Supporting Information Appendix Stigmergy, collective actions and animal social spacing

L. Giuggioli, J.R. Potts, D.I. Rubenstein, S.A. Levin

SI Appendix

The simulations were coded in the C programming language. Other than the conspecific avoidance rule (see below), animals were modeled as continuous time random walkers (1), where the time for each jump is drawn from an exponential distribution with a mean of 1 unit of time (henceforth called a 'time step'). To simulate the movement of all individuals, the Gillespie algorithm (2, 3) is implemented whereby each individual animal moves at random intervals of time. The locations of each individual are thus updated at random. The animals' locations are updated on a square lattice with periodic boundary conditions such that when an animal selection for the next move corresponds to a location beyond the outermost grid points, it reappears on the corresponding opposite lattice point of the grid. To measure the encounter rate (Fig. 3a), for each choice of parameter α and Z, 10 simulations were run for 110,000 time steps each, starting with 25 individuals uniformly distributed on the terrain and no marks present. Measurements of encounter rate began after a 10,000 step burn-in time. After this, the number of pairwise encounters were measured, averaged over the 10 simulations, and divided by 100,000 to give a rate R. Measuring the size of each marked area (Fig. 3d) is more computationally intensive, but requires less running time to obtain a good mean value, by averaging over every time-step, whereas encounters occur rarely. We started measuring after a burn-in time of 1,000 time steps, which is longer than the time required for the marked areas to reach a saturation size, starting with 25 individuals uniformly distributed on the terrain and no marks present. Simulations were then run for a further

30,000 steps, taking the average size across all these time-steps. We averaged over 10 such simulation runs. The numbers of animals in each marked area (Fig. 3b) and the exclusive area sizes (Fig. 3c) were measured concurrently with the marked area sizes. For $Z = 9$, we have used $\rho = 0.0044$, $T = 2000$; for $Z = 40$ we have used $\rho = 0.01$, $T = 4000$; for $Z = 122$, we have used $\rho = 0.0204$, $T = 6000$; and for $Z = 400$, we have used $\rho = 0.04$, $T = 10000$. In all simulations the value of D has been set to 1/4.

The movement rules were such that an animal moves at random if it does not encounter any active foreign mark. When it occupies a location where a foreign mark is active, it retreats. The move away from foreign marks is towards the safety of more familiar surroundings and is represented by selecting a movement step with probability p in the direction of the centroid of its marked area. Computationally this is accomplished by having, at any given time, the probability of an animal to move left, right, up and down, respectively, l, r, u, and d, given by

$$l = \frac{1}{4}\left[1 + (2p-1)\frac{m-m_c}{\sqrt{(m-m_c)^2+(n-n_c)^2}}\right],$$

$$r = \frac{1}{4}\left[1 - (2p-1)\frac{m-m_c}{\sqrt{(m-m_c)^2+(n-n_c)^2}}\right],$$

$$u = \frac{1}{4}\left[1 - (2p-1)\frac{n-n_c}{\sqrt{(m-m_c)^2+(n-n_c)^2}}\right],$$

$$d = \frac{1}{4}\left[1 + (2p-1)\frac{n-n_c}{\sqrt{(m-m_c)^2+(n-n_c)^2}}\right],$$

where (m, n) and (m_c, n_c) represent, respectively, the current position of the animal and of the centroid of its marked area. The probability p may be some constant between 1/2 and 1, or it may have a functional dependence on the age τ of the encountered mark. Our choice of functional dependence has been described in the Results section.

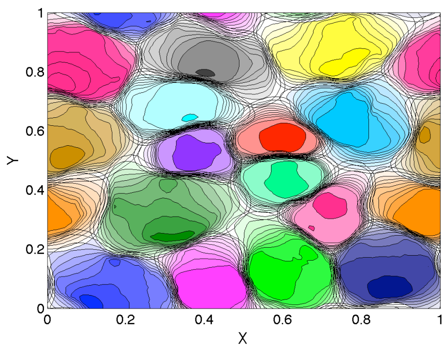
A good understanding of how α and Z affect the complex dynamics of the individuals in the population, we display the movement trajectories of a tagged individual relative to the locations of its neighbors. We have shown two such examples in Movies SV2 and SV3, where, respectively, for $Z = 400$ and $Z = 9$ and three different values of α, 10^{-5}, 0.1 and 100, the spatio-temporal dynamics of all animals are followed relative to a tagged red individual and its neighbors, which are colored in blue whenever they are within the marked area of the tagged animal, and black otherwise. Although the locations of the individuals are continually changing in time, the Movies indicate that the smaller the value of α or the larger the value of Z, the larger the number of animals present within the marked area of the tagged individual. As a larger number of individuals within an animal's marked area leads to a higher individual proximity, the Movies SV2 and SV3 indicate how the degree of gregariousness in a population of mobile individuals is affected by the degree of stigmergy and competition. Note that when $Z = 400$, the distance between adjacent lattice sites is smaller than when $Z = 9$, owing to a decrease in ρ. This makes the animals appear to move faster in the former case.

References

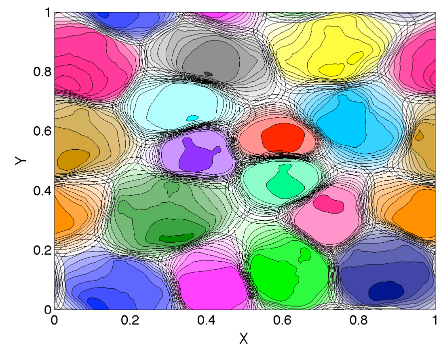
[1] Montroll EW, Weiss GH (1965) Random walks on lattices II. *J. Math. Phys.* 6:167–181.

[2] Gillespie DT (1976) General method for numerically simulating the stochastic time evolution of coupled chemical reactions. *J. Comput. Phys.* 22:403–434.

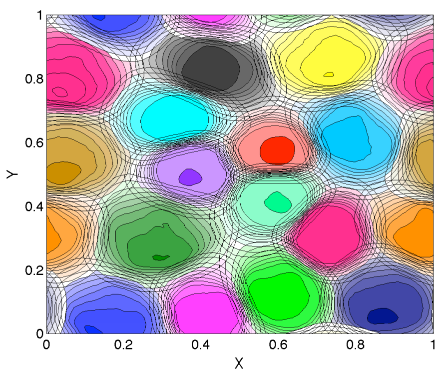
[3] Gillespie DT (1977) Exact stochastic simulation of coupled chemical reactions. *J. Phys. Chem.* 81:2340–2361.



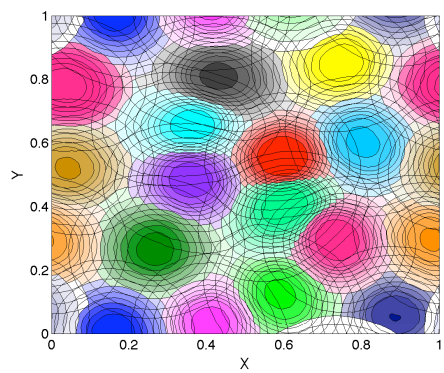
(a) Degree of stigmergy $\alpha = 100$.



(b) Degree of stigmergy $\alpha = 1$.



(c) Degree of stigmergy $\alpha = 0.1$.



(d) Degree of stigmergy $\alpha = 0.01$.

Figure S1: Utilization distribution reconstructed over a time equal to $2.5T$ for the entire set of individuals in a population with 16 individuals (density $\rho = 0.0016$) for different choice of the degree of stigmergy α and the competition parameter being $Z = 32$. In moving from panel (a) to (d), we progressively increase the stigmergy parameter, moving from a population where individuals nearly ignore one another in panel (a) to the opposite extreme, when individuals react strongly to foreign marks in panel (d). By sequentially looking at the panel (a)-(d) it is obvious that as α increases the animal home range overlap shrinks. The contour level values from the outer most to the inner most, when all present, are 10^{-4} multiplied, respectively, by the following factors: 1, 2, 4, 6, 8, 10, 12, 14, 20, 40, and 80.