A minimal model of predator-swarm dynamics

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Abstract. Many animals in nature form cohesive groups or swarms. One of the presumed benefits of swarm formation is predator avoidance. We propose a minimal model of predator-prey 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.

Significance Statement. We propose a model of predator-prey dynamics. Many such models already exist. So why add another? The main advantage of our model is that on one hand, it is simple enough as to be amenable to a full mathematical analysis. On the other hand, our model captures the essential features of predator-prey interactions. Many models of collective animal behavior found in literature include terms such as zone of alignment, angle of vision, acceleration etc. Our model captures the essential features of predator-prey interactions. 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 model swarms in general [16, 17, 18, 19, 20], and locusts [19], and fish populations [21, 13, 22, 23, 24] 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 $m \frac{d^2}{dt^2} x_j + \mu \frac{dx_j}{dt} = F_{j,\text{prey-prey}} + F_{j,\text{prey-predator}}$. Here, $F_{j,\text{prey-prey}} + F_{j,\text{prey-predator}}$ 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 simplification 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 [25] and other biological models [17, 26]. 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 $F_{j,\text{prey-prey}} = \ldots$

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\[
\frac{1}{N} \sum_{k=1, k \neq j}^{N} \left( \frac{x_j - x_k}{|x_j - x_k|^2} - a \right) (x_j - x_k).
\]
The term \( \frac{x_j - x_k}{|x_j - x_k|^2} \) 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 [27, 28].

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 \( F_{j, \text{prey-predator}} = b \frac{x_j - z}{|x_j - z|^2} \), with \( b \) being the strength of the repulsion. Finally, we model the predator-prey interactions as an attractive force in a similar way, \( \frac{dz}{dt} = F_{\text{predator-prey}} \). 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:

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

\[
\frac{dz}{dt} = c \sum_{k=1}^{N} \frac{x_k - z}{|x_k - z|^p}. \quad [2]
\]

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 first 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
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 $c_{hopf} = 0.7557$ (see result 2). Color corresponds to particle speed from blue (slowest) to red (highest). The velocity vector of the predator is also shown. First row: $c_0 < c < c_{hopf}$: predator catches up with the swarm but gets “confused” and the swarm forms a stable ring around it. Second row: $c < c_0$: the swarm escapes completely. Third row: $c$ is just above $c_{hopf}$: 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; chaotic behaviour is observed.

Our first result is to fully characterize this ring in the limit of large swarms; see result 1. Our main result (see result 2 below) is to show that this ring is in fact stable whenever

$$\frac{ba^{2/3}}{(1 + b)^{2/3}} < c < \frac{a^{2/3}}{b^{2/3} - (1 + b)^{2/3}}.$$  \[3\]

With parameters as chosen in figure 2 this corresponds to $0.2190 < c < 0.7557$. When $c$ is decreased below 0.2910 (row 2), 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 (rows 4), the motion becomes progressively chaotic until the predator is finally able to catch the prey (row 5). The main result of this paper is the stability analysis of the ring solution.

Our approach is to take the continuum limit $N \to \infty$ of [1]-[2], which results in the non-local integro-differential equation model; see SI text. Similar approach was taken by [20, 19, 18, 17]. By taking different pairwise endogenous forces, the steady state to [1]-[2] with no exogenous force $(b = 0)$ presents a wide variety of patterns [30, 31, 32]. Similar equations have been used to model animal aggregation in [33, 19, 34, 35, 36, 25]. The classical Keller-Segel model for chemotaxis also contains a Newtonian intra-species interaction [37, 38]. Aggregation models also appear in material science [39, 40, 41], vortex motion [42, 43, 44, 45] where Newtonian potential arises for vortex density evolution, and granular flow [46, 47].

“Confused” predator ring equilibrium state

Consider the steady state of the model [1]-[2], such as shown in top right corner of figure 2. For such an equilibrium, 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. In SI text we derive the following characterisation of this “ring” stage:

As discussed in the derivation of result 1, for large time, the swarm density rapidly approaches constant on its support, and tracking the evolution of the boundary and the predator is sufficient to determine the stability of the ring state.
Result 1. For large \( N \), the system [1]-[2] admits an equilibrium solution with the prey swarm located inside an annulus \( R_1 < |x| < R_2 \) whose inner radius \( R_1 \) and outer radius \( R_2 \) are given by

\[
R_1 = \sqrt{b/a}; \quad R_2 = \sqrt{(1 + b)/a},
\]

and with the predator \( z = 0 \) located at the center of the swarm. Moreover the swarm density is uniform inside the annulus.

Figure 2(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. Dashed curves show the continuum result [4], 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 derivation of result 1 follows closely [48, 45, 28] See SI text for details.

### 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 “chasing dynamics” which can lead to very complex periodic or chaotic behaviour. 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 transversal motion of the predator as well as the inner or outer boundary of the ring\(^1\). In SI text we derive the following result.

Result 2. Consider the ring equilibrium state of [1]-[2] as given in result 1. Define

\[
c_0 = \frac{b a^{2-q}}{(1 + b)^{2-q}}; \quad c_{hopf} = \frac{a^{2-q}}{b^{2-q} - (1 + b)^{2-q}}.
\]

The ring stability 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 \( c_0 < c < c_{hopf} \). It is unstable due to the presence of a negative real eigenvalue if \( c > c_0 \). As \( c \) is increased past \( c_{hopf} \), the ring is destabilized due to a oscillatory instabilities (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 \( c_{hopf} \), complex periodic or chaotic chasing dynamics result, but the predator is still unable to catch the prey. For even larger \( c \), the predator finally catches up with the prey; this is illustrated in figure 2.

### 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). The nonlinearities in [1] were carefully chosen so that the swarm has constant density; we have shown that a detailed mathematical analysis is possible in this case explaining different interactions.

Our model shows that swarming helps the prey to avoid the predator. For example in figure 2 rows 3 and 4, the speed of individual prey is slower than that of the predator; nonetheless the prey are able to take evasive action and avoid being caught. We verified that smaller swarm size leads to more chances of capture even for the same parameter values.

There are many possible extensions of this model which we now discuss.

#### Non-uniform State

The first extension is to replace the prey-predator interaction in [1] by a more general power nonlinearity, such as

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

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 of the equilibrium state is given by

\[
p(x) = \begin{cases} \frac{a}{\pi} - \frac{b(2-q)}{2x^q} & \text{when } R_1 < |x| < R_2 \\ 0 & \text{otherwise} \end{cases}
\]

with \( R_1, R_2 \) satisfying

\[
R_1 = (b/a)^{1/q}, \quad a (R_2^q - R_1^q) - b/2 (R_2^{2-q} - R_1^{2-q}) = 1; \quad [9]
\]

**Fig. 3.** Steady state for model [1]-[2] for parameters as given and with \( p = q, c = 10 \). These states were computed by starting with random initial conditions and as such they appear to be stable. Dashed blue lines correspond to the continuum-limit asymptotics [9]. (a) \( q = 2 \), constant density swarm. (b) \( q > 2 \), swarm is denser towards the inner boundary. (c) \( q < 2 \), swarm is denser towards the outer boundary.

**Fig. 4.** Symmetric steady states for [10] with \( a = 1, b = 2, N = 500 \), and with \( M = 2 \) two predators located at \( z_1 = (-d, 0) \) and \( z_2 = (d, 0) \) with \( d \) as given in the figure. Steady states are represented by the dots. The solid line is the boundary computed by using the continuum formulation (see SI text). Note that on the right figure, the swarm separates into two groups.

\[
\begin{align*}
(a) & \quad d = 2 \\
(b) & \quad d = 1.5 \\
(c) & \quad d = 1
\end{align*}
\]
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result 1 is recovered by choosing $q = 2$ in [9].

From [8] 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 2. 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

$$
\frac{dx_i}{dt} = \frac{1}{N} \sum_{k=1, k \neq j}^{N} \left( \frac{x_j - x_k}{|x_j - x_k|} - a (x_j - x_k) \right) + \sum_{k=1}^{M} \frac{x_j - z_k}{|x_j - z_k|^2},
$$

and replace $z$ by $z_j$ 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 [49, 50], decision making in the group with strong leaders [51] and generalization of Keller-Segel model to multi-species in chemotaxis [52, 53, 54].

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 2 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 2 shows the continuum limit of [10] which is obtained by computing the evolution along the boundary $\partial D$ of the swarm, while assuming that swarm density $\rho = |D|$ is constant. The algorithm to do this is outlined in SI text.

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

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

$$+ G (|x_j - z|) \frac{x - z}{|x - z|} \quad [11]$$

$$M \frac{d^2 z}{dt^2} + \mu_0 \frac{dz}{dt} = \frac{1}{N} \sum_{k=1}^{N} H(|z - x_k|) \frac{z - x_k}{|z - x_k|} \quad [12]$$

where $\mu_j, \mu_0$ are friction coefficients of prey and predator respectively, and $m_j, M$ are their masses. Figure 5 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 [24, 55, 56].

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 [29, 57] for work on 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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