

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. Here we model the spatio-temporal dynamics and transitions between these two phases. [ABSTRACT TO BE DONE LATER].

locust | phase change | gregarious | solitary

Abbreviations:

A recent locust outbreak in Africa from 2003 - 2005 destroyed \$2.5 billion in crops and cost an additional \$400 million in control efforts, with crop loss rates nonetheless reaching 50% in some regions [1, 2]. The principal perpetrator of many such outbreaks is the desert locust *Schistocerca gregaria*. These insects can form devastating swarms comprising billions of individuals, covering thousands of kilometers of ground area, and traveling tens of miles or more each day [3, 4, 5, 6]. Locust swarms are a perplexing humanitarian problem. Points to include (need references for these):

- Many developing countries must rely on heavy irrigation to make their land arable.
- Consequently, food becomes concentrated in a small area that locusts congregate to, which then contributes to swarming behavior.
- Desert locusts wreak serious havoc on crops and simultaneously threaten the livestock that must now compete with them for food.
- Famine thus results.

Crucially, desert locusts are *phase polyphenic*, meaning that individuals of the same genotype display more than one phenotypic form depending on external influences [7, 8]. For desert locusts, a crucial phenotypic difference is behavior. Individuals usually exist in the *solitary* behavioral phase and seek isolation; *gregarious* individuals, however, are attracted to others. Behavioral phase is tremendously plastic [5, 9, 8], and the most important mediating external influence is local population density. In sufficiently sparse surroundings a gregarious locust eventually acquires the crowd-avoiding preferences of a solitary one [9]. Conversely, in crowded surroundings, a solitary locust develops attractive behavior. This can occur when resource scarcity forces locusts to gather at nutritional sources, overriding their solitary tendency.

At a more mechanistic level, experimentalists have uncovered several types of stimuli responsible for gregarization, including visual, olfactory, and tactile. However, it is tactile stimulus that is most effective in inducing gregarization, and more specifically, stimulation of the outer face of the insects' hind femora [9, 10, 11]. Areas of the body such as the mouth, face, and abdomen are often self-stimulated by locusts during common behaviors such as walking, feeding, and grooming, and thus should not induce phase change [10]. The hind femora, however, are touched only by other insects, and it is plausible that the frequency of touching increases in crowds. Mechanosensory stimulation of nerves on the hind femora cause a cascade of serotonin in the brain, leading to gregarious behavior [10, 11, 12].

Patchy clumps of vegetation that lead to crowding of locusts also enhance their levels of activity and induce them to become gregarious [13]. (This was often quantified as a correlation between the fractal dimension of the vegetation and the locust behaviour [14]. Contact or sight of locusts coming from behind enhances the tendency of a

locust to move [15]. A transition from solitary to gregarious type can be evoked by rubbing the hind leg of a locust for 5 sec every 60 sec during a period of 4 hrs [10]. Leaving a gregarious locust on its own (unstimulated) for 4 hours results in a transition back to solitary.

There have been relatively few mathematical studies of locusts. Both [16] and [17] constructed models for the rolling pattern formed by flying locust groups. Work in [18] describes locust population density with the logistic map (with no spatial dependence) and models phase change via a birth rate and a carrying capacity that depend on population density and on stochastic effects. Work in [19] describes locusts within a confined arena using a self-propelled particle model similar to the seminal one [20] in which the velocity of every particle comes from averaging the velocities of neighboring particles within a fixed interaction radius (plus a small amount of noise).

It is of critical importance to understand how an initially dispersive, solitary population transitions to an aggregated, gregarious one. Thus, our goal in this paper is to model and understand the interplay of the phase change dynamics that cause locusts to gregarize or solitarize according to their local population density, and the spatial dynamics that cause locusts to clump or disperse depending on their behavioral phase.

Our mathematical framework follows the swarm modeling approach taken in, e.g., [21, 22]. A key element in swarms is social interaction. Social forces such as attraction and repulsion [23, 24] result when animals communicate directly by sound, sight, smell or touch, or indirectly via chemicals, vibrations, or other signals. A given communication may be unidirectional (e.g., narrow sight) or omnidirectional (e.g. hearing). Many organisms process a combination of inputs, which effectively results in omnidirectional communication [25, 26]. Modelers commonly assume that social interactions are pairwise, and that the effect of multiple organisms on a given one is given by superposition. Consider a swarm that is well-described by a continuum density $\rho(\mathbf{x}, t)$ and subject only to social interactions. A simple model is

$$\rho_t + \nabla \cdot (\rho \mathbf{v}) = 0, \quad \mathbf{v} = -\nabla Q * \rho. \quad [1]$$

Here, ρ is the population density, and the velocity \mathbf{v} is determined via a convolution (denoted by the asterisk). More explicitly,

$$\mathbf{v} = \int_{\Omega} -\nabla Q(\mathbf{x} - \mathbf{y}) \rho(\mathbf{y}, t) d\mathbf{y}, \quad [2]$$

where Q is a social interaction potential describing the social influence of the population at location \mathbf{y} on that at location \mathbf{x} . If

Reserved for Publication Footnotes

sensing is omnidirectional then \mathbf{Q} has the appropriate symmetry. Eq. (1) has been studied in [27, 28, 29] for specific choices of K , and in a two-dimensional setting in [30]. More generally, [21] showed that (1) manifests at least three different asymptotic behaviors, namely spreading, steady state, and blow-up. The compactly supported steady states, which may include jump discontinuities at the swarm's edges, are studied in depth in [22] in one spatial dimension.

The model that we presently consider extends (1) in two ways. First, it couples together two density fields which each obey their own (different) social interaction potential. Second, it incorporates reaction terms, so that the model is no longer purely advective. Our primary results are as follows... (need to complete once paper is finished).

The rest of this paper is organized as follows... (need to complete once paper is finished).

The model

Consider a spatial domain Ω . Let $s(\mathbf{x}, t)$ represent the density of solitary locusts, and $g(\mathbf{x}, t)$ the density of gregarious ones. The model equations are

$$\dot{s} + \nabla \cdot (v_s s) = -f_2(\rho)s + f_1(\rho)g, \quad [3a]$$

$$\dot{g} + \nabla \cdot (v_g g) = f_2(\rho)s - f_1(\rho)g. \quad [3b]$$

Define the total density

$$\rho = s + g. \quad [4]$$

Assume that velocities arise from pairwise, superposed social interactions, and model them as

$$v_s = -\nabla(Q_s * \rho), \quad v_g = -\nabla(Q_g * \rho). \quad [5]$$

Since solitary locusts avoid crowds, they should display social repulsion. Gregarious locusts should display attraction coupled with short range repulsion, in order to form finite aggregations. The solitary potential Q_s and the gregarious potential Q_g are

$$Q_s(\mathbf{x}) = R_s \exp(-|\mathbf{x}|/r_s), \quad Q_g(\mathbf{x}) = R_g \exp(-|\mathbf{x}|/r_g) - A_g \exp(-|\mathbf{x}|/a_g). \quad [6]$$

The parameters in $Q(g)$ must be chosen in the clumping regime, per the conditions stated in [21].

Now consider the density dependent rates of phase change. The solitarization rate f_1 should be high when local density is low, and should approach zero when density is high. Conversely, the gregarization rate f_2 should approach zero when local density low, and should be significant when density is high. Adopt the functional forms

$$f_1(\rho) = \frac{\delta_1}{1 + (\rho/k_1)^2}, \quad f_2(\rho) = \frac{\delta_2 (\rho/k_2)^2}{1 + (\rho/k_2)^2}. \quad [7]$$

Parameter Values

The African locust *Schistocerca gregaria* has body size of up to 7-8cm. A recent paper by Bazazi et al [31] gives many parameters that are directly useful in our model. The authors state that the speed of a locust when it is alone varies from 2 to 6 cm/sec depending on diet. At the upper end, this is roughly 1 body length (BL) per second. When it is moving in a group, the speed varies in a tighter range of 4-6 cm/sec. The critical density for the onset of collective motion is given in the range of 50 to 80 locusts /m². Further, according to Bazazi et al [31] and [19], the sensing range of a locust is 14 cm, and

the repulsion range is 4 cm, which coincides roughly with the body size of the locust.

We used these parameters as follows: We used the experiments in [10] to infer that the rate of transition from gregarious to solitary and vice versa is 1 per 4 hours, i.e. $\delta_1 \approx \delta_2 \approx 0.25h^{-1}$. We converted the critical area-density to a linear (1D) equivalent, obtaining $\rho_{crit} \approx \sqrt{50}$ to $\sqrt{80}$ which gives $\rho_{crit} \approx 7$ to 9 individuals per meter. We thus took $k_1, k_2 \approx 8$ locusts per meter as typical (1D) locust density level at which 1/2-max transition rates take place. We took the value of the repulsion ranges to be $r_s = r_g = 4\text{cm} = 0.04\text{m}$, and the range of attraction (for the gregarious locust form) as $a_g = 14\text{cm} = 0.14\text{m}$.

In order to obtain estimates for the magnitudes of the Morse potential terms R_s, R_g, A_g (for the repulsive and attractive parts of each potential) we made the following ansatz: We assumed that any locust at $x = 0$ in a density field $\rho = Heaviside(x)$ would move away due to repulsion at rate $v = -\nabla Q_s * \rho = 6\text{cm/sec} = 216\text{m/hr}$. Evaluating the integral and solving for R_s leads to $R_s = [\text{insert value}]$. We similarly assumed that a gregarious locust at $x = 0$ in a density field $\rho(x) = Heaviside(x - a_g)$ (i.e. with a group just at the edge of its sensing range) would move in the direction of that group with speed $v \approx 4\text{cm/sec} = [??]$. Combining the two equations for R_g and A_g obtained thereby, we got []. **THE LATTER PART OF THIS NEEDS RETHINKING AND REVISION**

Steady states and linear stability

There is a family of homogeneous steady states parameterized by the total homogeneous density ρ_0 . For any given ρ_0 , the homogeneous steady state is

$$s_0 = \frac{\rho_0 \delta_1 k_1^2 (k_2^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}, \quad g_0 = \frac{\delta_2 \rho_0^3 (k_1^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}. \quad [8]$$

In the small ρ_0 limit,

$$s_0 \approx \rho_0 - \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3, \quad g_0 \approx \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3. \quad [9]$$

and thus the low-density steady state is composed mostly of solitary locusts. In the large ρ limit,

$$s_0 \approx \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad g_0 \approx \rho_0 - \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad [10]$$

and thus the high-density steady state is composed mostly of gregarious locusts.

We now calculate the linear stability of the homogeneous steady state.

Let

$$s(\mathbf{x}, t) = s_0 + s_1(\mathbf{x}, t), \quad g(\mathbf{x}, t) = g_0 + g_1(\mathbf{x}, t). \quad [11]$$

Here, s_1 and g_1 are perturbations to the steady state. Also define

$$\rho(\mathbf{x}, t) = \rho_0 + \rho_1(\mathbf{x}, t) = s_0 + g_0 + s_1(\mathbf{x}, t) + g_1(\mathbf{x}, t). \quad [12]$$

Substitute (11) and (12) into (3), assume the perturbations s_1 and g_1 are small, i.e., $\mathcal{O}(\epsilon)$, and Taylor expand through $\mathcal{O}(\epsilon)$ to 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

$$A = f_2(\rho_0) + f_2'(\rho_0) s_0 - f_1'(\rho_0) g_0 \quad [14a]$$

$$B = f_1(\rho_0) + f_1'(\rho_0) g_0 - f_2'(\rho_0) s_0. \quad [14b]$$

Since f_1 is monotonically decreasing and f_2 is monotonically increasing, $f_1'(\rho_0) < 0$ and $f_2'(\rho_0) > 0$ (excluding the trivial possibility $\rho_0=0$). Hence, $A, B > 0$.

To further analyze the equations, Fourier expand the perturbations as

$$s_1(\mathbf{x}, t) = \sum_{\mathbf{k}} S_{\mathbf{k}}(t) \exp i\mathbf{k} \cdot \mathbf{x}, \quad s_2(\mathbf{x}, t) = \sum_{\mathbf{k}} G_{\mathbf{k}}(t) \exp i\mathbf{k} \cdot \mathbf{x}. \quad [15]$$

The admissible wave vectors \mathbf{k} depend on the chosen domain Ω . In the event that $\Omega = \mathbb{R}^n$ then all \mathbf{k} are admissible (per the Fourier transform). Substituting into (13) yields a set of ordinary differential equations for each Fourier mode amplitude. These are conveniently written in matrix form. Dropping the subscripts on S and G for simplification of notation, we have

$$\frac{d}{dt} \begin{pmatrix} S \\ G \end{pmatrix} = \mathbf{L}(k) \begin{pmatrix} S \\ G \end{pmatrix}, \quad \mathbf{L}(k) \equiv \begin{pmatrix} -s_0 k^2 \widehat{Q}_s(k) - A & -s_0 k^2 \widehat{Q}_s(k) + B \\ -g_0 k^2 \widehat{Q}_g(k) + A & -g_0 k^2 \widehat{Q}_g(k) - B \end{pmatrix}. \quad [16]$$

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

$$\widehat{Q}_s(k) = 2 \frac{R_s r_s}{1 + (r_s k)^2}, \quad \widehat{Q}_g(k) = 2 \left[\frac{R_g r_g}{1 + (r_g k)^2} - \frac{A_g r_a}{1 + (r_a k)^2} \right]. \quad [17]$$

The eigenvalues of $\mathbf{L}(k)$ are

$$\lambda_1(k) = -k^2 \left[s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) \right], \quad \lambda_2 = -(A + B). \quad [18]$$

The eigenvalue λ_2 is negative since $A, B > 0$. Thus, the constant density steady state is stable if $\lambda_1(k) < 0$ for all admissible k . If $\lambda_1(k) > 0$ for some k , then the constant density steady state is unstable to perturbations of those wave numbers. Factoring out a power of $-k^2$, the instability condition, then, is

$$s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) < 0. \quad [19]$$

Crucially, this condition does not depend on the functions $f_{1,2}$ which describe behavioral phase change. It only depends on the social interaction potentials and on the relative amounts of solitary and gregarious locusts.

Bulk theory for segregated states

In simulations of (3), we observe mass-balanced states in which gregarious and solitary locusts spatially segregate. We attempt a rough calculation of such solutions. The solitary locusts are spread throughout most of the domain Ω , covering an area we refer to as α_s . The gregarious locusts are concentrated in a clump whose area we call α_g , which may be estimated from the gregarious potential; see (6). For convenience, define the total number of solitary locusts and gregarious locusts,

$$S = \int_{\Omega} s \, d\Omega, \quad G = \int_{\Omega} g \, d\Omega, \quad [20]$$

and the total population mass $M = S + G$.

The local densities that solitary and gregarious locusts sense in their respective patches are

$$s = S/\alpha_s, \quad g = G/\alpha_g. \quad [21]$$

For a segregated state at mass balance, the number flux of gregarious locusts becoming solitarized per unit time is $Gf_1(G/\alpha_g)$. Similarly, the number flux of solitary locusts becoming gregarized is $Sf_2(S/\alpha_s)$. Equating these expressions and substituting from (7) yields

$$\frac{\delta_2 S^3}{\alpha_s^2 k_s^2 + S^2} = \frac{\delta_1 k_1^2 \alpha_g^2 G}{\alpha_g^2 k_g^2 + G^2}. \quad [22]$$

To find the mass-balanced states, we must solve (22). To simplify this calculation, we define the solitary and gregarious mass fractions

$$\phi_s = S/M, \quad \phi_g = G/M, \quad [23]$$

$$\phi_s + \phi_g = 1. \quad [24]$$

Substituting (23) into (22) and dividing through by M yields

$$\frac{c_1 \phi_s^3}{1 + c_2 \phi_s^2} = \frac{c_3 \phi_g}{1 + c_4 \phi_g^2}. \quad [25]$$

where

$$c_1 = \frac{\delta_2 M^2}{\alpha_s^2 k_s^2}, \quad c_2 = \frac{M^2}{\alpha_s^2 k_s^2}, \quad c_3 = \delta_1, \quad c_4 = \frac{M^2}{\alpha_g^2 k_g^2}. \quad [26]$$

Discussion

THIS MATERIAL FROM LEK IS TEMPORARY AND NEEDS TO BE EDITED, RERGANIZED, ETC] A recent general review of models for aggregation based on attraction and repulsion is provided by [32]. Purely theoretical models for swarming include integro-differential equations [24]. Application of such ideas to flying locust swarms include [16] and [17].

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 [33, 19, 34] as well as proportion of locusts moving at a given time [15, 31] 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. [33] formulated an abstract model of collective motion, with repulsion and attraction that was then modified by [31] 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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