Desert locust dynamics: Behavioral phase change and swarming

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The African Locust Schistocerca gregaria **has two interconvertible phases, solitary and gregarious. Individuals are repelled (attracted) by others depending on their solitary (gregarious) state, and crowding tends to bias conversion towards the gregarious form. Here we use nonlocal (integro-partial) differential equations to model the interplay of spatial dynamics and phase change dynamics to understand swarm formation. Steady state and linear stability analysis reveal conditions for the onset of a locust plague, characterized by mass transition to the gregarious form. A model reduction to describe the bulk dynamics enables quantification of the proportion of the population that will gregarize, and of the time scale for this to occur. Numerical simulations reveal clumping behavior and provide descriptions of the swarm structure.**

locust | phase change | swarm | gregarious | solitary

Abbreviations:

Outbreaks of the desert locust *Schistocerca gregaria* regularly afflict vast areas of northern Africa, the Middle East and southwest Asia. Depending on climate and vegetation conditions, billions of voracious locusts aggregate into destructive swarms that span areas up to a thousand square kilometers. A locust swarm can travel a few hundred kilometers per day, stripping crops and vegetation in its desolate path [1–4]. The latest locust plague in West Africa (2003–2005) severely disrupted agriculture, destroying \$2.5 billion in crops destined for both subsistence and export. Despite control efforts totalling \$400 million, loss rates escalated to 50% in certain regions [5, 6]. These numbers alone attest to the urgency of finding better ways to predict, manage, and control locust plague outbreaks.

Between plagues, locusts are mainly solitary creatures who live in arid regions and lay eggs in small breeding grounds lush with vegetation. Occasionally, resources are abundant enough to support numerous hatchings, leading to a high density of adults. Overcrowding at resource sites promotes a transition to a gregarious phase, in a self-reinforcing process. The available supply of vegetation and water at the breeding ground is eventually exhausted, and locusts migrate *en masse* to other locations in search for nourishment. Within the newly formed swarm, individuals maintain their cohesiveness via direct sensory communication, or via chemical and vibrational signaling [7–9]. Newly settled feeding grounds are also inevitably depleted, leading to several stop-and-go cycles of traveling locust bands. Outbreaks may be exacerbated in periods of drought, when large numbers of locusts congregate on the same breeding or feeding grounds [10].

Desert locusts are *phase polyphenic:* while sharing the same genotype, individuals may display different phenotypes [11, 12] which incorporate variations in morphology [13], coloration [14], reproductive features [15] and, most significantly, behavior [16, 17]. Behavior can change from a *solitary* state, in which locusts seek isolation, to a *gregarious* one, in which they are attracted to other (gregarious or solitary) individuals. Behavioral state is plastic [3, 12, 16] and strongly dependent on local population density: in sparse surroundings, a gregarious locust transforms into the solitary state [16] and vice–versa in crowded environments. This is the phenotypic change that – crucially – takes place when large numbers of locusts gather at a site, promoting a massive change from solitary to gregarious form and initiating a destructive swarm plague [18, 19].

Locust gregarization may be induced by visual or olfactory cues, but a most potent stimulus is tactile: the repetitive stroking of the femora of hind legs [16, 17, 20] is believed to function as a crowding indicator. The mechanosensory stimulation of leg nerves leads to subsequent serotonin cascades in the brain, and in turn to the onset of gregarious behavior [17, 20, 21]. Furthermore, contact with individuals coming from behind enhances the tendency of a stationary locust to move [22]. In the laboratory, it has been shown that the solitary to gregarious switch can be induced by rubbing a locust's hind leg for 5s per minute during a period of 4h [20]. Cessation of physical contact leads to a transition back to the solitary state after 4h.

There have been relatively few mathematical studies of locust behavior, especially of the switch between solitary and gregarious phases in a spatio-temporal framework. Both [23] and [24] studied the dynamics of rolling patterns formed by migrating locust groups. Data driven models include the self-propelled particle model of [25] where the observed transition between disordered to ordered locust movement was described via well-known physics paradigms [26]. A logistic map was introduced in [27] to describe population switching via a birth rate and a carrying capacity dependent on population density modulated by stochastic effects. None of the previous studies however, have focused on how an initially disperse, solitary locust population spontaneously transitions into an aggregated, gregarious one. The goal of this paper is to provide a mathematical description of such behavioral phase changes by taking into account the most relevant biological findings and by including relevant spatial features that cause locusts to clump or disperse.

OUR MAIN FINDING IS...

The model

As described above, locusts in a group are subject to attractive and/or repulsive forces based on combined sensory, chemical, and mechanical cues that affect their motion. Here we assume that such sensing is directionally isotropic, an assumption used in many models [31, 32] and a reasonable approximation for organisms receiving sensory input of a variety of types. Rather than tracking individual locusts, we consider a locust population density field $\rho(\mathbf{x}, t)$ moving at velocity $\mathbf{v}(\mathbf{x}, t)$. In the spirit of seminal work on continuum population models [33–35] this standard continuum approach provides us with analytical tools to characterize the formation process and structure of a swarm. Our framework builds on a generic swarm model that

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Reserved for Publication Footnotes

assumes a conservation law for ρ and a representation for $\mathbf{v}$ given by

$$\rho_t + \nabla \cdot (\rho \mathbf{v}) = 0, \quad \mathbf{v} = -\int_{\Omega} \nabla \mathbf{Q}(\mathbf{x}, \mathbf{x}')\rho(\mathbf{x}', t)\, d\mathbf{x}' \qquad \textbf{[1]}$$

where $\mathbf{x} = (x, y)$ (e.g., in 2D). Here, we model $\mathbf{v}$ as a convolution between the density $\rho(\mathbf{x}, t)$ and the social interaction field $Q(\mathbf{x}, \mathbf{x}')$ that describes the influence of the locust population at location $\mathbf{x}'$ on that at location $\mathbf{x}$. We use the notation $\mathbf{v} = -\nabla Q * \rho$ to denote the convolution in Eqn. 1 and assume that $Q(|\mathbf{x} - \mathbf{x}'|)$ is radially symmetric and depends only on the distance between $\mathbf{x}$ and $\mathbf{x}'$. Eqns. **[1]** have been extensively studied in one and two dimensions for many specific interaction choices [36–39]. Solutions generally include distinct regimes such as steady state swarms, spreading, and blow-up [28, 29, 36].

To adapt Eqns. **[1]** to biphasic desert locust swarm dynamics, we denote the density of solitary and gregarious locusts by $s(\mathbf{x}, t)$ and $g(\mathbf{x}, t)$, respectively, and the total density by $\rho = s + g$. We also include a density-dependent rate $f_1(\rho)$ to model the transition from the gregarious to the solitary state and $f_2(\rho)$ for the opposite switch. Our model thus reads

$$\dot{s} + \nabla \cdot (\mathbf{v}_s s) = -f_2(\rho)s + f_1(\rho)g, \qquad \textbf{[2a]}$$

$$\dot{g} + \nabla \cdot (\mathbf{v}_g g) = \quad f_2(\rho)s - f_1(\rho)g, \qquad \textbf{[2b]}$$

where the velocities are given by

$$\mathbf{v}_s = -\nabla(Q_s * \rho), \quad \mathbf{v}_g - \nabla(Q_g * \rho). \qquad \textbf{[3]}$$

These equations are complete once we specify the form of the solitary and gregarious social interaction fields Q_s and Q_g. Since solitary locusts are crowd-avoiding, we model Q_s as purely repulsive. Gregarious locusts, on the other hand, are assumed to be attracted to others, except for short distance repulsion due to excluded volume effects. Hence, we model Q_s and Q_g with the following Morse-type interactions

$$Q_s(\mathbf{x}) = R_s \mathrm{e}^{-|\mathbf{x}|/r_s}, \quad Q_g(\mathbf{x}) = R_g \mathrm{e}^{-|\mathbf{x}|/r_g} - A_g \mathrm{e}^{-|\mathbf{x}|/a_g}, \qquad \textbf{[4]}$$

where R_s, R_g, A_g are interaction amplitudes and r_s, r_g and a_g are interaction length scales. For cohesiveness to occur, the parameters in Q_g must be chosen in the parameter regime that leads to clumping, per the conditions stated in [8, 28, 30]. Specifically, we require $R_g a_g - A_g r_g > 0$ so that repulsion dominates at short length scales, and $A_g a_g^2 - R_g r_g^2 > 0$ so that attraction dominates at longer ones. We model $f_{1,2}(\rho)$ via Hill-type functions so that

$$f_1(\rho) = \frac{\delta_1}{1 + (\rho/k_1)^2}, \quad f_2(\rho) = \frac{\delta_2\,(\rho/k_2)^2}{1 + (\rho/k_2)^2}. \qquad \textbf{[5]}$$

Here, $\delta_{1,2}$ are maximal rates and $k_{1,2}$ are characteristic locust densities at which the transitions occur at half of their maximal values. These choices allow f_1 to be a decreasing function of ρ and f_2 to increase with ρ, saturating at δ_2. Our complete model thus is represented by Eqs. **[2]**-**[5]**. We analyze them on an infinite domain with initial conditions that specify $s(\mathbf{x}, 0)$ and $g(\mathbf{x}, 0)$. The model and our later analysis are easily adapted to finite a periodic domain (which is mathematically convenient) or to a finite domain with no-flux boundaries.

Biological Parameter Values

To estimate the phase change parameters in Eq. **[5]** we draw upon the experimental results of [20]. Since phase change between states take approximately four hours we estimate $\delta_1 = \delta_2 = 0.25\ \mathrm{h}^{-1}$. The critical density for gregarization is reported to be about 50 - 80 locusts /m^2. We assume that the solitarization process has the same critical density, and set $k_1 = k_2 \approx 65$ locusts /m^2. To estimate the social interaction length scale parameters in Eqs. **[4]**, we apply the results of [25, 40], which identify the "sensing range" of a locust as 0.14 m, and the "repulsion range" as 0.04 m, of the same order of magnitude as the approximately 0.08 m body length of a mature individual. For the gregarious phase we thus set the repulsion length scale at $r_g = 0.04$ m and the attractive one at $a_g = 0.14$ m, corresponding to the experimental sensing range. These choices agree with field observations where insect attraction typically occurs at longer length scales compared to repulsion. We also assume that solitary locusts are repelled from others at their sensing range, so that $r_s = 0.14$ m. These choices satisfy $r_g < a_g = r_s$ which we will assume for certain results in the remainder of this paper.

Finally, we estimate R_s, R_g, and A_g from explicit velocity computations. The speed of a locust when it is alone varies between 72–216 m/hr, depending on diet [40]. At the upper end, this is roughly 1 body length per second. When it is moving in a group, the speed varies in a tighter range of 144–216 m/hr [40]. To estimate R_s we imagine a hypothetical semi-infinite density field $\rho(x) = \rho_0 \mathrm{H}(x)$ where $\mathrm{H}(x)$ is the Heaviside function and $\rho_0 = 65$ locusts /m^2, the approximate critical density of a gregarious group. A solitary locust placed at the swarm's edge at the origin, should move to the left with maximal velocity $v_s^{max} = -216$ m/hr. We use the velocity definition Eq. **[3]** to write

$$v_s(0, 0) = -\partial_x \left\{ Q_s * \rho_0 \mathrm{H}(x) \right\}\big|_{(0,0)} = v_s^{max}, \qquad \textbf{[6]}$$

which we solve to find $R_s = 11.87$ locusts·m^2/hr. Similarly, a gregarious locust at the origin should move to the right with maximal velocity $v_g^{max} = 216$ m/hr, so

$$v_g(0, 0) = -\partial_x \left\{ Q_g * \rho_0 \mathrm{H}(x) \right\}\big|_{(0,0)} = v_g^{max}. \qquad \textbf{[7]}$$

A gregarious locust placed at the attraction length scale $a_g = 0.14$ m should also move to the right, but with a slower velocity which we take to be the minimal velocity in a crowd, $v_g^{min} = 144$ m/hr. Thus

$$v_g(-0.14, 0) = -\partial_x \left\{ Q_g * \rho_0 \mathrm{H}(x) \right\}\big|_{(-0.14,0)} = v_g^{min}. \qquad \textbf{[8]}$$

Together, these two conditions determine $R_g = 5.13$ locusts·m^2/hr and $A_g = 13.33$ locusts·m^2/hr.

Homogeneous steady states

For any set of initial conditions the mean locust density ρ_0 is known, and corresponds to the the total density at the homogeneous steady state. Accordingly, there is a family of homogeneous steady states parameterized by ρ_0. The corresponding solitary and gregarious steady state solutions arising from Eqs. **[2]** are

$$s_0 = \frac{\rho_0 \delta_1 k_1^2 (k_2^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}, \qquad \textbf{[9a]}$$

$$g_0 = \frac{\delta_2 \rho_0^3 (k_1^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}. \qquad \textbf{[9b]}$$

In the small ρ_0 limit these can be approximated as

$$s_0 \approx \rho_0 - \frac{\delta_2}{\delta_1 k_2^2}\rho_0^3, \quad g_0 \approx \frac{\delta_2}{\delta_1 k_2^2}\rho_0, \qquad \textbf{[10]}$$

so that the low-density steady state is composed mostly of solitary locusts. In the large ρ_0 limit, on the other hand,

$$s_0 \approx \frac{\delta_1 k_2^2}{\delta_2 \rho_0}, \quad g_0 \approx \rho_0 - \frac{\delta_1 k_2^2}{\delta_2 \rho_0}, \qquad \textbf{[11]}$$

so that the high-density steady state is composed mostly of gregarious insects. These estimates point to the nonmonotonicity of s_0 with respect to total density ρ_0. Further evidence of this relationship is given in Fig. 1 where s_0, g_0 are shown as functions of the total density ρ_0. To obtain the three sets of curves, we took a uniform distribution around each parameter $\{\delta_1, \delta_2, k_1, k_2\}$, centered at our biological estimates ($k_1 = k_2 = 65$ locusts /m^2 and $\delta_1 = \delta_2 = 0.25\ \mathrm{h}^{-1}$), with a range from 0.7 to 1.3 times these estimated values. We drew 10,000 sample parameter sets and plotted three pairs of curves, corresponding to 25, 50, and 75 percentile levels of the steady state value of s_0 (in blue) and g_0 (in green).

As noted, s_0 at first increases with ρ_0, as both solitary and gregarious locusts accumulate. At a critical total density ρ_c, s_0 reaches a maximum, whereas g_0 keeps monotonically increasing. From a biological point of view, this model prediction implies that homogeneous solitary groups can only exist up to ρ_c, beyond which gregarization dominates. The algebraic form of the phase change terms $f_{1,2}$ makes closed form expressions for the maximum difficult to obtain; however, for our biologically estimated parameters $k_1 = k_2 = k$ and $\delta_1 = \delta_2 = \delta$, the maximum solitary density is attained at $\rho_0 = k$ when $s_0 = g_0 = k/2$. See [REFERENCE TO APPROPRIATE SECTION OF SUPPLEMENTARY INFORMATION] for a calculation that incorporates detuning from these parameter assumptions.

Linear stability analysis

To determine conditions under which a uniformly spread locust population aggregates or disperses, we now study the stability of the steady state solution in Eqs. **[9a]** and **[9b]**. Consider small perturbations s_1, g_1 about the s_0, g_0 values and let

$$s(\mathbf{x}, t) = s_0 + s_1(\mathbf{x}, t), \quad g(\mathbf{x}, t) = g_0 + g_1(\mathbf{x}, t), \qquad \textbf{[12]}$$

which leads to $\rho(\mathbf{x}, t) = s_0 + g_0 + s_1(\mathbf{x}, t) + g_1(\mathbf{x}, t)$. Substituting Eqn. **[12]** into Eq. **[2]** under the assumptions $s_1 \ll s_0$ and $g_1 \ll g_0$ for all values of $\mathbf{x}$ and expanding to first order in the perturbations we obtain the linearized equations

$$\begin{aligned} \dot{s}_1 &= s_0 Q_s * \nabla^2 (s_1 + g_1) - A s_1 + B g_1, & \textbf{[13a]} \\ \dot{g}_1 &= g_0 Q_g * \nabla^2 (s_1 + g_1) + A s_1 - B g_1, & \textbf{[13b]} \end{aligned}$$

where

$$\begin{aligned} A &= f_2(\rho_0) + f_2'(\rho_0) s_0 - f_1'(\rho_0) g_0, & \textbf{[14a]} \\ B &= f_1(\rho_0) + f_1'(\rho_0) g_0 - f_2'(\rho_0) s_0. & \textbf{[14b]} \end{aligned}$$

Here, $A, B > 0$ for all $\rho_0 > 0$ since f_1 is a monotonically increasing function of ρ_0 and f_2 is a monotonically decreasing one. To further analyze the linearized equations, we Fourier expand the perturbations as

$$s_1(\mathbf{x}, t) = \sum_{\mathbf{q}} \mathcal{S}_{\mathbf{q}}(t) \mathrm{e}^{i\mathbf{q}\cdot\mathbf{x}}, \quad s_2(\mathbf{x}, t) = \sum_{\mathbf{q}} \mathcal{G}_{\mathbf{q}}(t) \mathrm{e}^{i\mathbf{q}\cdot\mathbf{x}}. \qquad \textbf{[15]}$$

For each perturbation wave number $\mathbf{q}$ the components $\{q_x, q_y\}$ may be physically interpreted as the inverse of typical length scales on which the perturbation occurs. The most unstable of these may be interpreted as the typical size of an emerging gregarious or solitary locust patch. We allow for an infinitely large domain so that there are no restrictionds on $\mathbf{q}$; on other domains with boundary conditions, $\mathbf{q}$ must be suitably restricted. Substituting the Fourier expansion of Eqn. **[15]** into Eqn. **[13]** yields ordinary differential equations for each Fourier mode amplitude. These are conveniently written in the matrix form as

$$\frac{d}{dt} \begin{pmatrix} \mathcal{S}_q \\ \mathcal{G}_q \end{pmatrix} = \mathbf{L}(q) \begin{pmatrix} \mathcal{S}_q \\ \mathcal{G}_q \end{pmatrix}, \qquad \textbf{[16a]}$$

$$\mathbf{L}(q) \equiv \begin{pmatrix} -s_0 q^2 \widehat{Q}_s(q) - A & -s_0 q^2 \widehat{Q}_s(q) + B \\ -g_0 q^2 \widehat{Q}_g(q) + A & -g_0 q^2 \widehat{Q}_g(q) - B \end{pmatrix}. \qquad \textbf{[16b]}$$

Here, $q = |\mathbf{q}|$ is the perturbation wave number, and $\widehat{Q}_{s,g}(a)$ are the Fourier transforms of the two dimensional social interaction potentials, respectively

$$\begin{aligned} \widehat{Q}_s(q) &= \frac{2\pi R_s r_s^2}{(1 + r_s^2 q^2)^{3/2}}, & \textbf{[17]} \\ \widehat{Q}_g(q) &= \frac{2\pi R_g r_g^2}{(1 + (r_g^2 q^2)^{3/2}} - \frac{2\pi A_g a_g^2}{(1 + a_g^2 q^2)^{3/2}}. & \textbf{[18]} \end{aligned}$$

The eigenvalues $\lambda_{1,2}(q)$ of $\mathbf{L}(q)$ can be written as

$$\lambda_1(q) = -q^2 \left[s_0 \widehat{Q}_s(q) + g_0 \widehat{Q}_g(q) \right], \quad \lambda_2 = -(A + B). \qquad \textbf{[19]}$$

The eigenvalue λ_2 is q-independent and negative since $A, B > 0$. Thus, the constant density steady state is stable if $\lambda_1(q) < 0$ for all admissible q. If $\lambda_1(q) > 0$ for some q, then the constant density steady state is unstable to perturbations of those wave numbers. The pivotal eigenvalue $\lambda_1(q)$ embodies all physically relevant parameters and is written in the most general form. [GO FOR IT! COULD WE CONSIDER REORGANIZING STARTING HERE? I WOULD PRESENT THE NUMERICAL RESULTS FIRST, SINCE THEY ARE GENERAL. I WOULD THEN DO THE ANALYTICAL STUFF, STARTING WITH THE PARAMETER EQUALITY ASSUMPTION. I WOULD MOVE ALL THE ANALYSIS LEADING UP TO EQ. 23 TO SUPLEMENTARY INFO, AND I WOULD INCLUDE THE EQ. 23 RESULT AND ITS DISCUSSION IN THE BODY.] In order to make analytical progress, we let $k_1 = k_2 = k$, $\delta_1 = \delta_2 = \delta$ and $r_s = a_g$, which follow from our biological assumptions. Later it will be useful to recall that within our parameter estimates $r_g < a_g$. Inserting these simplifications, we rewrite $\lambda_1(q)$ as

$$\lambda_1(q) = \frac{2\pi R_g \rho_0^3 r_g^2 q^2}{(h^2 + \rho_0^2)(1 + q^2 a_g^2)^{3/2}} \left[H(\rho_0) - h(q) \right] \qquad \textbf{[20]}$$

where

$$H(\rho_0) = \frac{\rho_0^2 A_g a_g^2 - k^2 R_s a_g^2}{R_g \rho_0^2 r_g^2}, \quad h(q) = \frac{(1 + q^2 a_g^2)^{3/2}}{(1 + q^2 r_g^2)^{3/2}}. \qquad \textbf{[21]}$$

Since $h(q) > 0$, for instability to occur we must require $H(\rho_0) > 0$, otherwise $\lambda_1(q)$ will always be negative. This necessary - but not sufficient - condition translates to $\rho_0^2 > k^2 R_s / A_g$. Let us now look more carefully at the terms inside the square brackets of Eqn. **[20]**. Since $r_g < a_g$, the function $h(q)$ is monotonically increasing. Hence, for $\lambda_1(q)$ to be positive, it is also necessary that $H(\rho_0)$ be at least greater than the minimum value of $h(q)$, attained at $q = 0$. Thus, a more stringent condition for instability is

$$H(\rho_0) > h(q = 0) = 1. \qquad \textbf{[22]}$$

Using the fact that $h(q \to \infty) = a_g^3 / r_g^3 > 1$ we can now distinguish three cases:

- if $H(\rho_0) < 1$ then $\lambda_1(q) < 0$ for all q and the homogeneous steady state is stable to perturbations of all wave numbers.
- if $1 \leq H(\rho_0) \leq a_g^3 / r_g^3$ then $\lambda_1(q)$ will have a single root at $q = q_*$ and instabilities in the homogeneous steady state will arise for perturbations with small wave numbers $q < q_*$, giving rise to large clusters of gregarious or solitary patches.
- if $H(\rho_0) > a_g^3 / r_g^3$ then $\lambda_1(q) > 0$ for all q and the homogeneous steady state is unstable to perturbations of any wave number.

The condition $H(\rho_0) > 1$ that guarantees instability can be rewritten as

$$\rho_0 > \left(\frac{R_s}{A_g - R_g (r_g / a_g)^2} \right)^{1/2} k. \qquad \textbf{[23]}$$

This inequality is a key result, and means that for sufficiently dense populations, uniform distributions are no longer stable and concentrated patches of locusts of various sizes may form. The instability condition may be considered an indicator of the locust plague, where patches of high density locust groups may arise in confined spaces causing much more damage to vegetation and crops than if uniform locust populations were spread over the entire available domain. Note that in order for the instability to occur, not only must the density ρ_0 be sufficiently large, but also the clumping condition introduced earlier that represents long range locust attraction, $A_g r_g^2 - R_g r_g^2 > 0$, must hold.

For our locust parameter choices, the condition in Eq. 22 implies that the homogeneous solution is unstable as long as $\rho_0 > 59.9$, close to the 50th percentile value of $\rho_0 = 57.5$ in Fig. 1, which is the left border of the grey region. [CHAD IS CONSIDERING: WHY AREN'T THEY CLOSER?] The vertical black dashed lines indicate the 25th and 75th percentile values for the onset of instability. Note that at the 50th percentile level, instability occurs before g_0 overtakes s_0 in value. This means that instability (and as we will later show, mass gregarization) can take place even when solitary locusts outnumber gregarious ones.

THESE DISCUSSIONS HAVE TO BE MERGED

Fig. 2 shows the most unstable wave number k_{max} as a function of ρ_0. This wavenumber characterizes the swarm size as it is first initiated. For low densities, the most unstable wavenumber is 0, indicating that large wavelength aggregation zones destabilize first. As ρ_0 increases, there is a sharp transition region in which k_{max} grows rapidly. Here, clusters of some finite size would be seen. We further observe that k_{max} levels to a plateau value. (As before, the three curves in Fig. 2 are the 25th, 50th, and 75th percentile values as parameters are varied). At the 50th percentile value the large ρ_0 asymptotic value of k_{max} is $k_{max} = 8.9$. **[GIVE UNITS AND INDICATE PREDICTED CLUSTER DIAMETERS.]**

We can now estimate the typical patch size d over which when the uniform population is unstable to perturbations by finding the most unstable wavelength q_{max} that maximizes $\lambda(q)$. We can thus identify $d \simeq 1/q_{max}$. We thus calculate $\lambda'(q)$ under the instability condition $H(\rho) > 1$ to find

$$\lambda'(q) = \frac{2\pi R_g \rho_0^3 r_g^2 q}{(h^2 + \rho_0^2)} \left[H \frac{2 - a_g^2 q^2}{(1 + a_g^2 q^2)^{5/2}} - \frac{2 - r_g^2 q^2}{(1 + r_g^2 q^2)^{5/2}} \right]. \quad \textbf{[24]}$$

To find q_{max} we set the above expression to zero $\lambda(q_{max} = 0)$. Note that at $q = 0$ the term in parenthesis in Eqn. **[24]** is given by $2(H(\rho_0) - 1) > 0$ due the instability condition. Furthermore, at $q = \sqrt{2}/a_g$ the same term is $2a_g^3(r_g^2 - a_g^2)/(a_g^2 + 2r_g^2)^{5/2} < 0$ since $r_g < a_g$. These two limits imply that $\lambda'(q_{max}) = 0$ for $q_{max} < \sqrt{2}/a_g$.

THIS IS A BIT IFFY:

Numerical estimates show that for the parameters at hand the maximum is obtained in the vicinity of $\sqrt{2}/a_g$ so we let $q_{max} \simeq \sqrt{2}/a_g - q_{sh}$ with $0 < q_{sh} \ll \sqrt{2}/a_g$. After expanding Eqn. **[24]** to leading orders and in the limit of large ρ_0 we find

$$q_{sh} \simeq \frac{9\sqrt{3}}{\sqrt{2} r_s} \frac{R_g}{A_g} \frac{r_g^2}{r_s^2} \quad \textbf{[25]}$$

we thus expect typical clusters to extend over the range

$$d \simeq \frac{\sqrt{r_s}}{2\left[1 - \frac{9\sqrt{3}}{2\sqrt{2}} \frac{R_g}{A_g} \frac{r_g^2}{r_s^2}\right]} \quad \textbf{[26]}$$

which, for the parameters at hand is rougly $d \simeq 0.11$ m.

CHAD: NOTE THAT FOR SURE, THIS IS CLOSE TO KMAX = 8.9 WHICH YOU ALSO HAD IN THE PAPER AND D = 1/8.9 = 0.11, BUT WHAT DOES THIS MEAN PHYSICALLY? OUR CLUSTERS ARE MADE OF A COUPLE OF LOCUSTS, SINCE THEY ARE TYPICALLY 0.08 METERS???

Bulk theory for segregated states

In simulations of **[2]**, we observe mass-balanced states in which gregarious and solitary locusts spatially segregate into regions with disjoint support. This means that in the given regions $\rho \approx s$ or $\rho \approx g$. We can approximate this behaviour with the following "bulk" state model reduction. For convenience, we define the total number of solitary and gregarious locusts, S and G respectively as

$$S = \int_\Omega s \, d\Omega, \quad G = \int_\Omega g \, d\Omega, \quad \textbf{[27]}$$

where Ω is our spatial domain, the total population mass is $M = S + G$, and mass fractions are given as

$$\phi_s = S/M, \quad \phi_g = G/M, \quad \phi_s + \phi_g = 1. \quad \textbf{[28]}$$

We assume that solitary locusts are spread throughout most of the domain Ω, covering an area denoted α_s, whereas gregarious locusts clumped in a region whose area we call α_g. (This area can be estimated from the gregarious potential; see **[4]**.) Then in these regions, local densities are approximately

$$s = S/\alpha_s, \qquad g = G/\alpha_g. \quad \textbf{[29]}$$

[THE SUBSEQUENT DERIVATION OF THE BULK MODEL SHOULD GO IN THE SI, PROBABLY. WE SHOULD KEEP THE ODE RESULT IN THE BODY OF THE PAPER.] If we now integrate Eqs. **[2]** over the domain the spatial terms vanish, and using $\rho \approx s$ or $\rho \approx g$ in the disjoint regions, we find

$$\int \dot{s} = -\int f_2(s)s + \int f_1(g)g = -\int \dot{g} \quad \textbf{[30]}$$

Further assuming that s, g are approximately constant in the regions of their support, the above equations can be rewritten as

$$\dot{S} \quad = -f_2(S/\alpha_s)S + f_1(G/\alpha_g)G = -\dot{G} \quad \textbf{[31]}$$

We can write the above in terms of the mass fractions ϕ_s, ϕ_g from **[28]**

$$\dot{\phi_s} = -f_2(M\phi_s/\alpha_s)\phi_s + f_1(M\phi_g/\alpha_g)\phi_g = -\dot{\phi_g} \quad \textbf{[32]}$$

Finally, substituting the definitions of f_1, f_2 from **[5]** we obtain

$$\dot{\phi_s} = -\frac{c_1 \phi_s^3}{1 + c_2 \phi_s^2} + \frac{c_3 \phi_g}{1 + c_4 \phi_g^2} = -\dot{\phi_g} \quad \textbf{[33]}$$

where the c_i reduced parameters are given by

$$c_1 = \frac{\delta_2 M^2}{\alpha_s^2 k_2^2}, \quad c_2 = \frac{M^2}{\alpha_s^2 k_2^2}, \quad c_3 = \delta_1, \qquad c_4 = \frac{M^2}{\alpha_g^2 k_1^2}. \quad \textbf{[34]}$$

The ODEs **[33]** can be used to compute the steady state fractions ϕ_s, ϕ_g. First, we consider the dynamics of this system. It is possible to reduce the bulk model to a single equation using $\phi_s = 1 - \phi_g$, though the result is is complicated. Another approach is to consider the large M limit, in which **[33]** becomes (to leading order)

$$\dot{\phi_s} = -\delta_2 \phi_s + \frac{c_3}{c_4 \phi_g} = -\dot{\phi_g} \quad \textbf{[35]}$$

Noting the values of the constants in **[35]**, and the fact that $0 \leq \phi_s, \phi_g \leq 1$ are dimensionless, we observe that the first term is of $O(1)$ whereas the second term is of $O(1/M^2)$. This means that, to leading order, for large M, the mass fraction of the solitary locusts decays exponentially in time with rate δ_1. This is based on the assumption of a segregated state, and would be expected to occur once segregation is nearly complete.

In short, for large M, the entire population will eventually become gregarious. Thus, the level ρ_0 that leads to instability is crucial. If the population is in the stable regime, mass gregarization can be avoided. As soon as the population shifts beyond the border of stability (at which $\phi_s \approx \phi_g$), gregarization of the entire group is inevitable.

Discussion

TEMPORARY.. TO BE WRITTEN AFTER RESULTS COLLECTED] A recent general review of models for aggregation based on attraction and repulsion is provided by [41]. Purely theoretical models for swarming include integro-differential equations [9]. Application of such ideas to flying locust swarms include [23] and [24].

As far as marching locusts, there have been a number of studies in which data collected in the laboratory and theoretical models have been combined. Most models concerned with alignment of locusts moving in a group [25, 42, 43] as well as proportion of locusts moving at a given time [22, 40] depending on treatments such as diet and denervation. The motivation in many of these models is to explore the transition between a disordered and a coherent marching group capable of great destructive force. [42] formulated an abstract model of collective motion, with repulsion and attraction that was then modified by [40] for locusts. The authors describe an individual-based model with locust in 2 states (stopped, moving) with stochastic transitions. They consider that locusts sense others in a spatial range and that this leads to an escape-dominated response with a parameter χ that reflects the strength of social interactions. They take a repulsive range of 2 cm and assume that the strength of the repulsion is χ_r=10cm/s^2. They write a Langevin equation for the speed and orientation of each locust. The main output of the model is proportion of individuals moving and mean group speed as a function of the group density. (The mean group speed varies sigmoidally (over the range 0-7 cm/sec) with density in the range of 0-100 locusts /m^2.

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Fig. 1. Uniform steady state (SS) levels of solitary locusts, s_0 (blue) and gregarious locusts, g_0 (green) as functions of the mean locust density ρ_0 on a log-log plot. The three curves represent the 25, 50 and 75 percentile of the SS value obtained using a uniform distribution centered at parameter values estimated from biological data, with a range $\pm 30\%$. The steady state is stable in the white region and unstable in the red region. Vertical dashed lines are 25th and 75th percentile values for onset of instability. At the 50th percentile, instability occurs before the value of g_0 overtakes s_0.

Fig. 2. Maximally unstable wavelength. At low densities, only the wavenumber $k = 0$ is unstable. Near the critical density, k_{max} increases rapidly to some constant value as the density increases. Three curves correspond to same percentile values as in Fig 1

.

[PUT IN SUPPLEMENT?] We can look for an approximate solution when $k_{1,2}$ and $\delta_{1,2}$ are each slightly detuned from equality. The basic idea is to expand everything in a power series in a small parameter ϵ. Take the formula for s_0 from Eq. 9a, differentiate it, and set it equal to zero to look for the critical point. This is our governing equation. Then expand everything in a power series. Without loss of generality, we can do this as

$$k_1 = k + \epsilon K, \quad k_2 = k - \epsilon K, \tag{36a}$$

$$\delta_1 = \delta + \epsilon\Delta, \quad \delta_2 = \delta - \epsilon\Delta, \tag{36b}$$

$$\rho_0 = \rho_{00} + \epsilon\rho_{01}. \tag{36c}$$

Substituting the power series into the equation for s' and solving at $\mathcal{O}(1)$ and $\mathcal{O}(\epsilon)$ yields

$$\rho_{00} = k, \quad \rho_{01} = K + \frac{\Delta k}{\delta}. \tag{37}$$

Thus, the maximum solitary density occurs at $\rho_0 \approx k + K + \Delta k/\delta$. Substituting back into the original formula for s_0 and keeping through $\mathcal{O}(\epsilon)$ gives us the maximum steady state solitary density, which is $s_{max} \approx k/2 + \Delta k/(2\delta)$.

I've checked how good this approximation is vis-a-vis the parameter sensitivities. That is, I've set $k = 65$ and $\delta = 0.25$. I've let the deviation K be as large as $0.3k$ and the deviation Δ be as large as 0.3δ – that is, I've considered up to 30% deviation from the mean values. Comparing the exact (numerical) values for the critical point's coordinates to the approximate values, you get up to 20% error for the ρ_0 coordinate and 15% error for the s coordinate.

Another interesting feature of the graph of s_0 and g_0 is that there is a point of equality between the two curves. By setting $s_0 = g_0$ in Eq. 9 and rejecting the trivial case $\rho_0 = 0$, one finds one positive solution, which is that $s_0 = g_0$ when

$$\rho_0 = \frac{k_1}{2\delta_2}\left(\delta_1 - \delta_2 + \sqrt{(\delta_1 - \delta_2)^2 + 4\delta_1\delta_2(k_2/k_1)^2}\right). \tag{38}$$

This solution is exact (no assumptions or approximations are necessary). In the white and grey region of Fig. 9, $s_0 > g_0$ at the 50th percentile, and the reverse is true in the pink region. The solid, vertical purple lines lines show the 25th and 75th percentile of the equality point.