

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 | swarm | gregarious | solitary

Abbreviations:

Outbreaks of the desert locust *Schistocerca gregaria* have afflicted vast areas across northern Africa, the Middle East and south-west Asia for centuries. Depending on climate and vegetation conditions, billions of these voracious insects may aggregate into destructive swarms, typically covering a thousand of square kilometer areas and traveling hundreds of kilometers a day, while leaving land mostly outstripped of vegetation in their aftermath [1–4]. The latest locust plague occurred in West Africa between 2003–2005 and severely disrupted subsistence and export agriculture by destroying \$2.5 billion in crops. Despite \$400 million spent in control efforts, in certain regions loss rates escalated to 50% [5, 6]. These numbers alone attest to the urgency of finding optimal ways to control, manage and possibly predict outbreaks.

In their quiet periods, locusts are mainly solitary creatures who live in arid regions and lay eggs in small breeding grounds lush with vegetation, usually after seasonal rains or due to irrigation. Occasionally, resources at these breeding grounds are abundant enough to support a large number of hatchlings, giving rise to a large adult locust population in a crowded area. 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, leaving their typical trail of destruction behind. This phenomenon may be exacerbated in periods of food scarcity, when large numbers of locusts congregate in the same breeding and feeding ground.

From a biological point of view, desert locusts are *phase polyphenic*: individuals of the same genotype display more than one phenotypic form depending on external influences [7, 8]. For desert locusts, relevant phenotypic differences are morphology [9], coloration [10], reproductive features [11] and most significantly behavior [12, 13]. The latter can change from *solitary* where locusts seek isolation to *gregarious* where individuals attract each other. Behavioral phase is tremendously plastic [3, 8, 12] and is strongly dependent on local population density. In sufficiently sparse surroundings a gregarious locust eventually acquires the crowd-avoiding preferences of a solitary one [12] while in crowded surroundings, a solitary locust develops attractive behavior. It is this phenotype switching mechanism that takes place when large numbers of locusts gather at the same nutritional site, allowing them to override their solitary tendency, transform into the gregarious form and swarm together.

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 [12–14]. 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 [14]. 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 [13–15].

Patchy clumps of vegetation that lead to crowding of locusts also enhance their levels of activity and induce them to become gregarious [16]. (This was often quantified as a correlation between the fractal dimension of the vegetation and the locust behaviour [17]. Contact or sight of locusts coming from behind enhances the tendency of a locust to move [18]. 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 [14]. 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 [19] and [20] constructed models for the rolling pattern formed by flying locust groups. Work in [21] 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 [22] describes locusts within a confined arena using a self-propelled particle model similar to the seminal one [23] 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 disperse, 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.*, [24, 25]. A key element in swarms is social interaction. Social forces such as attraction and repulsion [26, 27] 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 [28, 29]. 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

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

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 sensing is omnidirectional then Q has the appropriate symmetry. Eq. (1) has been studied in [30–32] for specific choices of K , and in a two-dimensional setting in [33]. More generally, [24] 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 [25] 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

Let $s(\mathbf{x}, t)$, $\mathbf{x} \equiv (x, y)$ represent the density of solitary locusts on the ground, 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

$$v_s = -\nabla(Q_s^{2D} * \rho), \quad v_g = -\nabla(Q_g^{2D} * \rho). \quad [5]$$

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^{2D} and the gregarious potential Q_g^{2D} are

$$Q_s^{2D}(\mathbf{x}) = R_s e^{-|\mathbf{x}|/r_s}, \quad Q_g^{2D}(\mathbf{x}) = R_g e^{-|\mathbf{x}|/r_g} - A_g e^{-|\mathbf{x}|/a_g}. \quad [6]$$

Assume that variation in the swarm is negligible in one direction, which we take to be the y -direction. Then (3) reduces to one dimension with interaction potentials that we refer to as quasi-two-dimensional, as in [25]. The potentials are

$$Q_{s,g}(x) = \int_{-\infty}^{\infty} Q_{s,g}(x, y) dy. \quad [7]$$

and the velocity is

$$v_s = -\partial_x(Q_s * \rho), \quad v_g = -\partial_x(Q_g * \rho). \quad [8]$$

The parameters in Q_g must be chosen in the clumping regime, per the conditions stated in [24]. [Not the right condition anymore since we are using quasi-2d.]

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

$$f_1(\rho) = \frac{\delta_1}{1 + (\rho/k_1)^2}, \quad f_2(\rho) = \frac{\delta_2 (\rho/k_2)^2}{1 + (\rho/k_2)^2}. \quad [9]$$

Parameter Values

We draw upon the experimental results of [14] to estimate phase change parameters in (9). Phase change from the gregarious to solitary state takes approximately four hours, and vice versa. Thus, $\delta_1 = \delta_2 = 1/4 = 0.25 h^{-1}$. The critical density for gregarization is 50 - 80 locusts $/m^2$. We assume that the solitarization process has the same critical density, and we set the characteristic density transition scales to be $k_1 = k_2 = 65$ locusts $/m^2$.

To estimate social interaction range parameters in (7), we apply results of [22, 34], which identify the ‘‘sensing range’’ of a locust as 0.14 m , and the ‘‘repulsion range’’ as 0.04 m , on order with the approximately 0.08 m body length of a mature individual. We set our repulsion length scales $r_s = r_g = 0.04 m$, corresponding to the experimental repulsion range. Since attraction typically operates over longer scales, we take $a_g = 0.14 m$, corresponding to the experimental sensing range.

We find R_s , R_g , and A_g from explicit computations of velocity under our model. The speed of a locust when it is alone varies from 72 - 216 m/hr , depending on diet [34]. At the upper end, this is roughly 1 body length per second. To estimate R_s we imagine the hypothetical semi-infinite density field $\rho(x) = \rho_0 H(x)$. Here, $H(x)$ 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 origin, at the swarm's edge, should move to the left with maximal velocity $v_s^{max} = -216 m/hr$. We use the velocity definition (8) to write

$$v_s(0) = -\partial_x \{Q_s * \rho_0 H(x)\} |_{x=0} = v_s^{max}, \quad [10]$$

which we solve to find $R_s = 41.54$ locusts $\cdot m^2/hr$. Similarly, a gregarious locust at the origin should move to the right with maximal velocity $v_g^{max} = 216 m/hr$, and so

$$v_g(0) = -\partial_x \{Q_g * \rho_0 H(x)\} |_{x=0} = v_g^{max}. \quad [11]$$

A gregarious locust placed a short distance away from the swarm equal to the attraction length scale 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

$$v_g(-0.14) = -\partial_x \{Q_g * \rho_0 H(x)\} |_{x=-0.14} = v_g^{min}. \quad [12]$$

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

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

$$s_0 = \frac{\rho_0 \delta_1 k_1^2 (k_2^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}, \quad g_0 = \frac{\delta_2 \rho_0^3 (k_1^2 + \rho^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}. \quad [13]$$

In the small ρ_0 limit,

$$s_0 \approx \rho_0 - \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3, \quad g_0 \approx \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3. \quad [14]$$

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

$$s_0 \approx \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad g_0 \approx \rho_0 - \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad [15]$$

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

$$s(\mathbf{x}, t) = s_0 + s_1(\mathbf{x}, t), \quad g(\mathbf{x}, t) = g_0 + g_1(\mathbf{x}, t). \quad [16]$$

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

$$\rho(\mathbf{x}, t) = \rho_0 + \rho_1(\mathbf{x}, t) = s_0 + g_0 + s_1(\mathbf{x}, t) + g_1(\mathbf{x}, t). \quad [17]$$

Substitute (16) and (17) into (??), 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

$$\dot{s}_1 = s_0 Q_s * \nabla^2 (s_1 + g_1) - A s_1 + B g_1, \quad [18a]$$

$$\dot{g}_1 = g_0 Q_g * \nabla^2 (s_1 + g_1) + A s_1 - B g_1 \quad [18b]$$

where

$$A = f_2(\rho_0) + f_2'(\rho_0) s_0 - f_1'(\rho_0) g_0 \quad [19a]$$

$$B = f_1(\rho_0) + f_1'(\rho_0) g_0 - f_2'(\rho_0) s_0. \quad [19b]$$

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

$$s_1(\mathbf{x}, t) = \sum_{\mathbf{k}} \mathcal{S}_{\mathbf{k}}(t) e^{i\mathbf{k}\cdot\mathbf{x}}, \quad s_2(\mathbf{x}, t) = \sum_{\mathbf{k}} \mathcal{G}_{\mathbf{k}}(t) e^{i\mathbf{k}\cdot\mathbf{x}}. \quad [20]$$

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 (18) yields a set of ordinary differential equations for each Fourier mode amplitude. These are conveniently written in matrix form. Dropping the subscripts on \mathcal{S} and \mathcal{G} for simplification of notation, we have

$$\frac{d}{dt} \begin{pmatrix} \mathcal{S} \\ \mathcal{G} \end{pmatrix} = \mathbf{L}(k) \begin{pmatrix} \mathcal{S} \\ \mathcal{G} \end{pmatrix}, \quad \mathbf{L}(k) \equiv \begin{pmatrix} -s_0 k^2 \widehat{Q}_s(k) - A & -s_0 k^2 \widehat{Q}_s(k) + B \\ -g_0 k^2 \widehat{Q}_g(k) + A & -g_0 k^2 \widehat{Q}_g(k) - B \end{pmatrix}. \quad [21]$$

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,

$$\widehat{Q}_s(k) = 2 \frac{R_s r_s}{1 + (r_s k)^2}, \quad \widehat{Q}_g(k) = 2 \left[\frac{R_g r_g}{1 + (r_g k)^2} - \frac{A_g r_a}{1 + (r_a k)^2} \right]. \quad [22]$$

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

$$\lambda_1(k) = -k^2 \left[s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) \right], \quad \lambda_2 = -(A + B). \quad [23]$$

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

$$s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) < 0. \quad [24]$$

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 (??), 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 (7). For convenience, define the total number of solitary locusts and gregarious locusts,

$$S = \int_{\Omega} s \, d\Omega, \quad G = \int_{\Omega} g \, d\Omega, \quad [25]$$

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

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

$$s = S/\alpha_s, \quad g = G/\alpha_g. \quad [26]$$

For a segregated state at mass balance, the number flux of gregarious locusts becoming solitarized per unit time is $G f_1(G/\alpha_g)$. Similarly, the number flux of solitary locusts becoming gregarized is $S f_2(S/\alpha_s)$. Equating these expressions and substituting from (9) yields

$$\frac{\delta_2 S^3}{\alpha_s^2 k_2^2 + S^2} = \frac{\delta_1 k_1^2 \alpha_g^2 G}{\alpha_g^2 k_1^2 + G^2}. \quad [27]$$

To find the mass-balanced states, we must solve (27). To simplify this calculation, we define the solitary and gregarious mass fractions

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

so that

$$\phi_s + \phi_g = 1. \quad [29]$$

Substituting (28) into (27) and dividing through by M yields

$$\frac{c_1 \phi_s^3}{1 + c_2 \phi_s^2} = \frac{c_3 \phi_g}{1 + c_4 \phi_g^2}. \quad [30]$$

where

$$c_1 = \frac{\delta_2 M^2}{\alpha_s^2 k_2^2}, \quad c_2 = \frac{M^2}{\alpha_s^2 k_2^2}, \quad c_3 = \delta_1, \quad c_4 = \frac{M^2}{\alpha_g^2 k_1^2}. \quad [31]$$

Discussion

THIS MATERIAL FROM LEK IS TEMPORARY AND NEEDS TO BE EDITED, REORGANIZED, ETC] A recent general review of models for aggregation based on attraction and repulsion is provided by [35]. Purely theoretical models for swarming include integro-differential equations [27]. Application of such ideas to flying locust swarms include [19] and [20].

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 [22, 36, 37] as well as proportion of locusts moving at a given time [18, 34] 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. [36] formulated an abstract model of collective motion, with repulsion and attraction that was then modified by [34] 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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