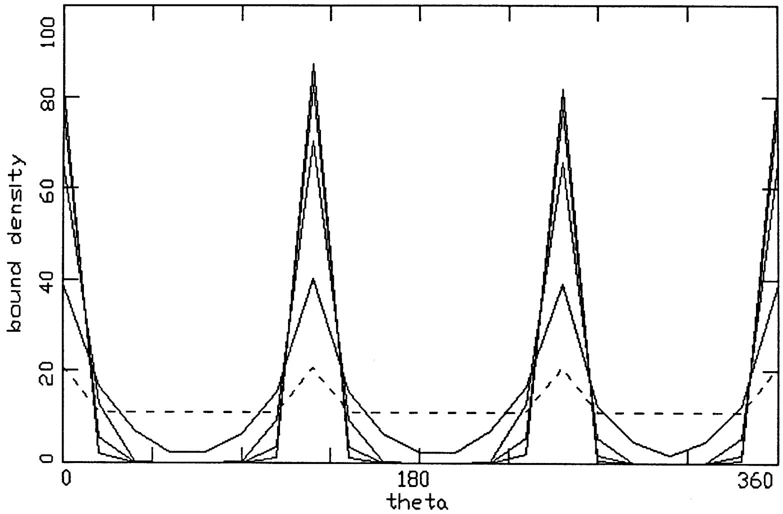


Fig. 5. As in Fig. 4, but with a kernel whose range is 55°. (See text for the exact form.) Note that now all three initial peaks can grow and coexist, since their interaction (mainly through angular diffusion) is very weak

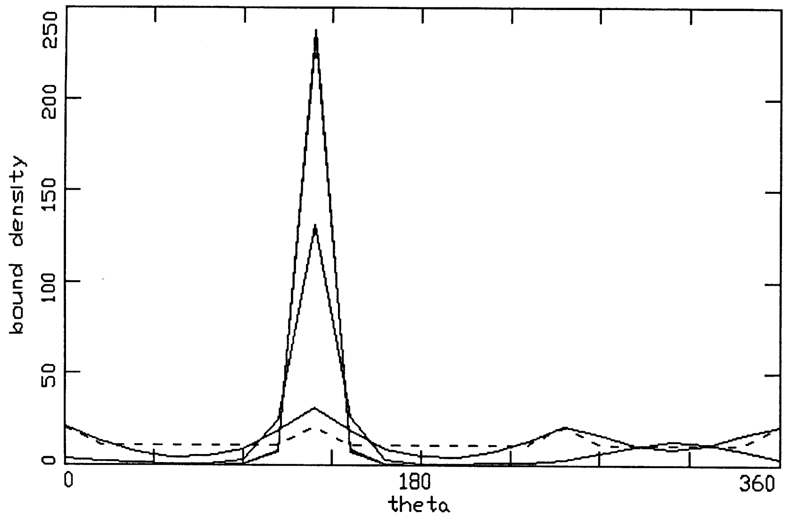


Fig. 6. Same as Fig. 5, but with an increased rate of diffusion, and simulated for longer time. $\varepsilon = 1.0$, 750 time units. Increased diffusion enhances the interactions of the peaks, and leads to the above situation

provide a sufficiently strong equalizing effect on the two peaks, in real time. Note, that the angle between the peaks in this experiment is as that predicted analytically. This is the consequence of an effective communication between the peaks during formation period.

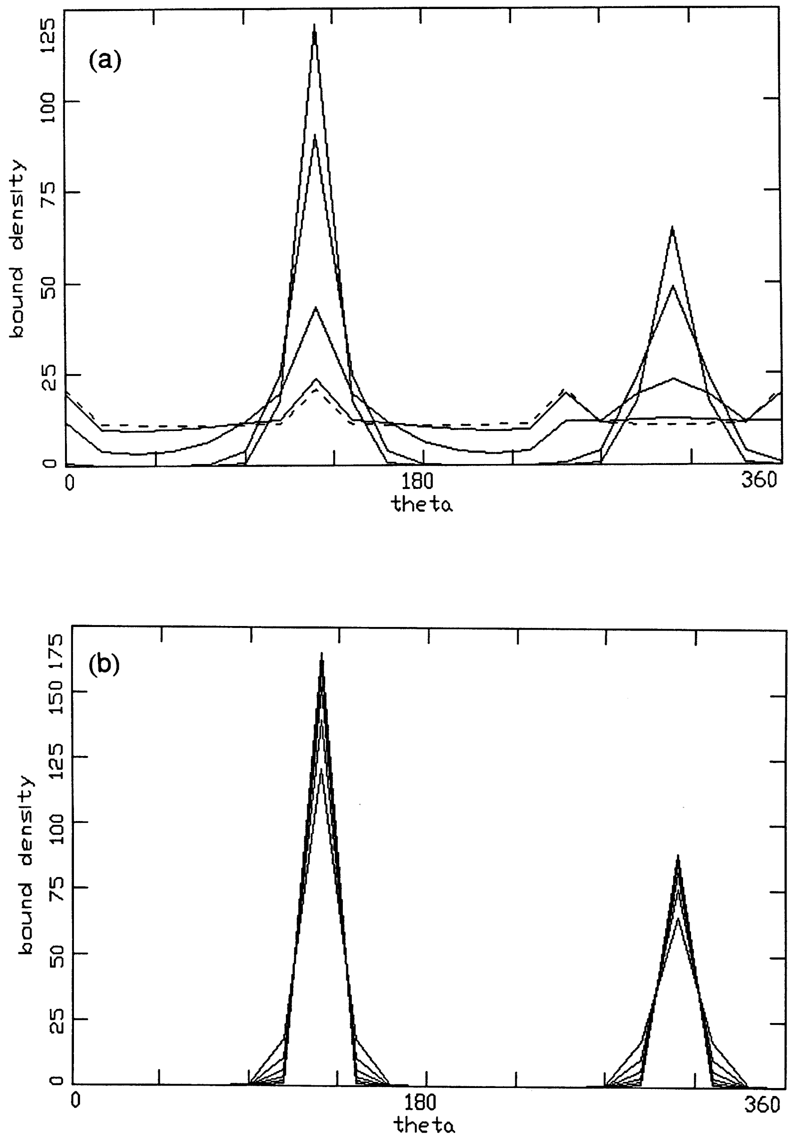


Fig. 7a, b. We used a double-humped kernel $K(\theta) = 1.5 + \cos 2\theta$, and diffusion rate $\varepsilon = 0.001$. **a** after 150 time units, **b** the next 150 time units. Two unequal peaks evolved. Because the diffusion is so small, the peaks do not essentially communicate with one another

In Fig. 8 we have the same case as in Fig. 7, but with much larger diffusion. Evolution of two equal peaks at a mutual angle π can be clearly seen, as will be mentioned in the discussion. Note that diffusion in this case is much larger than in the previous cases, providing effective communication between the

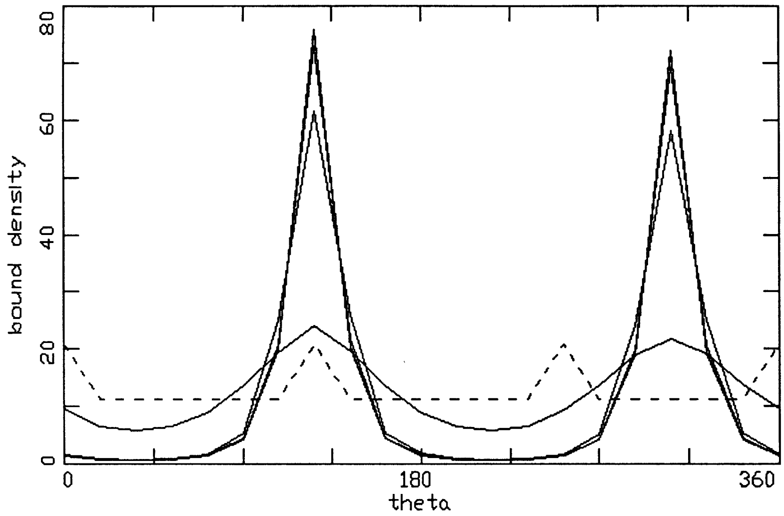


Fig. 8. Similar to Fig. 7, but with large diffusion, $\varepsilon = 1$. Two peaks at relative angle π evolve. Their heights are gradually equalized by the rotational diffusion. (Here shown up to 750 time units)

peaks at all times. It is seen that the evolved peaks are slightly uneven as the relaxation time is very long.

The results indicate that if the kernel is effective only at a finite range (as in the case of Figs. 4 and 5) then in reality, a few metastable peaks will evolve at small diffusion. The lifetime of the peaks will be larger than the timescale of most realistic experiments. In real situations, this implies the possible existence of a few different directions of alignment.

9 Discussion

The cases considered in this paper all pertain to phenomena in which individuals achieve strong alignment with one another. This stems from the fact that interaction terms dominate over random rotation. The alignment is an active one, stemming from forces, rather than a result of packing constraints due to crowding. This does not imply that all individuals align in the same direction. They can be distributed among a few directions, depending on symmetry features of the interaction terms. The actual directions along which alignment occurs are arbitrary (unless we incorporate some bias due to external influences), but the relative angles of separation of two or more peaks result from the interactions. These results imply that mild non-homogeneities in the angular distribution occurring close to bifurcation (see MEK, 1995) evolve into peaks. The number of the maxima of the weakly non-homogeneous distribution is equal to the number of peaks in the limiting case of this paper.

We explored three distinct models for alignment in which turning was instantaneous (Model I, III) and gradual (Model II). In Models I and III a number of peaks of constant location and variable heights was found but the only stable configuration consists of a single peak. This fact is established definitively for Model III and in a few simple cases in Model I. For Model II, peaks of constant heights appear, and gradually drift towards each other, and finally converge into a single peak. To place these results into a biological context, recall that the angular densities represent concentrations of filaments (e.g. actin) or cells (e.g. fibroblasts) at various orientations. In Models I and III, these objects cluster at several directions, but small fragments are exchanged, so that one or another of the clusters grow and eventually win over the others. In Model II, clusters are gradually "pulled" by one another, so that, eventually, all have the same orientation.

It follows from the qualitative theoretical reasoning in this paper that the case of weak angular diffusion is characterized by a hierarchy of times in the dynamics of alignment. One may speculate that first, on a relatively short timescale of order 1, an "initial" configuration of peaks evolves from the initial distribution. Then these peaks undergo slow evolution, changing their location and heights on an exponentially large timescale (i.e. $\exp(1/\varepsilon)$). (The proof of this assertion is one of the goals of future research.) The important fact for applications is that this large timescale can be comparable, or even larger, than the characteristic biological times. In this case, the system just does not have "enough time" to reach a globally stable configuration. Thus, it may happen that the system aligns, but that the type of alignment seems to depend on initial conditions. There is an analogue to this scenario in small noise perturbation theories (Gardiner, 1985). There, also a hierarchy of relaxation times in the system appears. The connection is that the Fokker-Planck equation with small diffusion is considered there, and the smallness of the diffusion results in this hierarchy.

The nonlinearity of the problem results in great difficulty in preforming a full treatment of the singular perturbation problem. Even the enumeration of all possible equilibria in the non-perturbed model is challenging. For this reason, we do not try to construct the full perturbational expansion and consider only the first approximation. In this approximation we have estimated the width of the peaks (see (4.9, 6.6)). We are not aware of theorems on the existence and uniqueness of solutions (or of Lyapunov functions) for Models I and III.

This nonlinearity makes the problem of the stability of the peak ansatz solution problematic. It is not clear how to prove global stability. Moreover, analytically only the local stability to shifts of the peaks, and their splitting can be checked. Theoretically, other perturbational modes may exist, breaking the stability of the peaks. However, there is a posteriori strong evidence for the stability of the peak solutions from numerical experiments. Further, there is no proof that the peak solutions are in a basin of attraction (with respect to most initial conditions), but again, numerical experiments point to this fact.

Finally, we briefly describe expected results on first, parallel alignment due to a double-humped kernel and, second, orthogonal alignment that occurs in Model I for kernels representative of the alignment of actin filaments in the cytoskelleton of the cell (see Civelekoglu and Edelstein-Keshet, 1994; MEK, 1995).

Case a: Parallel alignment. In this case we expect that the only stable situation is two equal peaks at relative angle of π in 2D (see Fig. 8) and similarly antiparallel in 3D.

Case b: Orthogonal alignment. It is natural to assume, based on our experience with the single and double humped kernels, that an even, non-negative double humped kernel having humps at $-\pi/2$ and $\pi/2$ leads to orthogonal alignment. (Alignment occurs along angles where the kernel has maxima). We expect in this case the formation of four equal and mutually orthogonal narrow peaks. In the 3D case, in the limiting case of weak diffusion, $\varepsilon \to 0$, six equal, mutually orthogonal narrow peaks evolve from the corresponding bumps. In the most convenient case, when one of the peaks is located at the pole, their location is given by the set of coordinates $\{\phi = 0\}$, $\{\phi = \pi\}$, $\{\phi = \pi/2;\ \theta = 0, \pi, -\pi/2, \pi/2\}$.

It is plausible that the stable configurations of peaks in 2D and 3D situations described above in the weak diffusion limit are the only stable ones. The stability analysis of the other configuration, however, is too complicated.

Appendix A: calculations for the peak ansatz

Derivation of equations (3.2). Plugging the expression $P = (M - C)$ into the dimensionless equation for C (the first equation in (2.1)) and assuming $\varepsilon = 0$, we obtain

$$\begin{aligned}\frac{\partial C}{\partial t} &= -C(K*C) - C(K*M) + C(K*C) + a(M - C)\\ &= C(a + (K*M)) + aM\ .\end{aligned} \tag{A.1}$$

Plugging $P = (M - C)$ into both equations (2.1) and adding leads to

$$\begin{aligned}\frac{\partial M}{\partial t} &= \frac{\partial P}{\partial t} + \frac{\partial C}{\partial t}\\ &= P(K*C) - C(K*P)\\ &= M(K*C) - C(K*C) - C(K*M) + C(K*C)\\ &= M(K*C) - C(K*M)\ .\end{aligned} \tag{A.2}$$

Proof that $F(\theta)$ is constant. The aim now is to show that $F(\theta)$ defined in (3.3) is a constant, i.e., that $F(\theta_1) = \ldots = F(\theta_n)$ where $\theta_1 \ldots \theta_n$ are the angles at which $M \neq 0$. We argue by contradiction: Suppose that $F(\theta)$ is not constant. Then there is some angle θ_1 such that

$$F_1 \equiv F(\theta_1) > F(\theta)\ , \tag{A.3}$$

for all $\theta \neq \theta_1$. Then from equation (3.8), it follows that

$$F_1 = \sum_{j=1}^{n} \frac{a + F_1}{a + F(\theta_j)} K(\theta_1 - \theta_j) M(\theta_j) \,. \tag{A.4}$$

But on the right hand side, the ratio

$$\frac{a + F_1}{a + F(\theta_j)} > 1, \quad j \neq 1 \,. \tag{A.5}$$

But then since

$$\begin{aligned} K(\theta - \theta_j) &> 0 \,, \\ M(\theta_j) &> 0 \,, \end{aligned} \tag{A.6}$$

the right hand side of the above sum is greater than the expression

$$\sum_{j=1}^{n} K(\theta_1 - \theta_j) M(\theta_j) \equiv (K * M)(\theta_1) \equiv F_1 \,. \tag{A.7}$$

Thus we have $F_1 > F_1$ which is a contradiction, and therefore it must follow that $F(\theta)$ is constant at the steady state.

Appendix B: stability of two peaks

The linearized system of equations for the perturbations c_1, c_2, m has the form:

$$\begin{cases} \dot{m} = 2K_1\bar{C}m - \dfrac{K_1 M}{2} c_1 + \dfrac{K_1 M}{2} c_2 \,, \\ \dot{c}_1 = (a + \bar{C}(K_1 - K_0))m - \left(a + \dfrac{MK}{2}\right) c_1 \,, \\ \dot{c}_2 = -(a + \bar{C}(K_1 - K_0))m - \left(a + \dfrac{MK}{2}\right) c_2 \,, \end{cases} \tag{B.1}$$

where $\bar{C} = \bar{C}_1 = \bar{C}_2$. We rewrite the system of equations (B.1) in the vector form

$$\dot{\boldsymbol{q}} = \boldsymbol{A}\boldsymbol{q} \,. \tag{B.2}$$

where

$$\boldsymbol{q} = \begin{pmatrix} m \\ c_1 \\ c_2 \end{pmatrix}, \qquad \boldsymbol{A} = \begin{pmatrix} b & -d & d \\ f & e & 0 \\ -f & 0 & e \end{pmatrix} \tag{B.3}$$

and where

$$\begin{aligned} b &= 2K_1\bar{C} \,, \\ d &= \frac{K_1 M}{2} \,, \\ f &= (a + \bar{C}(K_1 - K_0)) \,, \\ e &= -\left(a + \frac{\bar{K}M}{2}\right), \end{aligned} \tag{B.4}$$

Then a simple calculation reveals that the characteristic equation associated with the above matrix is

$$\begin{aligned}\det\{A-\lambda I\} &= (b-\lambda)(e-\lambda)^2 + df(e-\lambda) + df(e-\lambda)\\ &= (e-\lambda)[(b-\lambda)(e-\lambda)+2df]\\ &= 0\,. \end{aligned} \tag{B.5}$$

Thus one of the eigenvalues, λ_1 is simply $\lambda_1 = e = -(a + \bar{K}\frac{M}{2}) < 0$ and the other two satisfy the quadratic equation

$$[(b-\lambda)(e-\lambda)+2df] = 0\,. \tag{B.6}$$

An elementary calculation reveals that

$$\lambda_{\max} = \frac{1}{2l}\left(k - l^2 + \sqrt{(k-l^2)^2 - 4kl'l}\right), \tag{B.7}$$

where

$$k = K_1 aM, \qquad l = a + \frac{\bar{K}M}{2}, \qquad l' = \frac{(K_1 - K_0)M}{2}\,. \tag{B.8}$$

Since $K_1 < K_0$, $l' < 0$, and $-kl'l > 0$, it follows that at least one of the eigenvalues is positive. Thus, small deviations from the stationary steady state grow exponentially and two peaks are hence unstable.

Appendix C: stability of one peak

We now consider the stability of one peak. The linearized system of equations for the perturbations $\tilde{m}$, c_1, c_2 has the form:

$$\begin{cases} \dot{\tilde{m}} = K_1\bar{C}\tilde{m} + K_1 M c_2\,,\\ \dot{c}_1 = (a + \bar{C}(K_1 - K_0))\tilde{m} - (a + K_0 M)c_1\,,\\ \dot{c}_2 = -a\tilde{m} - (a + K_1 M)c_2\,. \end{cases} \tag{C.1}$$

If we rewrite these in the vector form

$$\dot{\boldsymbol{q}} = \boldsymbol{B}\boldsymbol{q}\,,$$

where $\boldsymbol{q}$ is the column vector $(\tilde{m}, c_1, c_2)$ then the matrix $\boldsymbol{B}$ is

$$\boldsymbol{B} = \begin{pmatrix} b & 0 & d\\ e & g & 0\\ f & 0 & h \end{pmatrix}. \tag{C.2}$$

Here

$$\begin{aligned} b &= K_1\bar{C}\,,\\ d &= K_1 M\,,\\ e &= a + \bar{C}(K_1 - K_0)\,,\\ g &= -(a + K_0 M)\,, \end{aligned}$$

$$\begin{aligned} f &= -a\,, \\ h &= -(a + K_1 M)\,. \end{aligned} \tag{C.3}$$

We now find that the characteristic equation is

$$\begin{aligned} \det\{\boldsymbol{B} - \lambda \boldsymbol{I}\} &= (b-\lambda)(g-\lambda)(h-\lambda) - df(g-\lambda) \\ &= (g-\lambda)[(b-\lambda)(h-\lambda) - df] \\ &= 0\,. \end{aligned} \tag{C.4}$$

Thus $\lambda_1 = g < 0$ is one eigenvalue, and the others are solutions of the quadratic equation

$$\lambda^2 - (b+h)\lambda + (bh - df) = 0\,. \tag{C.5}$$

This leads to

$$\lambda = \tfrac{1}{2}((b+h) \pm \sqrt{((b+h)^2 + 4(df - bh))} = \tfrac{1}{2}[-\gamma \pm \sqrt{\gamma^2 + 4\xi}]\,, \tag{C.6}$$

where

$$\gamma = +a + \frac{K_1 K_0 M^2}{(a + K_0 M)} > 0\,, \qquad \xi = \frac{a K_1 M^2}{(a + K_0 M)}(K_1 - K_0) < 0\,. \tag{C.7}$$

As $\gamma > 0$, and $\xi < 0$, both eigenvalues are negative. So one peak is stable to small perturbations which would tend to decrease it in favour of another peak.

Appendix D: stability of three peaks

The masses at the three peaks satisfy the system of equations:

$$\begin{cases} \dot{M}_1 = K_1(M_1(C_2 + C_3) - C_1(M_2 + M_3))\,, \\ \dot{M}_2 = K_1(M_2(C_1 + C_3) - C_2(M_1 + M_3))\,, \\ \dot{M}_3 = K_1(M_3(C_1 + C_2) - C_3(M_1 + M_2))\,, \\ \dot{C}_1 = -C_1(a + K_0 M_1 + K_1 M_2 + K_1 M_3) + a M_1\,, \\ \dot{C}_2 = -C_2(a + K_0 M_2 + K_1 M_1 + K_1 M_3) + a M_2\,, \\ \dot{C}_3 = -C_3(a + K_0 M_3 + K_1 M_1 + K_1 M_2) + a M_3\,. \end{cases} \tag{D.1}$$

A stability calculation in the case of these equations now leads to the 6×6 matrix

$$\begin{pmatrix} 2b & -b & -b & -2f & f & f \\ -b & 2b & -b & f & -2f & f \\ -b & -b & 2b & f & f & -2f \\ d & -b & -b & -e & 0 & 0 \\ -b & d & -b & 0 & -e & 0 \\ -b & -b & d & 0 & 0 & -e \end{pmatrix} \tag{D.2}$$

where

$$\begin{aligned} b &= K_1\bar{C}\,, \\ f &= K_1 M/3\,, \\ d &= a - K_0\bar{C}\,, \\ e &= a + \bar{K}M/3\,, \end{aligned} \tag{D.3}$$

and where $\bar{K} = K_0 + K_1 + K_1$, $\bar{C} = (aM/3)/(a + \bar{K}M/3)$. Observe that this matrix has a block structure,

$$\begin{pmatrix} 2b & -b & -b & & -2f & f & f \\ -b & 2b & -b & \vdots & f & -2f & f \\ -b & -b & 2b & & f & f & -2f \\ & \cdots & & \cdots & & \cdots & \\ d & -b & -b & & -e & 0 & 0 \\ -b & d & -b & \vdots & 0 & -e & 0 \\ -b & -d & d & & 0 & 0 & -e \end{pmatrix} \tag{D.4}$$

or,

$$\begin{pmatrix} A & \vdots & B \\ \cdots & \cdots & \cdots \\ C & \vdots & D \end{pmatrix} \tag{D.5}$$

where A, B, C, D are 3×3 matrices and D is diagonal. This fact is useful since it permits us to use a fact from matrix theory, namely that

$$\det\begin{pmatrix} A & \vdots & B \\ \cdots & \cdots & \cdots \\ C & \vdots & D \end{pmatrix} = \det(AD - BC)\,. \tag{D.6}$$

The eigenvalues of the block matrix can then be calculated by letting

$$\begin{aligned} A' &= A - \lambda I\,, \\ D' &= D - \lambda I\,, \end{aligned} \tag{D.7}$$

in the matrix $(A'D' - BC)$, with the result

$$(A'D' - BC) = \begin{pmatrix} \chi & \mu & \mu \\ \mu & \chi & \mu \\ \mu & \mu & \chi \end{pmatrix}, \tag{D.8}$$

where

$$\begin{aligned} \chi &= -(e + \lambda)(2b - \lambda) + 2f(d + b)\,, \\ \mu &= (e + \lambda)b - f(d + b)\,. \end{aligned} \tag{D.9}$$

This leads to

$$\det(A'D' - BC) = (\mu - \chi)[2\mu^2 - \mu\chi - \chi^2] \,. \tag{D.10}$$

The equation

$$2\mu^2 - \mu\chi - \chi^2 = 0 \,, \tag{D.11}$$

has four roots, and the case $(\mu = \chi)$ gives two roots. An expanded form of this last equation is

$$\lambda^2 + (e - 3b)\lambda + 3(fb + fd - eb) = 0 \,. \tag{D.12}$$

The roots of this equation are given by the expression:

$$\lambda = \tfrac{1}{2}(-(e - 3b) \pm \sqrt{(e - 3b)^2 + 4\tau} \tag{D.13}$$

where $\tau = K_1 M\bar{C}(K_0 - K_1) > 0$. Thus at least one of the eigenvalues is positive, and three equal, evenly spaced peaks are unstable.

Three unevenly spaced peaks

As a specific example, we took the following arbitrary values, for the parameters: $K(0) = 6$, $K(\theta_1 - \theta_2) = 2$, $K(\theta_1 - \theta_3) = 3$, $K(\theta_2 - \theta_3) = 4$, $\bar{M}_1 = 10$, $\bar{M}_2 = 9$, $\bar{M}_3 = 4$. Then $KM = 90$. We assume $a = 10$, then $\bar{C}_1 = 1$, $\bar{C}_2 = 0.9$, $\bar{C}_3 = 0.4$. Using the software Mathematica we found that in this case the 6×6 stability matrix has the form

$$\begin{pmatrix} 3 & -2 & -3 & -30 & 20 & 30 \\ -1.8 & 3.6 & -3.6 & 18 & -36 & 36 \\ -1.2 & -1.6 & 6.6 & 12 & 16 & -66 \\ 4 & -2 & -3 & -100 & 0 & 0 \\ -1.8 & 4.6 & -3.6 & 0 & -100 & 0 \\ -1.2 & -1.6 & 7.6 & 0 & 0 & 100 \end{pmatrix} .$$

Further, the six eigenvalues of this matrix are:

$$\begin{aligned} \lambda_1 &= -92.74 \ , \\ \lambda_2 &= -96.92 \ , \\ \lambda_3 &= 2.05 \ , \\ \lambda_4 &= 0.00 \ , \\ \lambda_5 &= 0.81 \ , \\ \lambda_6 &= -100.0 \ . \end{aligned} \tag{D.14}$$

Two of these eigenvalues are positive, so that this situation of three uneven peaks is unstable. Notice that one of the eigenvalues is zero since $M = M_1 + M_2 + M_3 = \text{const.}$

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