Supplementary Information

We consider cell density (n) and concentration of an activator (a). Cells undergo random motion, and also chemotaxis - moving preferentially up gradients in activator concentration. The activator is produced by cells, it undergoes linear decay and also random motion. This behaviour can be described using a system of partial differential equations:

$$\underbrace{\frac{\partial n}{\partial t}}_{\text{Rate of change of cell density}} = \underbrace{D_n \nabla^2 n}_{\text{Random motion}} - \underbrace{\chi \nabla.(n \nabla c),}_{\text{Chemotactic movement}} \tag{1}$$

$$\underbrace{\frac{\partial c}{\partial t}}_{\text{Rate of change of activator concentration}} = \underbrace{D_c \nabla^2 c}_{\text{Random diffusion}} + \underbrace{\frac{sn}{\beta + n} - \gamma c,}_{\text{Production and decay of activator}} \tag{2}$$

where D_n, D_c, χ, s, β and γ are positive constants. The first term on the RHS of each equation represents random motion/diffusion. The second term on the RHS of the cell density equation represents chemotactic movement, with cells moving up gradients in activator concentration. The remaining terms on the RHS of the activator equation represent activator production, which saturates for high cell density, and activator removal/decay.

We consider a two dimensional feather field, rectangular in shape, given by cells lying in the region $\mathcal{D} = [0, L_x] \times [0, L_y]$. We assume that there can be no loss of cells or activator through the boundaries of the field, which results in zero flux boundary conditions of the form $\boldsymbol{n}.\nabla u = 0$ and $\boldsymbol{n}.\nabla v = 0$ for $\boldsymbol{x} \in \partial\mathcal{D}$, where $\boldsymbol{n}$ is the unit normal to the boundary, $\partial\mathcal{D}$.

Non-dimensionalisation. We non-dimensionalise the model in such a way as to keep γ, the parameter controlling the rate of activator decay/removal:

$$n = n_0 \hat{n}, \quad c = L\sqrt{\frac{s}{\chi}}\hat{c}, \quad t = \frac{L}{\sqrt{s\chi}}\hat{t}, \quad \boldsymbol{x} = L\hat{\boldsymbol{x}}, \quad D = \frac{D_n}{D_c}, \quad \beta = \hat{\beta} n_0, \quad \gamma = \frac{\sqrt{s\chi}}{L}\hat{\gamma}. \tag{3}$$

Dropping the $\hat{}$ notation the result is the system

$$\frac{\partial n}{\partial t} = D\nabla^2 n - \nabla.(n\nabla c), \tag{4}$$

$$\frac{\partial c}{\partial t} = \nabla^2 c + \frac{n}{\beta + n} - \gamma c. \tag{5}$$

Steady states. Since there are no terms for cell production or decay, the total cell number remains constant over time. Hence the steady state levels of cell density and activator concentration in the spatially uniform case are given by

$$n = n_0 \quad \text{and} \quad c = c_0 = \frac{n_0}{\gamma(\beta + n_0)}, \tag{6}$$

where n_0 is the initial cell density.

Linear stability. To investigate whether, and if so, which type of patterns may be formed due to small fluctuations away from the steady states, we linearise the system about the steady states. We take $n = n_0 + u$ and $c = c_0 + v$, where $|u|, |v| \ll 1$, and substitute these expressions into our equations for the evolution of n and c:

$$\frac{\partial(n_0+u)}{\partial t} = D\nabla^2(n_0+u) - \nabla.[(n_0+u)\nabla(n_0+u)], \tag{7}$$

$$\frac{\partial(c_0+v)}{\partial t} = \nabla^2(c_0+v) + \frac{(n_0+u)}{\beta+(n_0+u)} - \gamma(c_0+v). \tag{8}$$

Expanding the quotient and ignoring all quadratic and higher order terms in u and v we arrive at the linearised system:

$$\frac{\partial u}{\partial t} = D\nabla^2 u - n_0\nabla^2 u, \tag{9}$$

$$\frac{\partial v}{\partial t} = \nabla^2 v + \frac{\beta u}{(\beta+n_0)^2} - \gamma u, \tag{10}$$

which describes the behaviour of the system whilst $|u|, |v| \ll 1$. In order that small perturbations to the system to give rise to a spatially heterogeneous field, we seek solutions for u and v of the form $u, v \propto \exp(\lambda t + ik\boldsymbol{x})$ for which $\mathcal{R}(\lambda) > 0$.

Searching for solutions of the above form the linearised equations (9)-(10) gives

$$\begin{pmatrix} \lambda u \\ \lambda v \end{pmatrix} = \begin{pmatrix} -k^2 D & k^2 n_0 \\ \frac{\beta}{(\beta+n_0)^2} & -k^2-\gamma \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}, \tag{11}$$

which has solutions if and only if

$$\lambda^2 + [k^2(D+1)+\gamma]\lambda + h(k^2) = 0, \tag{12}$$

where

$$h(k^2) = Dk^2(k^2+\gamma) - \frac{k^2 n_0 \beta}{(\beta+n_0)^2}. \tag{13}$$

Hence we can see that solutions with $\mathcal{R}(\lambda) > 0$ exist if the following condition on the critical wave number, k_{crit} is satisfied:

$$k_{crit}^2 = \frac{1}{D}\left[\frac{n_0\beta}{(\beta+n_0)^2} - D\gamma\right] > 0. \tag{14}$$

In other words, a necessary condition for spatial patterns in cell density is that

$$\frac{n_0\beta}{D\gamma(\beta+n_0)^2} > 1. \tag{15}$$

Pattern types. We consider now finding the nature of the patterns which could arise. Taking into account the boundary conditions at $x = 0, L_x$ and $y = 0, L_y$ a general solution of the linearised system given by equations (9)-(10) can be written:

$$u(x,y,t) = \sum_{p_x,p_y} A_{p_x,p_y} e^{\lambda(k^2)t} \cos\left(\frac{p_x\pi x}{L_x}\right) \cos\left(\frac{p_y\pi y}{L_y}\right), \tag{16}$$

Parameter	Figure 1	Figure 2	Figure 3
D	0.001	0.001	0.001
n_0	1.0	1.0	1.0
β	2.0	2.0	2.0
γ	30	60	90

Table 1: Parameter values for the numerical simulations

where the $p_x, p_y = 0, 1, 2, \ldots$ and satisfy

$$0 < k^2 = \left(\frac{p_x \pi}{L_x}\right)^2 + \left(\frac{p_y \pi}{L_y}\right)^2 < k_{crit}^2 = \frac{1}{D}\left[\frac{n_0 \beta}{(\beta + n_0)^2} - D\gamma\right]. \tag{17}$$

If k_{crit}^2 is sufficiently small, the only way to satisfy equation (17) may be to take either p_x or p_y (or both) equal to zero. If one of p_x or p_y is zero, the resulting pattern will be stripes in cell density, but if both p_x and p_y are zero the cell density will remain homogeneous. We note that k_{crit}^2, and hence the possible pattern types, can be fully controlled by varying γ, the rate of activator removal/decay.

Numerical simulation. The model can be solved numerically using the FEMLAB package. We solve the system given by equations (4)-(5) on the interval $(x, y) \in [0, 10] \times [0, 1]$ with zero flux boundary conditions. The initial conditions are taken to be the steady states of the model, given by equation (6), with small fluctuations added to the chemical concentration. The parameter values used in the numerical simulations are shown in Table 1.

Results Figure 1: for for low decay rate, the critical wave number admits oscillation in both the x and y directions, resulting in spots of high cell density. Figure 2: as the decay rate is increased, k_{crit}^2 decreases. Since $L_y < L_x$ (the competent field is longer than it is wide for the primary row) oscillations in the medial-lateral direction disappear, resulting in stripes. Figure 3: as the decay rate is increased even further, oscillations are not permitted in either the x or y directions and the feather field remains homogeneous. These results are summarised in Figure 4.

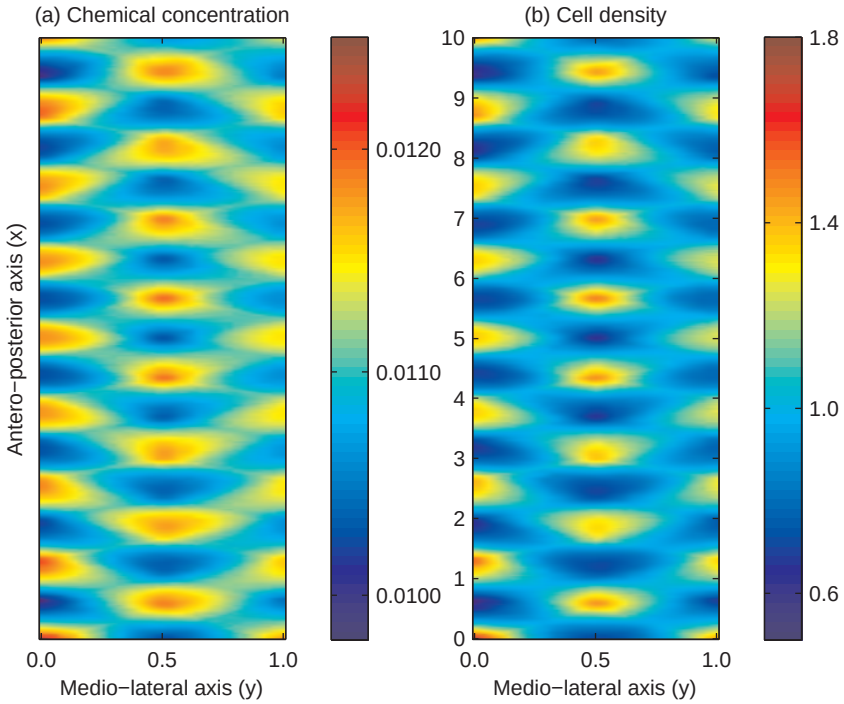

Figure 1: Numerical simulations of the control model result in a spotted pattern of feather buds. (a) shows activator concentration whilst (b) shows cell density.

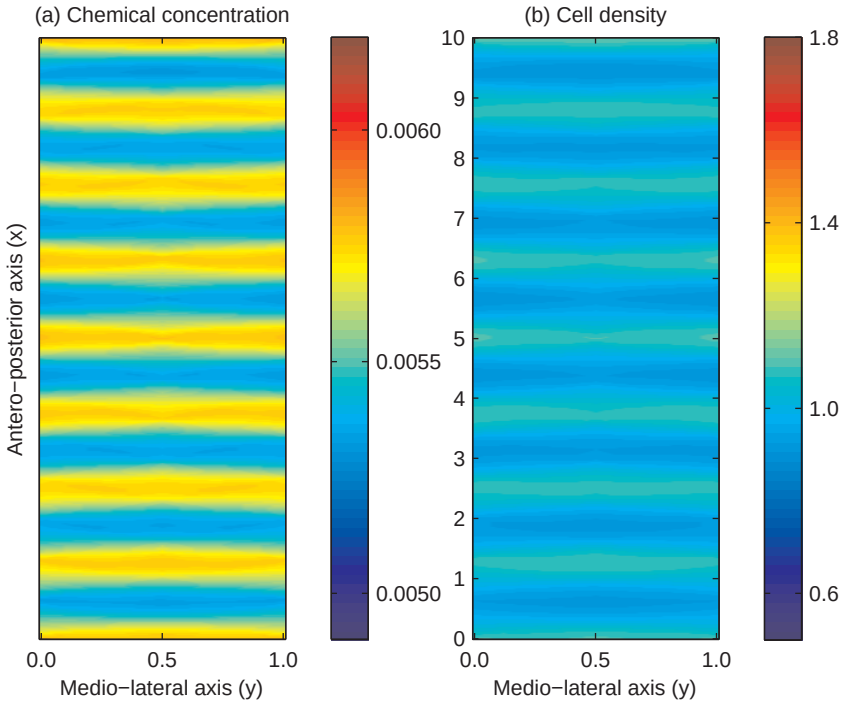

Figure 2: Numerical simulations with increased activator removal show a pattern of stripes in high cell density, which corresponds to elongation of the feather buds. (a) shows activator concentration whilst (b) shows cell density.

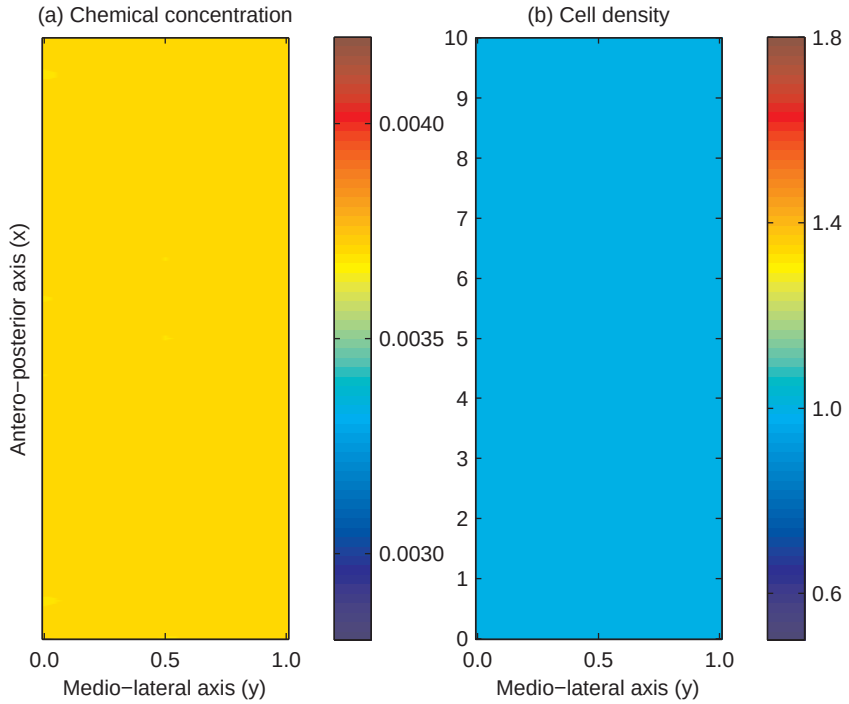

Figure 3: Numerical simulations result in a homogeneous feather field when the removal rate of the activator is too high. (a) shows activator concentration whilst (b) shows cell density.

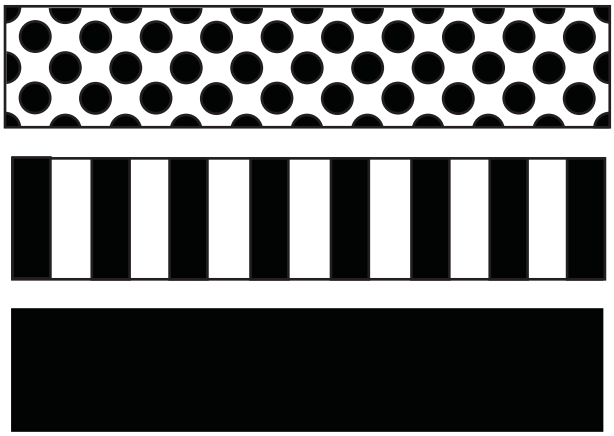

Figure 4: A diagram showing the feather patterns expected with numerical solution of the mathematical model. The top diagram shows the results for low activator removal rate: oscillations occur along both axes and the result is spots of high cell density. The middle diagram shows the results with increased activator removal: oscillations are no longer possible along the medio-lateral axis and stripes occur as a result. Finally the bottom diagram shows the results for high activator decay: oscillations are no longer possible along either axis and the field remains homogeneous.