A minimal model of predator-swarm interactions

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Many animals in nature form cohesive groups or swarms. We propose a minimal model of predator-swarm interactions which is able to capture many of the essential dynamics observed in nature. Different outcomes are observed depending on the predator strength. For a “weak” predator, the swarm is able to escape the predator completely. As the strength is increased, the predator is able to catch up with the swarm as a whole, but the individual prey is able to escape by “confusing” the predator: the prey forms a ring with the predator at the center. For higher predator strength, complex chasing dynamics are observed which can become chaotic. For even higher strength, the predator is able to successfully capture the prey. Our model is simple enough to be amenable to a full mathematical analysis which is used to predict the shape of the swarm as well as the resulting predator-prey dynamics as a function of model parameters. We show that as the predator strength is increased, there is a transition (due to Hopf bifurcation) from confusion state to chasing dynamics, and we compute the threshold analytically. Finally, the analysis indicates that the swarming behaviour is not helpful in avoiding the predator, suggesting that there are other reasons why the species may swarm. The chasing dynamics that we observe in our model are similar to behaviour observed in sheep flock avoiding a shepherd.

I. INTRODUCTION

Many species in nature form cohesive groups. Some of the more striking examples are schools of fish and flocks of birds, but various forms of collective behaviour occur at all levels of living organisms, from bacterial colonies to human cities. It has been postulated that swarming behaviour is an evolutionary adaptation that confers certain benefits on the individuals or group as a whole [1–5]. These benefits may include more efficient food gathering [6], predator avoidance in fish shoals [7] or zebra [4], and heat preservation in penguins huddles [8]. An example are defensive tactics used by a zebra herd against hyaenas or lions [4]. These defense mechanisms may include evasive maneuvers, confusing the predator, safety in numbers and increased vigilance [4, 9, 10]. On the other hand, a countervailing view is that swarming can also be detrimental to prey as it makes it easier for the predator to spot and attack the group as a whole [1].

Figure 1 gives some idea of the variety and complexity of predator-swarm interactions that occur in nature. A common characteristic is the formation of empty space surrounding the “predator” (or a human shephard as in figure 1(A)). There is also a presence of a relatively sharp boundary of the swarm.

In this paper we investigate a very simple particle-based model of predator-prey interactions which captures several distinct behaviours that are observed in nature. There are several well-known mechanisms whereby the prey try to avoid the predator. One well-studied example is predator confusion, which occurs when the predator is “confused” about which individual to pursue. Predator confusion decreases the predators’ ability to hunt their prey. To quote [3], “predator confusion effect describes the reduced attack-to-kill ratio experienced by a predator resulting from an inability to single out and attack individual prey”. In [12] the authors studied marching insects and demonstrated that their collective behavior function partly as an anti-predator strategy. During hunting, predators become confused when confronted with their prey swarm [13] and predator confusion has been observed in 64% of the predator prey systems to date [14]. Predator-prey dynamics were also studied using computer models, see for example [5, 15–17]. In [15] the authors studied a mathematical model of school of fish which demonstrates that collective evasion reduces predator’s success by confusing it. In [16] the authors used simulated co-evolution of predators and prey to demonstrate that predator confusion gives a sufficient selective advantage for swarming prey. Similar preference for swarming in the presence of confused predator was investigated in [5].

While there are many models in the literature that demonstrate complex predator-prey dynamics, most of these models are too complex to study except through numerical simulations. The goal of this paper is to present a minimal mathematical model which is carefully chosen so that (a) it is amenable to mathematical analysis; and (b) it captures the essential features of predator-prey interactions. A commonly used approach to swarm dynamics is to represent each prey by a particle that moves based on its interactions with other prey and its interaction with the predator. There is a large literature on particle models in biology, where they have been used to biological aggregation in general [1, 18–22] and locusts [21] or fish populations [15, 23–26] in particular. This is the approach that we take in this paper as well.

We now introduce the model that we will study in this paper. We assume that there are N prey whose positions \( x_j(t) \in \mathbb{R}^2 \), \( j = 1 \ldots N \) follow Newton’s law, so that

\[
m \frac{d^2 x_j}{dt^2} + \mu \frac{d x_j}{dt} = F_{j,\text{prey-prey}} + F_{j,\text{prey-predator}}.
\]

Here, \( F_{j,\text{prey-prey}} \) and \( F_{j,\text{prey-predator}} \) is the total force acting on the \( j \)-th particle, \( \mu \) is the strength of “friction” force and \( m \) is its mass. We make a further simplifica-
tion that the mass $m$ is negligible compared to the friction force $\mu$. After rescaling to set $\mu = 1$, the model is then simply $\frac{d}{dt}x_j = F_{j,\text{prey-prey}} + F_{j,\text{prey-predator}}$, so that the prey moves in the direction of the total force. This reduces the 2nd order model to a 1st order model which makes it easier to analyse mathematically. Similar reduction was used for example in the analysis of locust populations [27] and other biological models [19, 28]. Various forms can be considered for prey-prey interactions. To keep cohesiveness of the swarm we consider the interactions which exhibit pairwise short-range repulsion and long-range attraction, averaged over all of the particles. For concreteness, we consider the endogenous prey-prey interaction of the form

$$F_{j,\text{prey-prey}} = \frac{1}{N} \sum_{k=1,k\neq j}^N \left( \frac{1}{|x_j - x_k|^2} - a \right) (x_j - x_k).$$

The term $\frac{1}{|x_j - x_k|^2}$ represents Newtonian-type short-range repulsion that acts in the direction from $x_j$ to $x_k$, whereas $-a (x_j - x_k)$ is a linear long-range attraction in the same direction. While more general attraction-repulsion dynamics can be considered, we concentrate on this specific form because more explicit results are possible. In particular, in the absence of exogenous prey-predator force, this particular interaction has been shown to result in uniform swarms [29, 30]. In general, the distribution inside the swarm can vary and have fluctuations; however uniform density of swarm is often a good first-order approximation for many swarms. For example in [31] the authors found that the flocks of Sandhill Cranes feed-
The prey-predator interactions are modelled in a similar fashion: again for concreteness assume that there is a single predator whose position we denote by \( z(t) \in \mathbb{R}^2 \). Assuming that the predator acts as a repulsive particle on the prey, we take \( F_{\text{predator-prey}} = b \frac{x_j - x_k}{|x_j - x_k|^2} \), with \( b \) being the strength of the repulsion. Finally, we model the predator-prey interactions as an attractive force in a similar way, \( \frac{d}{dt} z = F_{\text{prey-predator}} \). We consider the simplest scenario where \( F_{\text{predator-prey}} \) is the average over all predator-prey interactions and each individual interaction is a power law which decays at large distances; the prey then moves in the direction of the average force.

These assumptions result in the following system:

\[
\frac{dx_j}{dt} = \frac{1}{N} \sum_{k=1, k \neq j}^{N} \left( \frac{x_j - x_k}{|x_j - x_k|^2} - a (x_j - x_k) \right) + b \frac{x_j - z}{|x_j - z|^2} \\
\frac{dz}{dt} = \frac{c}{N} \sum_{k=1}^{N} \frac{x_k - z}{|x_k - z|^p}.
\]

To illustrate the results and motivate the analysis in this paper, consider the numerical simulations of the particle model (1-2) shown in figure 2. We use the strength \( c \) of the predator-prey attraction as the control parameter, with other parameters as given in the figure. In the second row with \( c = 0.4 \), random initial conditions for prey and predator positions are taken inside a unit square. The swarm forms a “ring” of constant density with a predator at the center of the ring. Our first re-

FIG. 2: Predator-prey dynamics using the model (1-2). Parameters are: \( n = 400, a = 1, b = 0.2, p = 3 \) and \( c \) is as given. The bifurcation values for \( c \) are \( c_0 = 0.2190 \) and \( c_{\text{hopf}} = 0.7557 \) (see result 2). Color (online only) corresponds to particle speed from blue (slowest) to red (highest). The velocity vector of the predator is also shown. First row: \( c < c_0 \); the swarm escapes completely. Second row: \( c_0 < c < c_{\text{hopf}} \); predator catches up with the swarm but gets “confused” and the swarm forms a stable ring around it. Third row: \( c \) is just above \( c_{\text{hopf}} \); regular oscillations are observed. Fourth row: \( c \) is further increased leading to complex periodic patterns. Fifth row: the predator is able to “catch” the prey (see section IV); chaotic behaviour is observed.
result is to fully characterize this ring in the limit of large swarms; see result 1. Our main result is characterize the stability of this ring. In result 2 we show that the ring is stable whenever $2 < p < 4$ and

$$\frac{ba^{2-\frac{p}{2}}}{(1 + b)^{\frac{p}{2}}} < c < \frac{a^{2-\frac{p}{2}}}{b^{2-\frac{p}{2}} - (1 + b)^{\frac{p}{2}}}. \quad (3)$$

With parameters as chosen in figure 2 this corresponds to $0.2190 < c < 0.7557$. When $c$ is decreased below $0.2910$ (row 1), the ring becomes unstable and the predator is “expelled” out of the ring; the swarm escapes completely. A very different instability appears if $c$ is increased above $0.7557$ (row 3). In this case, we show that the ring also becomes unstable due to the presence of oscillatory instabilities, whereby the predator “oscillates” around the “center” of the swarm. After some transients, the system settles into a “rotating pattern” where the predator is continually chasing after its prey, without being able to fully catch up to it. As $c$ is further increased (row 4), the motion becomes progressively chaotic until the predator is finally able to catch the prey (row 5).

Our approach is to take the continuum limit $N \to \infty$ of (1-2), which results in the non-local integro-differential equation model [19–22]:

$$\rho(x, t) + \nabla \cdot (\rho(x, t)v(x, t)) = 0; \quad \int_{\mathbb{R}^2} \rho(y, t)dy = 1 \quad (4)$$

$$v(x, t) = \int_{\mathbb{R}^2} \left( \frac{x - y}{|x - y|^2} - a(x - y) \right) \rho(y, t)dy + b \frac{x - z}{|x - z|^2} \quad (5)$$

$$\frac{dz}{dt} = c \int_{\mathbb{R}^2} \frac{y - z}{|y - z|^p} \rho(y, t)dy. \quad (6)$$

Here, $\rho(x, t)$ denotes the density distribution of the prey swarm at position $x \in \mathbb{R}^2$ so that $\int_{\mathbb{R}^2} \rho(y, t)dy = 1$ and $v(x, t)$ is the swarm’s velocity field. The system (4-6) is obtained by choosing the initial density to be

$$\rho(x) = \frac{1}{N} \sum_{j=1}^{N} \delta(x - x_j)$$

where $\delta$ is the delta function. Equation (4) simply reflects the conservation of mass of the original prey system (1) (since no prey particles are created or destroyed); with the mass normalized so that $\rho(x, t)$ represents a probability distribution. By taking different pairwise endogenous forces, the steady state to (1-2) with no exogenous force ($b = 0$) presents a wide variety of patterns [32–34]. Similar equations have been used to model animal aggregation in [21, 27, 35–38]. The classical Keller-Segel model for chemotaxis also contains a Newtonian intra-species interaction [39, 40]. Aggregation models also appear in material science [41–43], vortex motion [44–47] where Newtonian potential arises for vortex density evolution, and granular flow [48, 49].

We now summarize the paper. In section II we construct the steady state solution consisting of a ring of prey particles of uniform density that surround the predator at the center. In section III we study its stability. We conclude with some extensions of the model and discussion of some open problems in section IV.

II. “CONFUSED” PREDATOR RING EQUILIBRIUM STATE

We start by constructing the “ring” steady state of the model (4-6), such as shown in the last picture of the second row of figure 2. Consider a steady state for which the predator is at the center of the swarm, surrounded by the prey particles. The predator is “trapped” at the center of the prey swarm while the prey forms a concentric annulus where the repulsion exerted by the predator cancels out due to the symmetry. We state the main result as follows:

Result 1 Define

$$R_1 = \sqrt{b/a}; \quad R_2 = \sqrt{(1 + b)/a}. \quad (7)$$

The system (4-6) admits a steady state for which $z = 0$, $\rho$ is a positive constant inside an annulus $R_1 < |x| < R_2$, and is otherwise.

Figure 6(a) illustrates this result. For parameters as shown in the figure, the discrete model (1-2) generates a stable ring steady state, which is shown with dots. Solid curves show the continuum result (7), in excellent agreement with the discrete model (1-2).

The fact that the density is constant inside a swarm is a result of the careful choice of the forces in (1): namely the nonlinearities are both Newtonian. The proof of result 1 follows closely [30, 50] and uses the method of characteristics, a common technique to find steady states in aggregation model.

Derivation of result 1. Define the characteristic curves $X(X_0, t)$ which start from $X_0$ at $t = 0$:

$$\frac{dX}{dt} = v(X, t); \quad X(X_0, 0) = X_0. \quad (8)$$

Using (4), along the characteristic curves $x = X(X_0, t)$, $\rho(x, t)$ satisfies:

$$\frac{d\rho}{dt} = - (\nabla_x \cdot v) \rho \quad (9)$$

Note that $\nabla_x \cdot \left( \frac{x - z}{|x - z|^2} \right) = \Delta_x (\ln |x - z|) = 2\pi \delta(x - z)$ so that from (5) we obtain

$$\nabla_x \cdot v = \int_{\mathbb{R}^2} [2\pi \delta(x - y) - 2a] \rho(y)dy + 2\pi b \delta(x - z)$$

$$= 2\pi \rho(x) - 2aM, \quad x \neq z \quad (10)$$

where $M = \int_{\mathbb{R}^2} \rho(y)dy$, is conserved. Then (9) becomes

$$\frac{d\rho}{dt} = (2aM - 2\pi \rho)\rho, \quad (11)$$

which has a solution $\rho(X(X_0, t), t)$ approaching $aM/\pi$ as $t \to \infty$ and independent of the location, as long as $\rho(X_0, 0) > 0$. 
Next we seek a steady state such that \( \rho \) is constant inside \( A \), \( \rho \) zero outside \( A \), where \( A \) is an annulus \( R_1 \leq |x| \leq R_2 \), with \( R_1, R_2 \) and \( z \) to be determined. Using the identity

\[
\int_{|y| \leq R} \frac{x - y}{|x - y|^2} dy = \left\{ \begin{array}{ll}
\frac{\pi R^2 x}{\pi x}, & |x| > R \\
0, & |x| < R
\end{array} \right.
\]  

and for \( x \in A \) we compute

\[
v(x) = \int_{A} \left[ \frac{x - y}{|x - y|^2} - a(x - y) \right] \rho(y, t) dy + \frac{b(x - z)}{|x - z|^2} = \pi px \left( 1 - \frac{R_2}{|x|^2} \right) - ax \rho \left( R_2^2 - R_1^2 \right) + \frac{b(x - z)}{|x - z|^2}.
\]  

The assumption of the steady state implies that (13) is zero for all \( x \in A \), which in turn implies that \( z = 0 \), \( \pi - a \pi \left( R_2^2 - R_1^2 \right) = 0 \), and \( \pi p \left( -R_1^2 \right) + b = 0 \), so that \( R_1 = \sqrt{b/a} \) and \( R_2 = \sqrt{(1+b)/a} \). Conversely, with this choice of \( R_1 \) and \( R_2 \), \( v = 0 \) whenever \( \rho \neq 0 \). Moreover by symmetry, \( dz/dt = 0 \), so that \( v, \rho, z \) as in result 1 constitute a true steady state of (4-6).

III. TRANSITION TO CHASING DYNAMICS

As illustrated in figure 2, the ring steady state configuration can transition to a moving configuration in two ways: If the predator strength \( c \) is sufficiently decreased the swarm will escape the predator. If \( c \) is increased past another threshold, the predator becomes more “focused” and less “confused” resulting in “chas ing dynamics” which can lead to very complex periodic or chaotic behaviour. Similar dynamics can be observed in nature as figure 3 illustrates. The onset of these dynamics can be understood as a transition from stability to an instability (i.e. bifurcation) of the ring steady state. The destabilizing perturbation corresponds to the translational motion of the predator as well as the inner or outer boundary of the ring [62].

To understand these bifurcations, we consider the perturbations of the inner boundary, outer boundary, as well as the predator itself. These perturbations are of the form

Inner boundary: \( x = R_1 e^{it} + \varepsilon_1 e^{\lambda t} \)  

Outer boundary: \( x = R_2 e^{it} + \varepsilon_2 e^{\lambda t} \)  

Predator: \( z = 0 + \varepsilon_3 e^{\lambda t} \)

where \( \varepsilon_i \ll 1 \). Note that this form of perturbation preserves the total mass which is an invariant of the model. In Appendix A we show that \( \lambda \) satisfies the eigenvalue problem

\[
(R_2^2 - R_1^2) \lambda \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{pmatrix} = A \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{pmatrix}
\]

where

\[
A = \begin{pmatrix}
-b - \frac{1}{1+b} & \frac{b}{1+b} & \frac{1}{1+b} \\
-b - \frac{1}{1+b} & \frac{b}{1+b} & \frac{1}{1+b} \\
-c \left( \frac{2-p}{a} \right) & c \left( \frac{2-p}{a} \right) + c & c \left( \frac{2-p}{a} \right)
\end{pmatrix}.
\]

The eigenvalues of \( A \) are given by \( \lambda = 0 \) and \( \lambda = \lambda_{\pm} \) which satisfy \( \lambda_{\pm}^2 + B \lambda_{\pm} + C = 0 \) where \( B = 1 - c \left( \frac{2-p}{a} \right) - \left( \frac{1+b}{a} \right) \), \( C = \frac{c(1+b)2-p}{a}. \) The eigenvalues \( \lambda_{\pm} \) are stable (i.e. \( \text{Re}(\lambda_{\pm}) < 0 \)) if and only if \( B > 0 \) and \( C > 0 \). Note when \( c = 0 \), we get \( B = 1, C < 0 \), so that \( \lambda_{\pm} < 0 < \lambda_{\pm} \) and the ring is unstable. As \( c \) is increased, either \( \lambda_{+} \) or \( \lambda_{-} \) cross zero. This occurs precisely when \( c = c_0 \) where

\[
c_0 = \frac{ba^{2-p}}{(1+b)^{2-p}},
\]

with \( C > 0 \) if \( c > c_0 \). If \( p \leq 2 \) then \( B > 0 \) for all \( c > c_0 \) so that \( \text{Re}(\lambda_{\pm}) < 0 \). If \( 2 < p \), a Hopf bifurcation occurs when \( B = 0 \) with \( C > 0 \); i.e. when \( c = c_{\text{hopf}} > c_0 \) where

\[
c_{\text{hopf}} = \frac{a^{2-p}}{b(1+b)^{2-p}}.
\]

Note \( 0 < c_0 < c_{\text{hopf}} \) if and only if \( 2 < p < 4 \) (with \( c_0 > c_{\text{hopf}} \) if \( p > 4 \), \( c_{\text{hopf}} = \infty \) if \( p = 2 \) and \( c_{\text{hopf}} < 0 \) if \( p < 2 \)). Therefore \( \text{Re}(\lambda_{\pm}) < 0 \) if and only if one of the following holds: (a) \( p \leq 2 \) and \( c > c_0 \); (b) \( 2 < p < 4 \) and \( c_0 < c < c_{\text{hopf}} \).

We summarize as follows.

**Result 2** Consider the ring steady state of (4-6) given in result 1. Let \( c_0, c_{\text{hopf}} \) be as defined by (18) and (19), respectively. The ring stability with respect to translational perturbations is characterized as follows.

- If \( p \leq 2 \): The ring is translationally stable if \( c_0 < c \), and unstable if \( c < c_0 \).
If $2 < p < 4$: The ring is translationally stable if $c_0 < c < c_{\text{hopf}}$. It is unstable due to the presence of a negative real eigenvalue if $c < c_0$. As $c$ is increased past $c_{\text{hopf}}$ the ring is destabilized due to a Hopf bifurcation.

If $p > 4$: The ring is unstable for all positive $c$.

This analysis reveals that there are three distinct regimes, which depends on the power exponent $p$ of the of the predator-prey attraction. If $p < 2$ then at close range the prey moves faster than the predator and can always escape. As a result, the predator can never catch the prey no matter how large $c$ is. The most interesting regime is $2 < p < 4$. As $c$ is increased just past $c_{\text{hopf}}$, complex periodic or chaotic chasing dynamics result, but the predator is still unable to catch the prey. The shape of the perturbation is reflected in the actual dynamics when $c$ is close to $c_{\text{hopf}}$ (such as in figure 2 row 3); however as $c$ is further increased, nonlinear effects start to dominate and linear theory is insufficient to describe the resulting dynamics (see figure 2 rows 4 and 5). For even larger $c$, the predator finally “catches” the prey; this is illustrated in figure 2 row 5, see section IV for further discussion of this.

Note that $c_0 = c_{\text{hopf}}$ when $p = 4$ in which case the stable band dissapears. If $p > 4$ then $c_{\text{hopf}} < c_0$ and the ring configuration is unstable for any $c$. In this case, the swarm escapes completely if $c < c_{\text{hopf}}$ but chasing dynamics and catching of the prey can still be observed if $c > c_{\text{hopf}}$.

IV. DISCUSSION AND EXTENSIONS

The minimal model (1-2) supports a surprising variety of predator-swarm dynamics, including: predator confusion, predator evasion, and chasing dynamics (with rectilinear, periodic, or chaotic motion).

Biologically, our model is useful in two ways. First, despite its simplicity, our model has an uncanny ability to reproduce the actual spatio-temporal dynamics of predator-prey systems observed in nature. This is illustrated in figure 3. Second, the mathematical analysis of this model provides some rudimentary biological insight into general forces at play, which we now discuss.

Formula (19) shows that the prey-prey attraction that is responsible for prey aggregation, controlled by a parameter $a$ in (1-2), is detrimental to prey: $c_{\text{hopf}}$ is a decreasing function of $a$ so that increasing $a$ makes it easier for the predator to catch the prey. This is also in agreement with several other studies. For example in [51, 52] the authors observed groups of about 20-30 dolphins surrounding a school of fish and blowing bubbles underneath it in an apparent effort to keep the school from dispersing, while other members of the dolphin group swam through the resulting ball of fish to feed. In a survey [1] the authors suggest that factors other than predator avoidance, such as food gathering, ease of mating, energetic benifits, or even constraints of physical environment are responsible for prey aggregation. Our model also supports this conclusion.

The parameter $b$ in the model (1-2) can be thought of as the strength of prey-predator repulsion. Formula (19) shows that $c_{\text{hopf}}$ is an increasing function of $b$, so that increasing $b$ is beneficial to the prey.
and suppose there are $N$ simulations here: [63].

For several values of $N$, while fixing the other parameters to be $p = 3, a = 1, b = 0.2$. The results are summarized in the following table.

<table>
<thead>
<tr>
<th>$N$</th>
<th>50</th>
<th>100</th>
<th>200</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c_{catch}$</td>
<td>0.9</td>
<td>1.1</td>
<td>1.4</td>
</tr>
</tbody>
</table>

Let $c_{catch}$ be the smallest value of predator strength $c$ for which the predator is able to catch the prey. We compute this value using full numerical simulations of (1-2) for several values of $N$, while fixing the other parameters to be $p = 3, a = 1, b = 0.2$. The results are summarized in the following table.

Note that $c_{catch}$ is increasing with $N$, which is also consistent with figure 5 showing that the kill rate increases when there are fewer particles. This suggests that all else being equal, having more individuals is beneficial to prey, in that a higher predator strength $c$ is required to catch the prey when $N$ is increased. This may be due to the fact that the predator becomes more “confused” by the various individuals inside the swarm when there are more of them.

From mathematical point of view, our analysis is rather nonstandard: the main result is obtained by doing a stability on the entire swarm in the continuum limit, which can be thought of as an infinite-dimensional dynamical system, or alternatively, a non-local PDE-ODE system (4-6). Below we discuss several possible extensions of the model.

Non-uniform state. The first extension is to replace the prey-predator interaction in (1) by a more general power nonlinearity, such as

$$\frac{dx_j}{dt} = \frac{1}{N} \sum_{k=1,k\neq j}^N \left( \frac{x_j - x_k}{|x_j - x_k|^q} - a (x_j - x_k) \right) + \frac{b}{|x_j - z|^q},$$

(21)

with equation for the predator unchanged; the original model corresponds to $q = 2$. As before, there is a steady state with the predator $z = 0$ at the center with swarm forming a ring around it. Unlike the $q = 2$, the density of the swarm is no longer uniform. Using a computation similar to the $q = 2$ case, we find that in the continuum limit, the density is given by

$$\rho(x) = \begin{cases} \frac{a}{\pi} & \text{when } R_1 < |x| < R_2 \\ 0 & \text{otherwise} \end{cases}$$

(22)

with $R_1, R_2$ satisfying

$$R_1 = (b/a)^{1/q} \quad a (R_2^q - R_1^q) - b/2 \left( R_2^{2-q} - R_1^{2-q} \right) = 1;$$

(23)

result 1 is recovered by choosing $q = 2$ in (23).

From (22) we note that for $q < 2$, the density is higher further away from the predator; conversely for $q > 2$ the density is higher closer to the predator. This compares favorably to full numerical simulations as shown in Figure 6. However the computation of stability for the non-constant density state remains an open problem.

Multiple predators. It is easy to generalize (1-2) to include multiple predators. For example, replace (1) by

$$\frac{dx_j}{dt} = \frac{1}{N} \sum_{k=1,k\neq j}^N \left( \frac{x_j - x_k}{|x_j - x_k|^q} - a (x_j - x_k) \right) + \sum_{k=1}^M \frac{x_j - z_k}{|x_j - z_k|^q},$$

(24)

and replace $z$ by $z_k$ in (2) (more complex predator-predator interactions can similarly be added). Even more
complex dynamics can be observed. Multi-species interaction has been studied in several other contexts recently, including crowd dynamics and pedestrian traffic \cite{53, 54}, decision making in the group with strong leaders \cite{55} and generalization of Keller-Segel model to multi-species in chemotaxis \cite{56–58}.

Here, we briefly consider the possible steady states of the swarm in the presence of two stationary predators (i.e. \( c = 0 \)). Consider two predators located symmetrically at \( z_1 = d \) and \( z_2 = -d \). Figure 7 shows some of the possible steady states for various values of \( d \). As \( d \) is decreased, the swarm splits into two. The swarm is symmetric with respect to \( x \) and \( y \) axes but is not radially symmetric.

The solid curve in figure 7 shows the continuum limit of (24) which is obtained by computing the evolution along the boundary \( \partial D \) of the swarm, while assuming that swarm density \( \rho = \frac{1}{|D|} \) is constant. Using the divergence theorem, the velocity can then be computed using only a one-dimensional integration:

\[
v(x) = \frac{1}{|D|} \int_{\partial D} \ln|x - y| \hat{n} dS(y) - ax + b \frac{x - z_1}{|x - z_1|^2} + b \frac{x - z_2}{|x - z_2|^2}
\]

where we assumed that the center of mass of the swarm is at the origin, and where the area \( |D| = \int_D dy = \frac{1}{2} \int_{\partial D} y \cdot \hat{n} dS(y) \) is also a one-dimensional computation.

**Acceleration and other effects.** Introducing acceleration allows for a more realistic motion. A more general model is

\[
m_j \frac{d^2 x_j}{dt^2} + \mu_j \frac{dx_j}{dt} = \frac{1}{N} \sum_{k=1, k \neq j}^{N} F(|x_j - x_k|) \frac{x_j - x_k}{|x_j - x_k|} + G(|x_j - z|) \frac{x - z}{|x - z|}
\]

(26)

\[
M \frac{d^2 z}{dt^2} + \mu_0 \frac{dz}{dt} = \frac{1}{N} \sum_{k=1}^{N} H(|z - x_k|) \frac{z - x_k}{|z - x_k|}
\]

(27)

where \( \mu_j, \mu_0 \) are friction coefficients of prey and predator respectively, and \( m_j, M \) are their masses. Figure 8 illustrates some of the possible dynamics of these models. Even more complex models exist in the literature. For example to obtain a more realistic motion for fish, an alignment term is often included which can lead to milling and flocking patterns even in the absence of predator \cite{26, 59, 60}.

Many models of collective animal behaviour found in literature include terms such as zone of alignment, angle of vision, acceleration etc. These terms may result in a more “realistic-looking” motion, although it can be difficult in practice to actually measure precisely how “realistic” it is \( \) (but see \cite{11, 61} for work in this direction). Moreover the added complexity makes it very difficult to study the model except through numerical simulations. Our minimal model shows that these additional effects are not necessary to reproduce complex predator-prey interactions.

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Appendix A

In this appendix we derive the eigenvalue problem (17) for the perturbations of the form (14-16). Let \( \omega_i = \varepsilon_i e^{i\lambda t} \).

The velocity then becomes

\[
v(x) = \rho \int_{B(o_2, R_2) \setminus B(o_1, R_1)} \left( \frac{x - y}{|x - y|^2} - a(x - y) \right) dy + b \frac{x - z}{|x - z|^2}.
\]

(28)

Using (12) with \( x \in B(o_2, R_2) \setminus B(o_1, R_1) \), we get

\[
v(x) = \rho \left[ \pi x - \pi o_2 + a\pi x(R_1^2 - R_2^2) - \frac{\pi R_1^2(x - o_1)}{|x - o_1|^2} + a\pi(R_2^2 o_2 - R_1^2 o_1) \right] + \frac{b(x - o_3)}{|x - o_3|^2}.
\]

(29)

At the steady state \( o_i = 0 \) and \( v = 0 \) so that (29) simplifies to

\[
v(x) = \rho \pi \left[ (aR_2^2 - 1)o_2 - aR_1^2 o_1 \right] + \rho \pi R_1^2 \left[ \frac{x}{|x|^2} - \frac{x - o_1}{|x - o_1|^2} \right] + b \left[ \frac{x - o_3}{|x - o_3|^2} - \frac{x}{|x|^2} \right].
\]

(30)

On the inner boundary, we have \( x = R_1 e^{i\theta} + \varepsilon_1 e^{i\lambda t} \) and linearizing we obtain

\[
v \sim \rho \pi \left[ (aR_2^2 - 1)o_2 - aR_1^2 o_1 \right] - \rho \pi \varepsilon_1 + \frac{b \varepsilon_3 e^{2i\theta}}{R_1^2}.
\]

Evaluating the perpendicular component \( v_\perp = v \cdot e^{i\varphi} \) yields

\[
v_\perp \sim \left\{ \rho \pi \left[ (aR_2^2 - 1)e_2 - aR_1^2 e_1 \right] - \rho \pi \varepsilon_1 + \frac{b \varepsilon_3}{R_1^2} \right\} e^{i\lambda t} \cos(\theta)
\]

We equate \( v = dx/dt = \lambda \varepsilon_1 e^{i\lambda t} \) along the perpendicular component to finally obtain

\[
\frac{\lambda}{\rho \pi} \varepsilon_1 = (-aR_1^2 - 1)e_1 + (aR_2^2 - 1)e_2 + \frac{b}{\rho \pi R_1^2} \varepsilon_3.
\]

(31)

The same computation along the outer boundary \( x = R_2 e^{i\theta} + \varepsilon_2 e^{i\lambda t} \) yields

\[
\frac{\lambda}{\rho \pi} \varepsilon_2 = \left( -aR_2^2 - \frac{R_2^2}{R_1^2} \right)e_1 + (aR_2^2 - 1)e_2 + \frac{b}{\rho \pi R_2^2} \varepsilon_3.
\]

(32)

Next we linearize the predator equation (6) around the ring steady state (7). We estimate:

\[
\int_{B(o_2, R_2) \setminus B(o_1, R_1)} \frac{x - o_3}{|x - o_3|^p} dx \sim \int_{B(o_2, R_2) \setminus B(o_1, R_1)} \frac{x}{|x|^p} dx + \int_{B(0, R_2) \setminus B(0, R_1)} \frac{px(x \cdot o_3 - o_3 |x|^2}{|x|^{p+2}} dx + h.o.t.
\]

where h.o.t. denotes higher order terms that are quadratic in \( o_i \). We then compute explicitly

\[
\int_{B(0, R_2) \setminus B(0, R_1)} \frac{px(x \cdot o_3 - o_3 |x|^2}{|x|^{p+2}} dx = -\pi o_3 \left( R_2^{2-p} - R_1^{2-p} \right)
\]

and approximate

\[
\int_{B(o_2, R_2) \setminus B(o_1, R_1)} \frac{x}{|x|^p} dx \sim \pi o_2 R_2^{2-p} - \pi o_1 R_1^{2-p}.
\]
Linearizing the predator equation (6) then yields

\[ \frac{\lambda}{\rho \pi} \epsilon_3 = -cR_1^{2-p} \epsilon_1 + cR_2^{2-p} \epsilon_2 + c(R_1^{2-p} - R_2^{2-p}) \epsilon_3. \]  

The three equations (33), (31), (32) then yield a closed three-dimensional eigenvalue problem,

\[ \frac{\lambda}{\rho \pi} \begin{bmatrix} \epsilon_1 \\ \epsilon_2 \\ \epsilon_3 \end{bmatrix} = \begin{bmatrix} -aR_1^2 - 1 & aR_2^2 - 1 & \frac{b}{\rho \pi R_1^2} \\ -aR_1^2 - \frac{R_1^2}{R_2^2} & aR_2^2 - 1 & \frac{b}{\rho \pi R_2^2} \\ -cR_1^{2-p} & cR_2^{2-p} & c(R_1^{2-p} - R_2^{2-p}) \end{bmatrix} \begin{bmatrix} \epsilon_1 \\ \epsilon_2 \\ \epsilon_3 \end{bmatrix} \tag{34} \]

The problem (17) is obtained by substituting (7) into (34).

References:


[62] As discussed in the derivation of result 1, for large time, the density \( p(x,t) \) rapidly approaches constant on its support, \( p \rightarrow aM/\pi \) and the equation for \( p \) along characteristics is independent of the boundary shape or the form of predator-prey interactions (parameters \( c \) and \( p \) in (2)). As such, tracking the evolution of the boundary and the predator is sufficient to determine the stability of the ring state.

[63] We created a website which contains the movies showing the simulations of predator-swarm interactions from this paper. These can be viewed by following the link: [http://goo.gl/BC6pyC](http://goo.gl/BC6pyC)