A Simple Predator-Prey Swarming Model

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Abstract

This paper describes an individual-based model for simulating the swarming behavior of prey in the presence of predators. Predators and prey are represented as agents that interact through radial force laws. The prey form swarms through attractive and repulsive forces. The predators interact with the prey through an anti-Newtonian force, which is a nonconservative force that acts in the same direction for both agents. Several options for forces between predators are explored. The resulting equations are solved numerically and the dynamics are described in the context of the swarm’s ability to realistically avoid the predators. The goal is to reproduce swarm behavior that has been observed in nature with the simplest possible model.

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INTRODUCTION

Animal aggregation is observed in a diverse range of organisms [1, 2]. It includes fish schooling, bird flocking, mammal herding, insect/bacterial swarming, and human crowding. Even predators have been known to act together in the form of hunting packs. There are shared similarities in all of these cases, such as the fact that the organisms act in unison and rapidly respond to obstacles. The universality of such features suggests simple mechanisms for its emergence. In this paper, swarming will refer to any such behavior in which organisms come together and act in a reasonably coordinated manner to produce an aggregate object.

Swarming has been studied extensively by computer simulation [3–7]. Many models are individual-based, where swarm members are represented as agents that interact with other agents as a function of their positions [8]. The use of force laws has been a general approach. These forces consist of a long-range attractive force that makes agents approach and form the swarm, coupled with a short-range repulsive force so that they do not collide with each other [9–11]. A self-propulsive force that pushes each agent forward toward some preferred velocity is often included [12–14]. Additionally, a mechanism to align the agents with each other is sometimes included, especially in application to flocking [12, 13, 15, 16].

These models have succeeded in reproducing some aspects of swarming observed in nature. The premise has been extended to study similar problems such as pedestrian control [17]. Features such as evolution can be included to facilitate the search for optimal parameters [13]. Furthermore, the possibility of implementing such algorithms into systems of robots has been explored [18, 19].

The model described in this paper has similarities with those in the literature. However, it differs in a few regards. First of all, there will be an emphasis on keeping the model simple at the expense of making it an accurate predictor of natural behavior. The intent is to reproduce swarming behavior without including the features dependent on the traits of the organism. The set of adjustable parameters is kept to a minimum to facilitate exploration of the dynamics. Secondly, the model will be focused on the swarming of prey in the presence of predators. Although predators have been implemented into some models [13, 15], it is less common than studying single species. Since a primary purpose of swarming is for protection from predators, the predator is important to include. Thirdly, the model does not include alignment or self-propulsion mechanisms, which are found in nearly all other models. This
is justified because of the presence of the predators. The interaction with the predators is expected to align the prey motions. If a predator is a distance away from the swarm, the force will act similarly upon each agent in the swarm and thus give uniform motion. This is confirmed in the results. More interesting effects can also emerge as a predator approaches the swarm. Thus, self-propulsion and other alignment mechanisms are assumed to be less important in this context.

MODEL

The system consists of two types of agents: predator and prey. The environment is a two-dimensional infinite Cartesian plane that represents the surface of the earth. Three-dimensional environments, such as the sky for birds or the water for fish, usually contain the most stunning swarming behavior but are not described in this paper since the dynamics do not appear to differ significantly from the two-dimensional model. There is assumed to be no interaction between the agents and the environment except for uniform friction. To facilitate computation, there are no more than a dozen agents in our simulations. In addition, there are more prey than predators to reflect the general situation in nature.

With the exception of friction, all forces are directed radially between agents and are power laws of the distance between the agents. The prey pairs interact through long-range attractive and short-range repulsive forces. The forces between the predator pairs are not as obvious since there is no general tactic that they follow in nature. Choosing the same forces as between prey allows the predators also to form swarms (i.e. hunting packs), which might be appropriate for a species such as wolves. Another option is a repulsive force so that the predators spread around and trap the swarm. The simplest option would be to have no force between predators, which implies that the predators do not coordinate with each other when attacking prey. All three possibilities will be considered. Lastly, there is an anti-Newtonian force between predator-prey pairs [20]. This force is equal in magnitude for both agents and acts in the direction from predator to prey. The anti-Newtonian force is nonconservative, which allows the system to stay in motion indefinitely despite the loss of energy from friction.

The long-range force \( f \) and short-range force \( g \) acting on agent \( i \) due to agent \( j \) are:
\( f_{ij} = r_{ij}^{\gamma - 1}(r_j - r_i) \) \hspace{1cm} (1)

\( g_{ij} = r_{ij}^{\alpha - 1}(r_j - r_i) \) \hspace{1cm} (2)

The vector \( r \) denotes the position of the agent, and \( r_{ij} \) is the distance between the agents. The force parameters are \( \gamma \) for the long-range force and \( \alpha \) for the short-range force, with \( \alpha < \gamma \). The short-range force is only used for repulsion. The long-range force is used for the attraction between prey pairs, the interaction between predator pairs, and the anti-Newtonian force between unlike agents. A value of \( \gamma = -1 \) tends to give the most realistic dynamics. With an inverse-squared dependence (\( \gamma = -2 \)), the force falls off too fast so that there is often an unnatural range of accelerations. With \( \gamma = 0 \), the predator has no preference for close prey over far away ones. A fractional value of \( \gamma \) is possible, but is not explored in this paper. The choice of \( \alpha \) is less critical, so \( \alpha = -2 \) is used here. The resulting equation of motion for prey is:

\[ m_o \ddot{r}_i = \sum_{\text{prey}} (f_{ij} - g_{ij}) - \sum_{\text{pred}} f_{ij} - b_o \dot{r}_i \] \hspace{1cm} (3)

The agent parameters are mass \( m \) and coefficient of friction \( b_o \), with indices \( x \) for predators and \( o \) for prey. The mass and coefficient of friction in the model roughly correspond to the physical mass and mobility of the organism. Additional coefficients may be introduced to weigh each contribution to the force differently, but this is avoided in this paper for simplicity. The first summation over \( j \) takes the indices of all other prey (\( j \neq i \)). This summation accounts for the attractive and repulsive forces that form the swarm. The second summation over \( j \) takes the indices of the predators and accounts for the anti-Newtonian forces. The final term accounts for friction, which is taken to be proportional to the velocity.

Three similar equations are considered for predators. The first gives no interaction between predators:

\[ m_x \ddot{r}_i = \sum_{\text{prey}} f_{ij} - b_x \dot{r}_i \] \hspace{1cm} (4)

The other two possibilities are either attraction or repulsion between predators. This corresponds to a plus or minus sign in the following equation:
\begin{equation}
m_x \ddot{r}_i = \sum_{pred} (\pm f_{ij} - g_{ij}) + \sum_{prey} f_{ij} - b_x \dot{r}_i
\end{equation}

The short-range repulsion is not essential for the predators when the long-range repulsive force is used.

The initial conditions are not critical in most cases. In our simulations, the prey are scattered randomly near the origin and the predators are placed a short distance outside. This corresponds to a situation where the predators approach an initially unorganized swarm. Initial velocities are taken to be zero.

RESULTS

Trivial case (no predator)

The trivial case has no predator in the system. The equations of motion simplify to the form:

\begin{equation}
m_o \ddot{r}_i = \sum_{j \neq i} (f_{ij} - g_{ij}) - b_o \dot{r}_i
\end{equation}

The result is that the prey form a stationary equilibrium cluster with agents evenly dispersed, as shown in Fig. 1. Animations corresponding to Fig. 1 and other figures can be found online at Ref [21]. The only situation in which the swarm does not come to a stationary equilibrium in the trivial case is when friction is removed, in which case energy is conserved and no stable equilibrium exists. The trivial case is not very interesting in itself, but it does show the type of organization to expect when predators are far away in the more complicated cases. Additional terms can be put into the equation of motion to make the trivial case more interesting, such as effects from an external field, self-propulsion for each agent, or possibly noise. However, the emphasis is on what happens once a predator is introduced, so there is no need to make the trivial case more realistic and complicated. Therefore, the trivial case is taken to be a rough approximation of a natural swarm with no predators around. A similar model for trivial swarming has been studied in Ref [22] in more mathematical detail.
Single predator

The next case has one predator with the multiple prey. It is observed that the general case no longer comes to a stable equilibrium. However, there are equilibrium cases where the predator travels into the center of the swarm and becomes trapped. Friction eventually brings it to a stop. One such equilibrium occurs when $m_x = 0.5$, $b_x = 1$, $m_o = 0.1$, $b_o = 0.5$ with seven prey. This is shown in Fig. 2 along with the path of the predator during the transient phase.

Other cases result in a prey swarm similar to that of the trivial case but perturbed by the predator. Although the equations do not include any alignment terms, the prey agents will generally move in a coordinated manner away from the predator. Once the predator gets near the swarm, the prey become less organized.

One simple solution is a quasiperiodic attractor that forms after a transient phase. As the predator approaches the swarm, the swarm divides in order to avoid it. The predator passes through and the pattern repeats, but shifted by a small angle. This attractor requires that the predator has more mass and less friction than the prey. One such set of parameters is $m_x = 2.5$, $b_x = 1$, $m_o = 0.1$, $b_o = 0.5$ with seven prey. The trajectories of the predator and prey are shown separately in Fig. 3, along with the motion of the center of mass.

In addition, there exist chaotic solutions. These are of more interest since they better match nature’s unpredictability. One case has the predator weave a path through the prey
FIG. 2. The positions of a predator trapped between seven prey in a stable equilibrium, along with the predator trajectory during the transient phase. The parameters for this case are $m_x = 0.5$, $b_x = 1$, $m_o = 0.1$, and $b_o = 0.5$.

swarm. The predator remains relatively close to the swarm, which deforms the swarm from the lattice pattern seen in the trivial case. Parameters for this are $m_x = 0.2$, $b_x = 0.1$, $m_o = 0.3$, $b_o = 0.5$ with seven prey. The trajectories are shown in Fig. 4. The largest Lyapunov exponent [23] is computed to be $\lambda \approx 0.75$.

With minor adjustment of the parameters, the prey become even less organized and the attractor becomes unstable over long periods of time. Unlike the previous case, the predator will sometimes chase prey away from the swarm for brief moments. The predator trajectory is shown in Fig. 5 for $m_x = 0.2$, $b_x = 0.4$, $m_o = 0.1$, $b_o = 0.5$ with seven prey. The loops that protrude from the dense swarm region are the paths on which the predator follows prey out of the swarm.

In some cases, the predator will chase a prey away from the swarm. This results in a two-body predator-prey system that remains independent of the swarm. This can be interpreted as a successful capture for the predator. The lone prey has lost the security of the swarm, so the predator should have an easier time capturing it. Of course, this does not happen in the simulation since the two agents are locked in an interminable chase. Additional rules could be applied at this point if a more realistic model is desired.

However, there is another natural way that a predator can capture a prey. If a predator has more friction and less mass than the prey, then it may be drawn in towards the prey...
FIG. 3. The trajectories in a quasiperiodic solution with the parameters $m_x = 2.5$, $b_x = 1$, $m_o = 0.1$, and $b_o = 0.5$. The predator trajectory is shown on the top, the corresponding trajectories of the seven prey are shown in the center, and the trajectory of the center of mass for the system is shown on the bottom.
FIG. 4. The trajectories in a chaotic solution with $m_x = 0.2$, $b_x = 0.1$, $m_o = 0.3$, and $b_o = 0.5$. The predator trajectory is shown on the top, and the corresponding trajectories of the seven prey are shown on the bottom.

while the prey is unable to escape. This leads to the predator approaching a singularity. This case is not as interesting from a dynamics perspective, but has valuable connections to nature. It corresponds to situations in which a predator is in much better physical shape than the prey. The low mass means that it undergoes high accelerations. The high friction means that it has increased maneuverability and can change directions rapidly. Thus, the parameters required for a predator to successfully capture a prey can be characterized.

The effect of the parameters on the dynamics can be seen from a bifurcation plot, where the largest Lyapunov exponent is plotted as a function of the four agent parameters. Such a bifurcation plot is shown in Fig. 6, where the four parameters were individually varied from the chaotic case in Fig. 4. Three distinct regions are visible. Periodic and quasiperiodic
FIG. 5. The trajectories in a chaotic solution with $m_x = 0.2$, $b_x = 0.4$, $m_o = 0.1$, and $b_o = 0.5$. The predator trajectory is shown on the top, and the corresponding trajectories of the seven prey are shown on the bottom. The predator occasionally pulls prey temporarily away from the swarm. This attractor is unstable over long periods of time.

Cases with $\lambda = 0$ are obtained for small values of $b_x$ and $m_o$ and large values of $b_o$ and $m_x$. This represents cases where the prey easily avoid the predator as it moves toward the swarm. The greater friction acting on prey allows them to change the direction of motion more rapidly than the predators, while the lower mass allows them to change position faster. At intermediate values, there is a region of robust chaos with $\lambda$ continuously increasing from $\lambda = 0$ at the first region. Within this chaotic region, there are a few windows where $\lambda = 0$ for values of $m_o$ and $m_x$. These windows correspond to quasiperiodic solutions. Finally, there is a sharp drop where $\lambda$ goes back to zero. In this region, the prey have difficulty escaping the predator. This leads to the cases where the predator chases one prey away from the
FIG. 6. A bifurcation plot showing the resulting largest Lyapunov exponent, $\lambda$, over a range of values for the four parameters when varied from the case in Fig. 4. There is a region of no chaos ($\lambda = 0$) for small $b_x$ and $m_o$ and large $b_o$ and $m_x$. Then there is a chaotic region for intermediate values where $\lambda$ varies smoothly except for some windows of quasiperiodicity. Finally, there is a sharp drop back to $\lambda = 0$ where the predator either chases one prey from the swarm or captures it.

swarm. After long times, $\lambda = 0$ since the swarm and two-body predator-prey system stop interacting because of drifting apart. Also in this region are cases where the prey is unable to escape the predator, resulting in a singularity that makes the computation of $\lambda$ difficult.
Multiple predators

The most complicated case has multiple predators with multiple prey. This is also the most difficult situation to model because the features of the predator become important.

The simplest option is to have no force between the predators, which corresponds to Eq. (4). This represents predators that do not explicitly cooperate. The resulting dynamics are generally chaotic. The dynamics are similar to the chaotic cases with one predator, except that the swarm is even more unorganized due to the extra predators. If forces between predators are added but are very weak, the outcome is similar.

The next option is to have short-range repulsion and long-range attraction between predators. This corresponds to Eq. (5) with the plus sign. This allows the predators to form swarms. Any combination of prey swarm and predator swarm can exist. When the force between predators is not quite strong enough to bind them together, the dynamics are similar to the case of no force between predators.

A more interesting outcome is to have a prey swarm and a predator swarm exist concurrently. In such a case, there is initially a transient chaotic phase where the predators orbit the swarm separately. This transient phase can exist for a long period of time depending on initial conditions. After some time, the predators approach each other and combine into a swarm. The final result is a two-body problem: a predator swarm in a circular orbit around a prey swarm. This quasiperiodic attractor is shown in Fig. 7 for three predators, seven prey with \( m_x = 1, b_x = 0.1, m_o = 0.5, b_o = 0.5 \).

The final option is to have a repulsive force between the predator agents, corresponding to the negative sign of Eq. (5). This might correspond to predators that prefer to spread around and herd the prey swarm. Herding is a complex behavior, but the basic features may be reproduced with this model. Within a range of parameters, the predators orbit the prey swarm while also avoiding each other. The prey swarm undergoes very little net motion since the predators tend to divide into all directions. Hence, the territory covered by the prey is very small compared to that of the predators. The trajectories for \( m_x = 1, b_x = 0.1, m_o = 0.5, b_o = 1 \) are shown for the three predators, seven prey in Fig. 8. The largest Lyapunov exponent for this case is \( \lambda \approx 0.32 \).

With one or more predators, some of the chaotic attractors break apart after long periods of time. This appears to be an inherent rather than numerical effect. The conditions under
FIG. 7. The trajectories for a quasiperiodic attractor formed by three predators, seven prey with \( m_x = 1, b_x = 0.1, m_o = 0.5, \) and \( b_o = 0.5 \) with an attractive force between predators. The prey swarm orbits inside of the circular predator swarm orbit.

which this happens are not clear, but eventually the agents arrange themselves so that the system splits into two or more distinct clusters. This outcome is influenced by the parameters, and it appears that the cases listed here are stable.

**Unrealistic results**

Along with the dynamics already presented, there are many other less realistic solutions. Some of these exhibit notable features despite not being useful models of nature. One especially unusual solution is shown in Fig. 9, where \( \gamma = 0, \alpha = -1 m_x = 0.2, b_x = 0.4, m_o = 0.2, b_o = 0.2 \) for one predator and five prey. This attractor forms after a transient phase independent of initial conditions. All of the prey orbit on a single path around the predator, while the predator itself has a periodic orbit inside of the prey’s orbit. Over longer periods of time, the orbit rotates and covers the area of a circle. This case is just one example of the unexpected solutions that can spring from the anti-Newtonian force.
FIG. 8. The chaotic trajectories for a system of three predators, seven prey with $m_x = 1$, $b_x = 0.1$, $m_o = 0.5$, and $b_o = 1$ with a repulsive force between predators. The predator trajectories are shown on top, and the corresponding prey trajectories on bottom.

CONCLUSION

The model presented in this paper manages to reproduce basic swarming behavior by using only friction and central forces between agents. Most other swarming models include additional complexity, usually in the form of directional forces or self-propulsion for each agent. This was found to be unessential for this model. This is largely due to the predator interacting with prey through the anti-Newtonian force, which has the tendency to cause the prey to move as a group when the predator is at a distance from the swarm. Additionally, the anti-Newtonian force keeps the system in motion despite energy loss to friction.

One of the most evident results was the unified motion of the swarms despite having each agent act autonomously. This is known to be feature of real swarms. Emergent behavior in-
FIG. 9. A peculiar solution with $\gamma = 0$, $\alpha = -1$, $m_x = 0.2$, $b_x = 0.4$, $m_o = 0.2$, and $b_o = 0.2$. The five prey orbit on an outer trajectory and a single predator orbits inside. The entire orbit slowly revolves, eventually filling a circular area.

cludes the temporary division of the swarm into two fragments when a predator approaches. This motion would confuse the predator since it must decide which fragment to chase.

There are three main outcomes that may occur. The first outcome is for the dynamics to be periodic or quasiperiodic. These are probably the least realistic solutions because naturally observed swarming near predators is complicated or unpredictable. The second outcome is chaos. The presence of chaotic solutions hints at the complexity that could arise in real systems. It was observed that some of the chaotic solutions are unstable over long times, which leads to the third outcome. The third outcome is for the system to be unbounded or encounter a singularity. Unbounded cases correspond to the predator chasing a prey away from the swarm. In such cases, the predator would have favorable chances to capture the prey in a more realistic model. Singularities occur when the predator approaches the prey faster than the prey can escape. The resulting singularity causes problems in the numerical simulation. This can be interpreted as the predator directly capturing the prey.

To make the model more complete, additional terms or degrees of freedom could be included in the equations. The best way to construct the model would be to match it to experimental data from nature. For example, rather than having a single parameter gamma that determines the range dependence for all three of the long-range forces, the dynamics might better match observed behavior with three separate parameters. Such changes would
make it more difficult to explore the entire parameter space, but might result in much more realistic dynamics. Furthermore, noise may be added to the equations. This may arise from mistakes made by the organisms or the unpredictable effects of the system [24]. This may perturb some of the solutions and make them appear to be more realistic.

A more realistic model would also incorporate basic hunting and evasion tactics that may arise from instincts or experience. For example, if one prey finds itself disconnected from the swarm, the predator should pursue it for an easy meal. In this model, the predator usually goes towards the swarm since there is a stronger force in that direction due to the larger number of agents. This can be remedied in a few different ways. One way would be to make the force proportional to the distance of the prey from the center of mass. Another option would be to include different sets of equations that depend on the situation at hand: the usual equations can be used when all prey are in the swarm, and then a transition to a new set of equations with completely different forces can take effect once a prey gets displaced. Any of these options would add considerable complexity to the model, so it would be important to be certain of one’s choice before exploring the dynamics.

Although the model is physically simple, it can become computationally inefficient with a larger number of agents. This suggests that approximations should be considered when studying larger systems. There could be ways to simplify the current differential equation while still retaining the essence of the dynamics. One idea that has worked well for large systems is to model the swarm as a continuum [7].

There are two promising applications of swarming models. The first is to understand how swarms act in nature and to explain the emergent patterns. The optimal parameters may be uncovered and these may be linked to the biological traits of the organism. It would be most appropriate for a biologist to do such work. The second application is to apply the algorithms to systems of robots. Although this option is still in the rudimentary phase due to initial difficulties in designing small robots, such possibilities are now being seriously considered [18, 19]. By understanding swarms at a fundamental level, the systems of robots can be engineered to best fit their purpose without causing harm. Even so, it is difficult to predict what will emerge with such technology.

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[21] See EPAPS Document No. [number will be inserted by publisher] for animations of the figures.