

# Desert locust dynamics: Behavioral phase change and swarming

Roberta Graff<sup>\*</sup>, Javier de Ruiz Garcia<sup>†</sup>, and Franklin Sonnerly<sup>†</sup>

<sup>\*</sup>University of Cambridge, Cambridge, United Kingdom, and <sup>†</sup>Universidad de Murcia, Bioquímica y Biología Molecular, Murcia, Spain

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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 areas of a thousand square kilometers, traveling a few hundred kilometers each day, and leaving behind land mostly stripped of vegetation [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, loss rates escalated to 50% in certain regions [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 are abundant enough to support numerous hatchings, leading to a large number of adult locusts who, due to crowding, acquire gregarious tendencies. 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. Newly settled feeding grounds are also inevitably depleted, leading to several stop-and-go cycles of traveling locust bands. This phenomenon 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 [7, 8] such as 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 they attract each other. Behavioral phase is tremendously plastic [3, 8, 12] and strongly dependent on local population density, so that in sparse surroundings a gregarious locust turns into a solitary one [12] and vice-versa in crowded environments. It is this phenotype switch that takes place when large numbers of locusts gather at the same nutritional site, allowing individuals to transform from solitary to gregarious and swarm together [14, 15].

At a more mechanistic level, locust gregarization is induced by tactile, visual and olfactory cues. One of the most potent stimuli has been shown to be the regular touching of an individual's hind legs by another [12, 13, 16]. Although other areas of the body such as mouth, face, and abdomen may be self-activated while performing common tasks such as walking, feeding or grooming [16], the hind femora are touched only by other insects in the field so that intense leg rubbing may function as an indicator of crowding conditions. The mechanosensory stimulation of leg nerves leads to subsequent serotonin cascades in the brain, and in turn to the onset of gregarious behavior [13, 16, 17]. Furthermore, contact with individuals coming

from behind enhances the tendency of a stationary locust to move [18]. It has been shown that the solitary to gregarious switch can be induced by rubbing a locust's hind leg for 5 seconds per minute during a period of four hours [16]. Similarly, cessation of physical contact leads to a transition back to the solitary state after four hours.

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 Refs. [19] and [20] studied the dynamics of rolling patterns formed by migrating locust groups. Data driven models include the self-propelled particle model of Ref. [21] where the observed transition between disordered to ordered locust movement was described via well-known physics paradigms [22]. A logistic map was introduced in Ref. [23] to describe population switching via a birth rate and a carrying capacity dependent on population density modulated by stochastic effects.

None of these studies have focused on how an initially disperse, solitary locust population transitions to 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 paper is organized as follows/our main results/conclusions.

## The model

Individuals in a swarm are subject to attractive or repulsive forces resulting either from direct sensory communication or via the indirect signaling provided by chemical or vibrational sources [26–28]. While communications may be unidirectional (*e.g.*, narrow sight) or omnidirectional (*e.g.* hearing), many organisms process a combination of inputs, effectively resulting in omnidirectional sensing [29, 30]. Social forces are typically cast in the form of superimposed pairwise interactions, although many-body choices are also possible. In this work we will consider a traveling swarm that is well-described by a continuum population density  $\rho(\mathbf{x}, t)$  subject to social interactions. The continuum assumption holds well in the context of locust gregarization due to the large population numbers involved, both in the gregarious and solitary phases (IS THIS TRUE?). A simple model commonly used is

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

where the velocity  $\mathbf{v}$  is determined via a convolution with the social interaction field  $Q(\mathbf{x} - \mathbf{x}')$  that describes the influence of the popu-

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lation at location  $\mathbf{x}'$  on that at location  $\mathbf{x}$ . For notational simplicity we denote the convolution via an asterisk, so that  $\mathbf{v} = -\nabla Q * \rho$ . If sensing is omnidirectional then  $\mathbf{Q}$  has the appropriate symmetry (DO WE NEED THIS LINE?) Eq. 1 has been studied in Refs. [31–33] for specific choices of  $Q$ , and in a two-dimensional setting in [34]. Generally, the dynamics arising from Eq. 1 include at least three different asymptotic behaviors: spreading, steady state, and blow-up [24]. The compactly supported steady states, which may include jump discontinuities at the swarm's edges, are studied in depth in Ref. [25] in one spatial dimension.

In the context of biphasic desert locust swarms we denote the density of solitary and gregarious locusts by  $s(\mathbf{x}, t)$  and  $v(\mathbf{x}, t)$  respectively, where  $\mathbf{x} = (x, y)$ . We also denote the total density by  $\rho = s + g$ . Extending Eq. 1 to include switching transitions between the solitary and gregarious phases we write

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

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

where the velocities are given by

$$v_s = -\nabla(Q_s^{2D} * \rho), \quad v_g = -\nabla(Q_g^{2D} * \rho). \quad [3]$$

in accordance to Eq. 1.

STOP FOR TODAY

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

$$Q_s^{2D}(\mathbf{x}) = R_s e^{-|\mathbf{x}|/r_s}, \quad Q_g^{2D}(\mathbf{x}) = R_g e^{-|\mathbf{x}|/r_g} - A_g e^{-|\mathbf{x}|/a_g}. \quad [4]$$

Assume that variation in the swarm is negligible in one direction, which we take to be the  $y$ -direction. Then (2) reduces to one dimension with interaction potentials that we refer to as quasi-two-dimensional, as in [25]. The potentials are

$$Q_{s,g}(x) = \int_{-\infty}^{\infty} Q_{s,g}(x, y) dy. \quad [5]$$

and the velocity is

$$v_s = -\partial_x(Q_s * \rho), \quad v_g = -\partial_x(Q_g * \rho). \quad [6]$$

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

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

## Parameter Values

We draw upon the experimental results of [16] to estimate phase change parameters in (7). Phase change from the gregarious to solitary state takes approximately four hours, and vice versa. Thus,  $\delta_1 = \delta_2 = 1/4 = 0.25 \text{ h}^{-1}$ . The critical density for gregarization is  $50 - 80 \text{ locusts/m}^2$ . We assume that the solitarization process has the same critical density, and we set the characteristic density transition scales to be  $k_1 = k_2 = 65 \text{ locusts/m}^2$ .

To estimate social interaction range parameters in (5), we apply results of [21, 35], which identify the ‘‘sensing range’’ of a locust as  $0.14 \text{ m}$ , and the ‘‘repulsion range’’ as  $0.04 \text{ m}$ , on order with the approximately  $0.08 \text{ m}$  body length of a mature individual. We set our repulsion length scales  $r_s = r_g = 0.04 \text{ m}$ , corresponding to the experimental repulsion range. Since attraction typically operates over longer scales, we take  $a_g = 0.14 \text{ m}$ , 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  $72 - 216 \text{ m/hr}$ , depending on diet [35]. 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  $\rho_0 = 65 \text{ locusts/m}^2$ , 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  $v_s^{max} = -216 \text{ m/hr}$ . We use the velocity definition (6) to write

$$v_s(0) = -\partial_x \{Q_s * \rho_0 H(x)\} |_{x=0} = v_s^{max}, \quad [8]$$

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

$$v_g(0) = -\partial_x \{Q_g * \rho_0 H(x)\} |_{x=0} = v_g^{max}. \quad [9]$$

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,  $v_g^{min} = 144 \text{ m/hr}$ . Thus

$$v_g(-0.14) = -\partial_x \{Q_g * \rho_0 H(x)\} |_{x=-0.14} = v_g^{min}. \quad [10]$$

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

## Steady states and linear stability

There is a family of homogeneous steady states parameterized by the total homogeneous density  $\rho_0$ . For any given  $\rho_0$ , the homogeneous steady state is

$$s_0 = \frac{\rho_0 \delta_1 k_1^2 (k_2^2 + \rho_0^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}, \quad g_0 = \frac{\delta_2 \rho_0^3 (k_1^2 + \rho^2)}{\delta_1 k_1^2 k_2^2 + \delta_1 k_1^2 \rho_0^2 + \delta_2 k_1^2 \rho_0^2 + \delta_2 \rho_0^4}. \quad [11]$$

In the small  $\rho_0$  limit,

$$s_0 \approx \rho_0 - \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3, \quad g_0 \approx \frac{\delta_2}{\delta_1 k_2^2} \rho_0^3. \quad [12]$$

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

$$s_0 \approx \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad g_0 \approx \rho_0 - \frac{\delta_1 k_1^2}{\delta_2} \frac{1}{\rho_0}, \quad [13]$$

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

$$s(\mathbf{x}, t) = s_0 + s_1(\mathbf{x}, t), \quad g(\mathbf{x}, t) = g_0 + g_1(\mathbf{x}, t). \quad [14]$$

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

$$\rho(\mathbf{x}, t) = \rho_0 + \rho_1(\mathbf{x}, t) = s_0 + g_0 + s_1(\mathbf{x}, t) + g_1(\mathbf{x}, t). \quad [15]$$

Substitute (14) and (15) 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

$$\dot{s}_1 = s_0 Q_s * \nabla^2 (s_1 + g_1) - A s_1 + B g_1, \quad [16a]$$

$$\dot{g}_1 = g_0 Q_g * \nabla^2 (s_1 + g_1) + A s_1 - B g_1 \quad [16b]$$

where

$$A = f_2(\rho_0) + f'_2(\rho_0)s_0 - f'_1(\rho_0)g_0 \quad [17a]$$

$$B = f_1(\rho_0) + f'_1(\rho_0)g_0 - f'_2(\rho_0)s_0. \quad [17b]$$

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

$$s_1(\mathbf{x}, t) = \sum_{\mathbf{k}} \mathcal{S}_{\mathbf{k}}(t) e^{i\mathbf{k}\cdot\mathbf{x}}, \quad s_2(\mathbf{x}, t) = \sum_{\mathbf{k}} \mathcal{G}_{\mathbf{k}}(t) e^{i\mathbf{k}\cdot\mathbf{x}}. \quad [18]$$

The admissible wave vectors  $\mathbf{k}$  depend on the chosen domain  $\Omega$ . In the event that  $\Omega = \mathbb{R}^r$  then all  $\mathbf{k}$  are admissible (per the Fourier transform). Substituting into (16) 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

$$\frac{d}{dt} \begin{pmatrix} \mathcal{S} \\ \mathcal{G} \end{pmatrix} = \mathbf{L}(k) \begin{pmatrix} \mathcal{S} \\ \mathcal{G} \end{pmatrix}, \quad \mathbf{L}(k) \equiv \begin{pmatrix} -s_0 k^2 \widehat{Q}_s(k) - A & -s_0 k^2 \widehat{Q}_s(k) + B \\ -g_0 k^2 \widehat{Q}_g(k) + A & -g_0 k^2 \widehat{Q}_g(k) - B \end{pmatrix} \quad [19]$$

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,

$$\widehat{Q}_s(k) = 2 \frac{R_s r_s}{1 + (r_s k)^2}, \quad \widehat{Q}_g(k) = 2 \left[ \frac{R_g r_g}{1 + (r_g k)^2} - \frac{A_g r_a}{1 + (r_a k)^2} \right]. \quad [20]$$

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

$$\lambda_1(k) = -k^2 \left[ s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) \right], \quad \lambda_2 = -(A + B). \quad [21]$$

The eigenvalue  $\lambda_2$  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

$$s_0 \widehat{Q}_s(k) + g_0 \widehat{Q}_g(k) < 0. \quad [22]$$

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  $\Omega$ , covering an area we refer to as  $\alpha_s$ . The gregarious locusts are concentrated in a clump whose area we call  $\alpha_g$ , which may be estimated from the gregarious potential; see (5). For convenience, define the total number of solitary locusts and gregarious locusts,

$$S = \int_{\Omega} s \, d\Omega, \quad G = \int_{\Omega} g \, d\Omega, \quad [23]$$

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

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

$$s = S/\alpha_s, \quad g = G/\alpha_g. \quad [24]$$

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 (7) yields

$$\frac{\delta_2 S^3}{\alpha_s^2 k_2^2 + S^2} = \frac{\delta_1 k_1^2 \alpha_g^2 G}{\alpha_g^2 k_1^2 + G^2}. \quad [25]$$

To find the mass-balanced states, we must solve (25). To simplify this calculation, we define the solitary and gregarious mass fractions

$$\phi_s = S/M, \quad \phi_g = G/M, \quad [26]$$

so that

$$\phi_s + \phi_g = 1. \quad [27]$$

Substituting (26) into (25) and dividing through by  $M$  yields

$$\frac{c_1 \phi_s^3}{1 + c_2 \phi_s^2} = \frac{c_3 \phi_g}{1 + c_4 \phi_g^2}. \quad [28]$$

$$c_1 = \frac{\delta_2 M^2}{\alpha_s^2 k_2^2}, \quad c_2 = \frac{M^2}{\alpha_s^2 k_2^2}, \quad c_3 = \delta_1, \quad c_4 = \frac{M^2}{\alpha_g^2 k_1^2}. \quad [29]$$

## 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 [36]. Purely theoretical models for swarming include integro-differential equations [28]. 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 [21, 37, 38] as well as proportion of locusts moving at a given time [18, 35] 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. [37] formulated an abstract model of collective motion, with repulsion and attraction that was then modified by [35] 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  $\chi$  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 /m<sup>2</sup>).

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