The emergent physics of growing active matter

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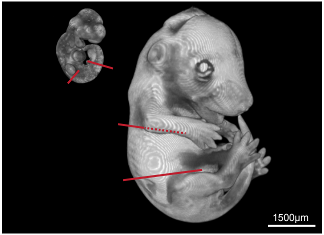
Why is growing active matter interesting?

- From a mathematical perspective, the timescales of growth and active matter dynamics cannot be separated.
- In particular, I am interested how the *implementation* of growth influences active matter dynamics.



ARTICLE

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Reconciling diverse mammalian pigmentation patterns with a fundamental mathematical model

Richard L. Mort[1,*], Robert J.H. Ross[2,*], Kirsten J. Hainey[1], Olivia J. Harrison[1], Margaret A. Keighren[1], Gabriel Landini[3], Ruth E. Baker[2], Kevin J. Painter[4], Ian J. Jackson[1,5] & Christian A. Yates[6]

Bands of colour extending laterally from the dorsal to ventral trunk are a common feature of mouse chimeras. These stripes were originally taken as evidence of the directed dorsoventral migration of melanoblasts (the embryonic precursors of melanocytes) as they colonize the

- Experimentally it is difficult to study how growth is ‘implemented’ in developing mammalian systems.

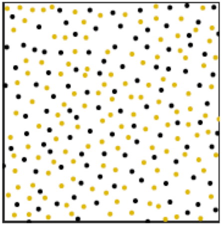
A potential model organism for growing active matter studies?

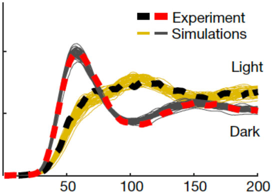
ARTICLE

https://doi.org/10.1038/s41586-018-0591-3

Elucidating the control and development of skin patterning in cuttlefish

Sam Reiter[1], Philipp Hülsdunk[1,2], Theodosia Woo[1], Marcel A. Lauterbach[1], Jessica S. Eberle[1], Leyla Anne Akay[1], Amber Longo[1], Jakob Meier-Credo[1], Friedrich Kretschmer[1], Julian D. Langer[1,3], Matthias Kaschube[2] & Gilles Laurent[1]*





A potential model organism for growing active matter studies?

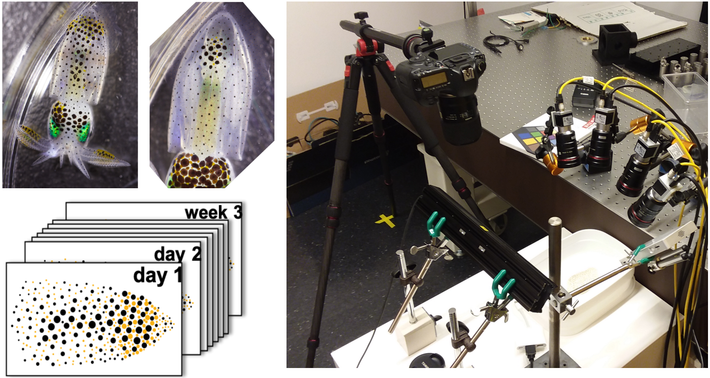
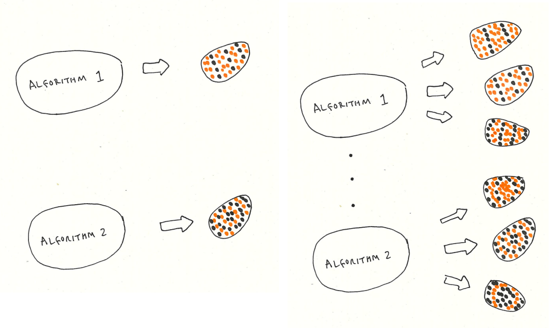


Figure 1: Hi-resolution squid chromatophore tracking.

- Can we infer how the dorsal mantle grows by tracking the chromatophores?

A grand theory..?

- Different cephalopods have different chromatophore patterns.

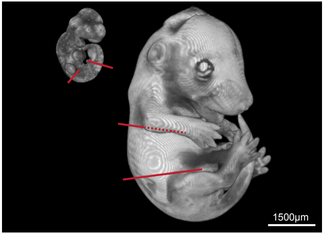


(a) Algorithm-centered perspective.

(b) Algorithm-via-growth perspective.

- To what extent can the *implementation of growth* funnel chromatophore patterning towards certain outcomes? Or, growing active matter systems in general?

In what ways can growth implementation influence active matter dynamics?



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Reconciling diverse mammalian pigmentation patterns with a fundamental mathematical model

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Bands of colour extending laterally from the dorsal to ventral trunk are a common feature of mouse chimeras. These stripes were originally taken as evidence of the directed dorsoventral migration of melanoblasts (the embryonic precursors of melanocytes) as they colonize the

- What physics might emerge from the interaction of active matter and the implementation of growth?

A simple cell motility and proliferation model

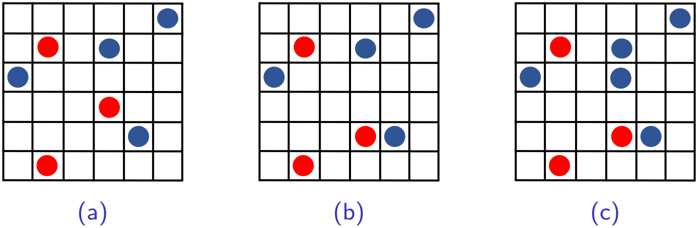

Figure 3: (a) t1, (b) t2 and (c) t3. Species R (red), high motility, low proliferation. Species B (blue), low motility, higher proliferation than species R. We employ periodic boundary conditions and have density-dependent proliferation.

Spatial correlations are established by agent proliferation

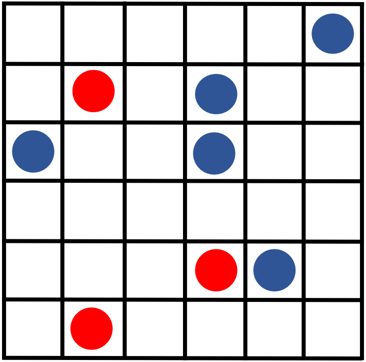

Figure 4: Adjacent agents prohibit proliferation, a form of density-dependent proliferation.

Spatial correlations affect the evolution of agent density

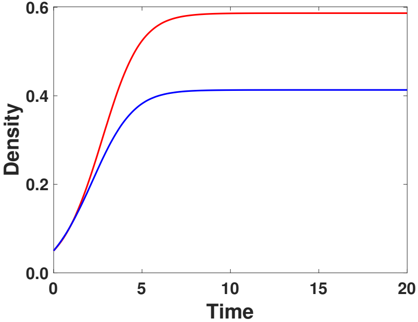

Figure 5: The evolution of the agent densities on a nongrowing lattice. Species R (red) dominates despite having a lower proliferation rate. The parameters are $P_m^R = 20$, $P_p^R = 0.9$, $P_m^B = 1$ and $P_p^B = 1$.

Two implementations of lattice growth

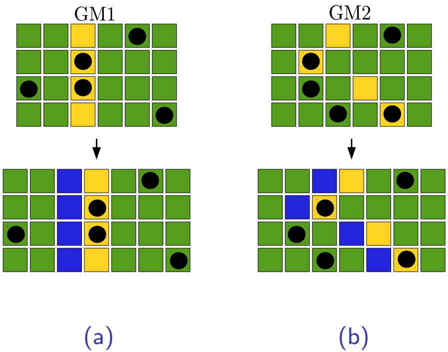

Figure 6: Before and after the growth events for both (a) GM1 and (b) GM2, in which growth is along the x-axis for a two-dimensional lattice. We study exponential growth.

Competition outcome is reversed depending on growth mechanism

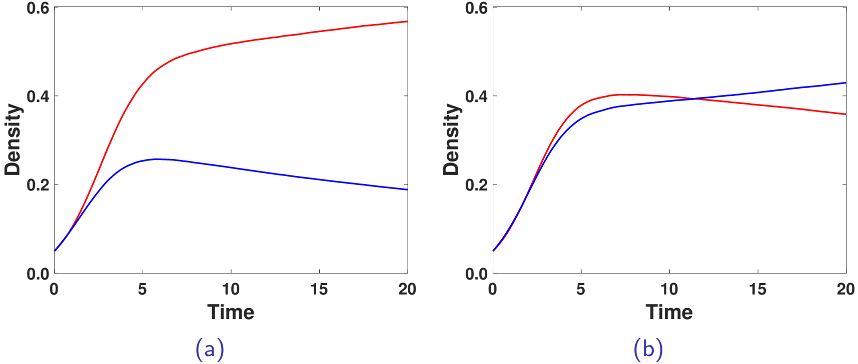

Figure 7: Species R (red) dominates when the lattice is grown with GM1, whereas species B (blue) ultimately dominates when the lattice is grown with GM2. The parameters for both panels (a) GM1 and (b) GM2 are $P_m^R = 20$, $P_p^R = 0.9$, $P_m^B = 1$, $P_p^B = 1$, $P_{g_x} = 0.1$ and $P_{g_y} = 0.1$.

GM1 is scale invariant, GM2 is not

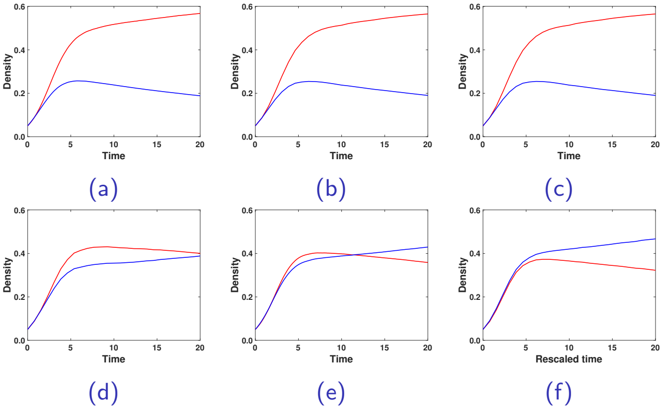

Figure 8: Altering the initial domain size causes the evolution of both species to change in GM2 but not in GM1. The initial lattice size in (a) and (d) is 50 by 50, in (b) and (e) 100 by 100, and in (c) and (f) 200 by 200. The parameters for all panels are $P_m^R = 20$, $P_p^R = 0.9$, $P_m^B = 1$, $P_p^B = 1$, $P_{g_x} = 0.1$ and $P_{g_y} = 0.1$.

Including pairwise correlations accounts for competition outcome reversal

The meanfield approximation does not work, however, if we take spatial correlations into account:

$$\frac{\mathrm{d}c_A(t)}{\mathrm{d}t} = P_p^R c_A(t)\Big(1 - F_{A,A}(1,0;t)c_A(t) - F_{A,B}(1,0;t)c_B(t)\Big) - \left(P_{g_x} + P_{g_y}\right)c_A(t).$$

The evolution of pairwise correlations in GM1 are independent of the size of the lattice.

$$\begin{aligned}\frac{\mathrm{d}\rho_{A,A}^{N_x\times N_y}(r_x, r_y; t)}{\mathrm{d}t} &= P_{gx}(r_x - 1)\rho_{A,A}^{N_x\times N_y}(r_x - 1, r_y; t) \\ &- P_{gx}(r_x + 1)\rho_{A,A}^{N_x\times N_y}(r_x, r_y; t) \\ &+ P_{gy}(r_y - 1)\rho_{A,A}^{N_x\times N_y}(r_x, r_y - 1; t) \\ &- P_{gy}(r_y + 1)\rho_{A,A}^{N_x\times N_y}(r_x, r_y; t).\end{aligned}$$

Mathematics for anyone interested.[1]

[1] 1. R Ross, C Yates, R Baker. Physica A 466, 334-345.
2. R Ross, R Baker, C Yates Physical Review E 94 (1), 012408.
3. R Ross, C Yates, R Baker. Physical Review E 95 (3), 032416.

Evolution of pairwise correlations in GM2

The evolution of pairwise correlations in GM2 are *not* independent of the size of the lattice.

$$
\begin{aligned}
&\frac{\mathrm{d}\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x, r_y; t)}{\mathrm{d}t} = \\
&P_{g_x}\left(-1-\frac{N_x(t)}{3}+r_x\left(\frac{r_x}{N_x(t)}-1\right)+\frac{1}{3N_x(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x, r_y; t) \\
&+P_{g_y}\left(-1-\frac{N_y(t)}{3}+r_y\left(\frac{r_y}{N_y(t)}-1\right)+\frac{1}{3N_y(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x, r_y; t) \\
&+P_{g_y}\left(-\frac{1}{2}+\frac{N_y(t)}{6}-\frac{r_y}{2}\left(\frac{r_y}{N_y(t)}-1\right)+\frac{1}{3N_y(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x, r_y-1; t) \\
&+P_{g_y}\left(-\frac{1}{2}+\frac{N_y(t)}{6}-\frac{r_y}{2}\left(\frac{r_y}{N_y(t)}-1\right)+\frac{1}{3N_y(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x, r_y+1; t) \\
&+P_{g_x}\left(-\frac{1}{2}+\frac{N_x(t)}{6}-\frac{r_x}{2}\left(\frac{r_x}{N_x(t)}-1\right)+\frac{1}{3N_x(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x-1, r_y; t) \\
&+P_{g_x}\left(-\frac{1}{2}+\frac{N_x(t)}{6}-\frac{r_x}{2}\left(\frac{r_x}{N_x(t)}-1\right)+\frac{1}{3N_x(t)}\right)\rho_{A,A}^{(N_x+1)\times(N_y+1)}(r_x+1, r_y; t).
\end{aligned}
$$

Including pairwise correlations accounts for competition outcome reversal

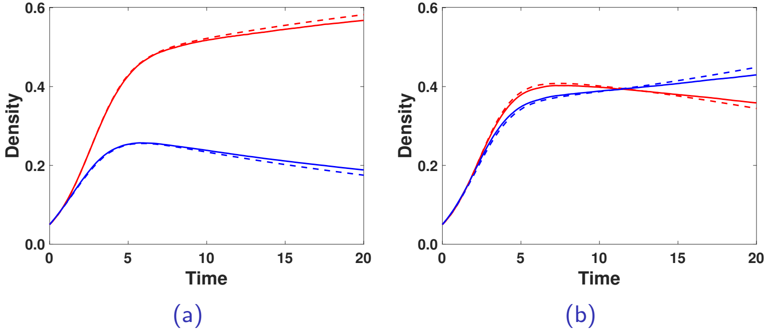

Figure 9: The dashed line is now the ODE model that includes pairwise correlations. Including the effects of pairwise correlations renders the correlations ODE model able to accurately approximate the averaged results from the stochastic simulation. The parameters for both panels (a) GM1 and (b) GM2 are $P_m^R = 20$, $P_p^R = 0.9$, $P_m^B = 1$, $P_p^B = 1$, $P_{g_x} = 0.1$ and $P_{g_y} = 0.1$.

Including pairwise correlations accounts for scale invariance

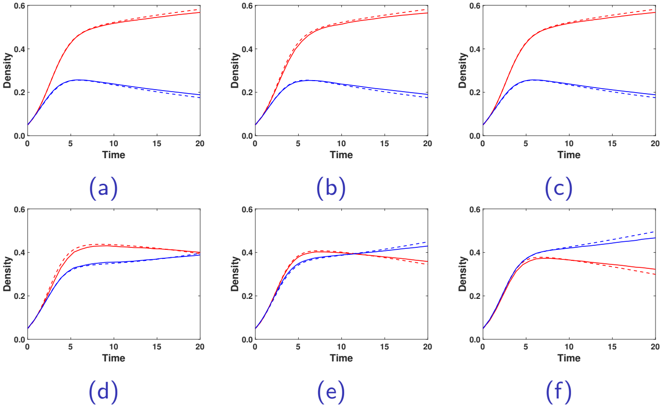

Figure 10: Including the effects of pairwise correlations renders the correlations ODE model able to accurately approximate the averaged results from the stochastic simulation. (a) and (d) 50 by 50, (b) and (e) 100 by 100, (c) and (f) 200 by 200. The parameters for all panels are $P_m^R = 20$, $P_p^R = 0.9$, $P_m^B = 1$, $P_p^B = 1$, $P_{g_x} = 0.1$ and $P_{g_y} = 0.1$.

Translational invariance of governing equations in GM1

In GM2 the rate at which spatial correlations are broken down depends on your location on the lattice, this is a boundary effect, as GM2 introduces an ‘origin of growth’.

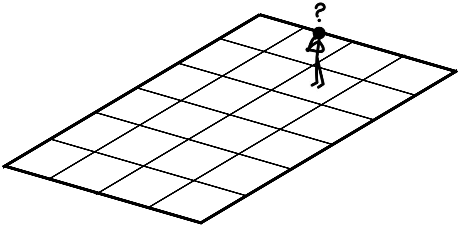

Figure 11: In GM2 the rate at which spatial correlations are broken down is a function of both position and domain size. In GM1 this is not the case.

How do GM1 and GM2 correspond to growth in continuous space?

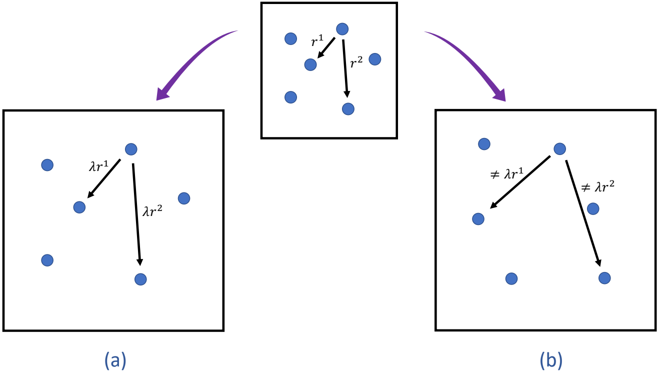

Figure 12: How pairwise distances evolve in (a) is equivalent to GM1, whereas how pairwise distances evolve in (b) is representative of GM2.

How else can the implementation of growth funnel active matter to different regions of its phase space in the large size (long-time) limit?

1. Growth-induced breaking and unbreaking of ergodicity in fully-connected spin systems, Morris & Rogers, *Journal of Physics A* (2014).
2. Compressibility of random walker trajectories on growing networks, *Physics Letters A* (2019).
3. Balancing conservative and disruptive growth in the voter model, to appear in the *Journal of Statistical Physics*.

Acknowledgements

1. University of Oxford - Ruth Baker and Kit Yates.
2. Harvard University - Walter Fontana