

Desert locust dynamics: Behavioral phase change and swarming

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The African Locust *Schistocerca gregaria* is known to have 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 model the spatio-temporal interactions and transitions between the two phases using nonlocal (integro-partial) differential equations. We use steady state and linear stability analysis to characterize the conditions for onset of a locust “plague”, characterized by mass transition to the gregarious form. Model reduction to approximate “bulk” theory allows us to quantify the size and density of the emergent gregarious clusters, and numerical simulations provide qualitative 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 south-west 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 hatchlings, 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.

Desert locusts are *phase polyphenic*: while sharing the same genotype, individuals may display different phenotypes [10, 11] such as morphology [12], coloration [13], reproductive features [14] and most significantly behavior [15, 16]. The latter can change from *solitary* where locusts seek isolation to *gregarious* where they attract one another. Behavioral state is plastic [3, 11, 15] and strongly dependent on local population density: in sparse surroundings, a gregarious locust transforms into the solitary state [15] and vice-versa in crowded environments. It is this phenotype switch that takes place when large numbers of locusts gather at a site, promoting a massive change from solitary to gregarious form and initiating the swarm plague [17, 18].

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 [15, 16, 19] 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 [16, 19, 20]. Furthermore, contact with individuals coming from behind enhances the tendency of a stationary locust to move [21]. 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 [19]. 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 [22] and [23] studied the dynamics of rolling patterns formed by migrating locust groups. Data driven models include the self-propelled particle model of [24] where the observed transition between disordered to ordered locust movement was described via well-known physics paradigms [25]. A logistic map was introduced in [26] 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, a simplification used in many similar models [30, 31]. We consider a locust population density $\rho(\mathbf{x}, t)$ moving at velocity $\mathbf{v}(\mathbf{x}, t)$ rather than individual locusts. This standard continuum approach provides us with analytical tools that can be brought to bear on the problem of characterizing the initiation and structure of a swarm. Our framework is based on a common swarm model that includes a conservation law for ρ and a representation for \mathbf{v} given by

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

Reserved for Publication Footnotes

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 [32–35]. Solutions generally include distinct regimes such as steady state swarms, spreading, and blow-up [27, 28, 32].

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

$$\dot{s} + \nabla \cdot (v_s s) = -f_2(\rho)s + f_1(\rho)g, \quad [2a]$$

$$\dot{g} + \nabla \cdot (v_g g) = f_2(\rho)s - f_1(\rho)g, \quad [2b]$$

where the velocities are given by

$$v_s = -\nabla(Q_s * \rho), \quad v_g = -\nabla(Q_g * \rho). \quad [3]$$

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 repulsions due to excluded volume effects. Hence, we let Q_s and Q_g be described by the following Morse-type interactions

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

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 so called “clumping regime”, per the conditions stated in [8, 27, 29]. 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 $f_{i=1,2}(\rho)$ via Hill-type functions so that

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

Here, $\delta_{i=1,2}$ are maximal rates and $k_{i=1,2}$ 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 Eqns. [2]–[5]. We analyze them in 1D and 2D, with appropriate boundary conditions in a finite domain and with initial conditions that specify $s(\mathbf{x}, 0)$ and $g(\mathbf{x}, 0)$.

Biological Parameter Values

In order to estimate the parameters in Eq. [5] we draw upon the experimental results of [19]. Since phase changes between states take approximately four hours we estimate $\delta_1 = \delta_2 = 0.25 \text{ h}^{-1}$. 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 $k_1 = k_2 \approx 65 \text{ locusts}/\text{m}^2$. To estimate the social interaction parameters in Eqns. [4], we apply instead the results of [24, 36], who 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 $r_g = 0.04 \text{ m}$ and the attractive one at $a_g = 0.14 \text{ m}$ corresponding to the experimental sensing range. These choices are in agreement with field

observations where attraction typically occurs at longer length scales compared to repulsion. We also assume that solitary locusts tend to repel others at their sensing range so that $r_s = 0.14 \text{ m}$. Due to these choices, in the remainder of this paper we will often be working under the assumption that $r_g < a_g = r_s$.

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 [36]. 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 [36]. To estimate R_s we imagine a hypothetical semi-infinite density field $\rho(x) = \rho_0 H(x)$ where $H(x)$ is the Heaviside function and $\rho_0 = 65 \text{ locusts}/\text{m}^2$, 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 $v_s^{max} = -216 \text{ m/hr}$. We use the velocity definition Eq. [3] to write

$$v_s(0, 0) = -\partial_x \{Q_s * \rho_0 H(x)\} \Big|_{(0,0)} = v_s^{max}, \quad [6]$$

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

$$v_g(0, 0) = -\partial_x \{Q_g * \rho_0 H(x)\} \Big|_{(0,0)} = v_g^{max}. \quad [7]$$

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

$$v_g(-0.14, 0) = -\partial_x \{Q_g * \rho_0 H(x)\} \Big|_{(-0.14,0)} = v_g^{min}. \quad [8]$$

Together, these two conditions determine $R_g = 5.13 \text{ locusts} \cdot \text{m}^2/\text{hr}$ and $A_g = 13.33 \text{ locusts} \cdot \text{m}^2/\text{hr}$.

Homogeneous steady states

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

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

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

In the small ρ_0 limit these can be approximated as

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

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

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

so that the high-density steady state is composed mostly of gregarious insects. These estimates already point to the nonmonotonicity of s_0 with total density. 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 $\{\delta_1, \delta_2, k_1, k_2\}$ parameter, centered at our biological estimates ($k_1 = k_2 = 65 \text{ locusts}/\text{m}^2$ and $\delta_1 = \delta_2 = 0.25 \text{ h}^{-1}$), 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. While for the chosen functions $f_{i=1,2}$, closed form expressions for the maximum cannot easily be obtained, for the biologically estimated parameters of this work, $k_1 = k_2 = k$ and $\delta_1 = \delta_2 = \delta$, we find that the maximum solitary density is attained at $\rho_0 = k$ when $s_0 = g_0 = k/2$.

Linear stability analysis

In this section we study the stability of the steady state solution in Eqs. [9a] and [9b], to determine under what conditions uniformly spread locust populations aggregate or disperse, creating local clusters or vacancies. We thus consider small perturbations s_1, g_1 about the s_0, g_0 values and let

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

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 $g_1 \ll g_0$ and expanding to first order in the perturbations we obtain the linearized equations

$$\dot{s}_1 = s_0 Q_s * \nabla^2 (s_1 + g_1) - A s_1 + B g_1, \quad [13a]$$

$$\dot{g}_1 = g_0 Q_g * \nabla^2 (s_1 + g_1) + A s_1 - B g_1, \quad [13b]$$

where

$$A = f_2(\rho_0) + f'_2(\rho_0)s_0 - f'_1(\rho_0)g_0, \quad [14a]$$

$$B = f_1(\rho_0) + f'_1(\rho_0)g_0 - f'_2(\rho_0)s_0. \quad [14b]$$

and where $A, B > 0$ for all $\rho_0 \neq 0$ 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

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

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 restrictions on \mathbf{q} . Thus, upon substituting the Fourier expansion of Eqn. [15] into Eqn. [13] we find a set of ordinary differential equations for each Fourier mode amplitude. These are conveniently written in the following matrix form

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

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

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

$$\widehat{Q}_s(q) = \frac{2\pi R_s r_s^2}{(1 + r_s^2 q^2)^{3/2}}, \quad [17]$$

$$\widehat{Q}_g(q) = \frac{2\pi R_g r_g^2}{(1 + (r_g^2 q^2)^{3/2})} - \frac{2\pi A_g a_g^2}{(1 + a_g^2 q^2)^{3/2}}. \quad [18]$$

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

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

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 $\lambda_1(q) \geq 0$ 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. 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

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

where

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

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

$$H(\rho_0) > h(q=0) = 1. \quad [22]$$

Using the fact that $h(q \rightarrow \infty) = a_g^3 / r_g^3 > 1$ 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

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

The above inequality is one of the most important results of this paper and states that for sufficiently large locust densities uniform distributions are no longer stable and concentrated patches of locusts of various sizes may form. In this work we do not include descriptions of vegetation or crops, but 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 than if uniform locust populations were spread over the entire available domain. Note that in order for the instability to occur not only the density has to be large enough, but also the ‘‘clumping condition’’ introduced earlier and that represents long range locust attraction, $A_g r_g^2 - R_g r_g^2 > 0$, must hold.

For the locust parameter choices specified in this work, Eq. refeq: homogeneous solution is instability 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.

Fig. 2 shows the most unstable wave number k_{max} as a function of ρ_0 . This wavenumber would be characterize the cluster diameter of the swarm as it is first initiated. **[BRIEFLY EXPLAIN HOW OBT'D]**. 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.]**

Typical locust patch size

We can now estimate the typical locust patch size d 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

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

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

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

we thus expect typical clusters to extend over the range

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

which, for the parameters at hand is roughly $d \simeq 0.11$ 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

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

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

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

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

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

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

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

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

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

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

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

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

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

where the c_i reduced parameters are given by

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

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

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

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. 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. This implies that the level ρ_0 that leads to instability is crucial. If the state of 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 $\phi_s \approx \phi_g$), there is no avoiding the gregarization of the entire group.

Discussion

TEMPORARY.. TO BE WRITTEN AFTER RESULTS COLLECTED] A recent general review of models for aggregation based on attraction and repulsion is provided by [37]. Purely theoretical models for swarming include integro-differential equations [9]. Application of such ideas to flying locust swarms include [22] and [23].

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 [24, 38, 39] as well as proportion of locusts moving at a given time [21, 36] 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. [38] formulated an abstract model of collective motion, with repulsion and attraction that was then modified by [36] 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 $\chi_r=10\text{cm/s}^2$. 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 /m².)

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References

- Kennedy JS (1951) The migration of the desert locust (*Schistocerca gregaria* Forsk). *Proc Roy Soc Lond B* 235:163–290.
- Albrecht FO (1967) Les grands problèmes de la biologie, in *Polymorphisme phasaire et biologie des acridiens migrants* (Masson, Paris).
- Uvarov B (1977) *Grasshoppers and locusts* (Cambridge Univ Press, London) Vol. 2.
- Rainey RC (1989) *Migration and Meteorology: Flight Behavior and the Atmospheric Environment of Locusts and other Migrant Pests*, Oxford Science Publications (Clarendon Press, Oxford).
- Bell M (2005) The 2004 desert locust outbreak. *Bull Am Meteor Soc* 86:S60.
- Brader L, et al. (2006) Towards a more effective response to desert locusts and their impacts on food security, livelihoods and poverty: Multilateral evaluation of the 2003–05 desert locust campaign, (United Nations Food and Agriculture Organization), Technical report.
- Breder CM (1954) Equations descriptive of fish schools and other animal aggregations. *Ecol* 35:361–370.
- D’Orsogna MR, Chuang YL, Bertozzi AL and Chayes L (2006) Self-propelled particles with soft-core interactions: patterns, stability and collapse. *Phys Rev Lett* 96:104302.
- Mogilner A, Edelstein-Keshet L (1999) A non-local model for a swarm. *J Math Biol* 38:534–570.
- Applebaum SW, Heifetz Y (1999) Density-dependent physiological phase in insects. *Ann Rev Entomol* 44:317–341.
- Pener MP, Simpson SJ (2009) Locust phase polyphenism: An update. *Adv Insect Physiol* 36:1 – 272.
- Dirsh VM (1953) Morphometric studies on phases of the desert locust (*Schistocerca gregaria* Forskal. *Antilocust Bull* 16:1–34.
- Islam MS, Roessingh P, Simpson S J and McCaffery AR (1994b) Parental effects on the behavior and coloration of nymphs of the desert locust *Schistocerca gregaria*. *J Insect Physiol* 40:173–181.
- Schmidt GH and Albutz R (1999) Identification of solitary and gregarious populations of the desert locust, *Schistocerca gregaria*, by experimental breeding. *Entomol Gen* 24:161–175.
- Simpson SJ, McCaffery AR, Hagele BF (1999) A behavioral analysis of phase change in the desert locust. *Biol Rev* 74:461–480.
- Rogers S, et al. (2003) Mechanosensory-induced behavioural gregarization in the desert locust *Schistocerca gregaria*. *J Exp Bio* 206:3991–4002.
- Despland E, Collett M, Simpson S (2000) Small-scale processes in desert locust swarm formation: how vegetation patterns influence gregarization. *Oikos* 88:652–662.
- Collett M, Despland E, Simpson S, Krakauer D (1998) Spatial scales of desert locust gregarization. *Proc Natl Acad Sci* 95:13052.
- Simpson SJ, Despland E, Hagele BF, Dodgson T (2001) Gregarious behavior in desert locusts is evoked by touching their back legs. *Proc Natl Acad Sci* 98:3895–3897.
- Anstey ML, Rogers SM, Ott SR, Burrows M, Simpson SJ (2009) Serotonin mediates behavioral gregarization underlying swarm formation in desert locusts. *Science* 323:627–630.
- Bazazi S, Buhl J, Hale JJ, Anstey ML, Sword GA, Simpson SJ, Couzin ID (2008) Collective motion and cannibalism in locust migratory bands. *Curr Biol* 18:735–739.
- Edelstein-Keshet L, Watmough J, Granbaum D (1998) Do travelling band solutions describe cohesive swarms? An investigation for migratory locusts. *J Math Bio* 36:515–549.
- Topaz CM, Bernoff AJ, Logan S, Toolson W (2008) A model for rolling swarms of locusts. *Eur Phys J Spec Top* 157:93–109.
- Buhl J, Sumpter DJT, Couzin ID, Hale JJ, Despland E, Miller ER, Simpson SJ (2006) From disorder to order in marching locusts. *Science* 312:1402.
- Czirok, A et al (1995) Novel type of phase transition in a system or self-driven particles. *Phys Rev Lett* 75:1226–1229.
- Holt J, Cheke R (1996) Models of desert locust phase changes. *Ecol Model* 91:131–137.
- Leverentz AJ, Topaz CM and Bernoff AJ (2009) Asymptotic dynamics of attractive-repulsive swarms. *SIAM J Appl Dyn Sys* 8:880–908.
- Bernoff AJ, Topaz CM (2011) A primer of swarm equilibria. *SIAM J Appl Dyn Sys* 10:212–250.
- Chuang, YL, D’Orsogna MR, Marthaler D, Bertozzi A, Chayes L, (2007) State transitions and the continuum limit for interacting, self-propelled particles. *Phys D* 232:33–51.
- Eftimie R, de Vries G, Lewis M A, Lutscher F (2007) Modeling group formation and activity patterns in self-organizing collectives of individuals. *Bull Math Biol* 69:1537–1565.
- Partan SR, Marler P, (2005) Issues in the classification of multimodal communication signals. *Am Nat* 166:231–245.
- Bertozzi AL, Laurent T, (2007) Finite time blow up of solutions of an aggregation equation in R^n . *Comm Math Phys* 274:717–735
- Bodnar M, Velasquez JLL, (2005) Derivation of macroscopic equations for individual cell-based models: a formal approach. *Math Meth Appl Sci* 28:1757–1779.
- Bodnar M, Velasquez JLL, (2006) An integro-differential equation arising as a limit of individual cell-based models. *J Diff Eq* 222:341–380.
- Topaz CM, Bertozzi AL, (2004) Swarming patterns in a two-dimensional kinematic model for biological groups. *SIAM J Appl Math* 65:152–174.
- Bazazi S, Romanczuk P, Thomas S, Schimansky-Geier L, Hale JJ, Miller GA et al. (2011) Nutritional state and collective motion: from individuals to mass migration. *Proc Roy Soc B* 278:356-363
- Schellinck J, White T (2011) A review of attraction and repulsion models of aggregation: Methods, findings and a discussion of model validation. *Ecol Mod* 222:1897–1911
- Romanczuk P, Couzin I, Schimansky-Geier L (2009) Collective motion due to individual escape and pursuit response. *Phys Rev Lett* 102:10602.
- Yates AC, Erban R, Escudero C, Couzin ID, Buhl J, Kevrekidis IG et al (2009) Inherent noise can facilitate coherence in collective swarm motion. *Proc Natl Acad Sci* 106:5464–5469.

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

$$k_1 = k + \epsilon K, \quad k_2 = k - \epsilon K, \quad [36a]$$

$$\delta_1 = \delta + \epsilon \Delta, \quad \delta_2 = \delta - \epsilon \Delta, \quad [36b]$$

$$\rho_0 = \rho_{00} + \epsilon \rho_{01}. \quad [36c]$$

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

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

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

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

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 show the 25th and 75th percentile of the equality point.