Aggregation increases prey survival time in group chase and escape

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Received 31 January 2014, revised 18 June 2014
Accepted for publication 25 June 2014
Published 4 August 2014

Abstract
Recently developed chase-and-escape models have addressed a fascinating pursuit-and-evasion problem that may have both theoretical significance and potential applications. We introduce three aggregation strategies for the prey in a group chase model on a lattice. Simulation results show that aggregation dramatically increases the group survival time, even allowing immortal prey. The average survival time $\tau$ and the aggregation probability $P$ have a power-law dependence of $\tau \sim (1 - P)^{-1}$ for $P \in [0.9, 0.997]$. With increasing numbers of predators, there is still a phase transition. When the number of predators is less than the critical point value, the prey group survival time increases significantly.

Online supplementary data available from stacks.iop.org/njp/16/083006/mmedia

Keywords: collective behaviors, group chase and escape, aggregation

Introduction
Many studies have investigated complex collective motion [1], in which simple rules can produce complex emergent behaviors. Related topics include collective navigation observed in the flight of birds [2], trail organization in ants [3], and swarming in locusts [4], fish [5] and bacteria [6]. These group behaviors bring new functionality to complex collective motion and
can be computed by simple interaction models [7, 8]. Each agent in these models acts according to the computation it performs on the locations of the other neighbor agents. Simple interaction models have been used to demonstrate and study the fundamental building blocks of complex collective motion [4, 7, 9].

Reynolds created the Boids model in 1986 to simulate swarm behavior with three simple rules: separation, alignment and cohesion [8]. It is considered the first computational model to demonstrate quantitative and qualitative features of flocking behavior observed in birds. As a special case of the Boids model, the self-propelled particles (SPP) model was introduced by Vicsek et al [7]. A swarm is modeled in the SPP model by a collection of particles that move with a constant speed but respond to a random perturbation by adopting at each time increment the average direction of motion of the other particles in their local neighborhood. The SPP model predicted random or coherent motion of group clusters depending on the particle density with some random perturbation added. Couzin et al built a model to show how information can be transferred within groups. They revealed that group size is inversely proportional to the number of informed individuals [9].

Chase and escape is a family of problems in the field of collective behavior research. A merchant vessel pursued by a pirate ship that it desperately tries to evade is a good example [10]. Issues relating to these problems have a long history and have often led to interesting mathematical results [11]. The classical setup involves two agents, and the goal is to choose a deterministic motion strategy, given their velocities and sighting ranges, that optimizes their respective chances of successful pursuit or evasion. As an improvement, when there is one prey chased by M predators in a lattice model, Oshanin et al analyzed the efficacy of a lazy, minimal-effort evasion strategy according to which the prey tries to avoid encounters with the predators by making a hop only when any of the predators appears within its sighting range [10]. Their study found a simple asymptotic relation $P_e(t) \sim (N/V)^2 \ln P_{imm}(t)$ between the survival probabilities of an evasive and an immobile prey.

The group chase and escape model proposed by Kamimura et al [12] in 2010 described an evasive group of prey chased by a group of predators on lattice. In their model, an optimal number of chasers exists for a given number of targets to minimize the cost of catching all targets. Vicsek rated this research highly in Nature [13]: ‘Hunting in groups or gregarious prey is such a widespread phenomenon in the animal kingdom that it comes as a surprise that the first simple model of the process has only just been published’. Angelani’s work in Phys. Rev. Lett. introduced an individual-based off-lattice model and changed the escape strategy by considering a weighted (power-law) average of neighboring predators with an optimal weight exponent [14]. They found that this strategy can benefit the prey and the effect is more pronounced when preys are faster than predators. They stated that the case of alignment has no relevant differences with respect to that of non-alignment. Yamamoto et al [15] proposed a strategy for prey and predator to maximize the distance from their mates, in order to avoid making a flock for the efficient escape in a honeycomb grid. Lin et al [16] developed a 3D off-lattice model to describe the predation process and found that prey have the maximum predation avoidance because they form localized large groups while interacting with low noise.

We argue, in this paper, that aggregation may benefit the prey rather than having no influence or even being totally harmful. To find inspiration from nature, we find that aggregation behaviors have been observed universally in animate and inanimate systems [17] and provide many benefits to group prey animals [18]. Animals in groups are believed to benefit from an increased probability of detecting a predator [19]. The herd can reduce the cost in
vigilance in springbok [20]. Observations of rainbowfish suggested that more information on the location of the escape route was available to fish in larger shoal sizes owing to social stimulation [21].

We introduce the aggregation strategy of the evader in the group chase and escape model. We focus on the changes of survival time distributions, the influence of aggregation probability on the survival time and the phase transition of survival time versus the number of predators.

The model

We consider a two-dimensional square lattice $L_x \times L_y$ with periodical boundary conditions, where $L_x = L_y = 100$ [12]. Each site in the lattice is either empty or occupied by a single particle: a prey or a predator. The distance of two particles is measured by Euclidean distance, considering the periodical boundary conditions, the distance between particle $i$ and $j$ is

$$D(\vec{c}_i, \vec{c}_j) = \sqrt{d^2(x_i, x_j) + d^2(y_i, y_j)},$$

where $\vec{c}_i = (x_i, y_i)$ is the coordinate of the site where the particle $i$ stays, $d(r_i, r_j) = \min(|r_i - r_j|, L - |r_i - r_j|)$, $r_i$ and $r_j$ are the coordinate components.

To initialize the model, $M$ predators and $N$ prey are randomly distributed in the lattice. During each time step, each predator and each live prey hops by one site, excluding the corner sites. For a single particle, the possible direction set is

$$U = \{[1, 0], [0, 1], [-1, 0], [0, -1]\}.$$ (2)

Predators hop first in a random order, followed by the live prey. The simulation stops when all the prey are eliminated from the system.

The particles follow the hopping rules described below:

Each predator will find its nearest prey as a target to chase. When two or more prey are at the same minimum distance from a predator, it randomly chooses one to chase after. The possible chasing direction set for predator $i$ is

$$U_i = \{\vec{u} \in U | D(\vec{c}_e + \vec{u}, \vec{c}_i) < D(\vec{c}_i, \vec{c}_e)\},$$ (3)

where $\vec{c}_i$ is the coordinate of its chasing target $e$. As shown in figure 1, there is only one site for predator 1 to get closer to its target, with $p = 1$. There are two possible sites for predator 2 to hop to in order to approach its target, with an equal probability of $p = 1/2$.

Each prey $i$ tries to evade its nearest predators $c$, who has the minimum distance from itself. When two or more predators are at the same minimum distance from a prey, the prey randomly selects one to escape from. The possible escaping direction set for prey is

$$U_i = \{\vec{u} \in U | D(\vec{c}_c + \vec{u}, \vec{c}_i) > D(\vec{c}_i, \vec{c}_c)\},$$ (4)

where $\vec{c}_i$ is the coordinate of its escaping target $c$. In figure 1, if the prey and its evading target are in the same row or the same column, as prey 1 and predator 1 in figure 1, there are three available sites with probability $p = 1/3$. In another case in figure 1, there are two nearest sites for prey 2 finding predator 1 as its escaping target to evade. In this case, the probability for each site is $p = 1/2$.

If a particle chooses a site occupied by another particle of the same species, it has to remain in its original site and waits for the next turn to hop.
A prey cannot hop to an adjacent site occupied by a predator. The predator, however, can hop to a next site occupied by a prey to catch it. Then, the prey is ‘dead’ and eliminated from the system.

Next, we introduce three aggregation strategies. We define $P$ as the aggregation probability to hop toward the prey group (prefer similar type neighbor agents). The first strategy is called aggregation toward the mass center (MC). The aggregation point, where the prey is trying to hop to, is the MC, computed as the average vector of coordinates of the current snapshot of the live prey including the prey under consideration:

$$ x_{ap} = \frac{\sum_{i}^{N_{t}} x_{i}}{N_{t}}, \quad y_{ap} = \frac{\sum_{i}^{N_{t}} y_{i}}{N_{t}}. $$

where $c_{ap} = (x_{ap}, y_{ap})$ is the aggregation point, $N_{t}$ is the number of live prey at $t$ time step. The aggregation direction set for prey $i$ is
\[ U_a = \left\{ \vec{u} \in U_e \mid \min D\left(\vec{c}_i + \vec{u}, \vec{c}_{ap}\right) \right\} . \]  

(6)

The plausible MC idea, however, may be not-well defined when the group is moving across the borders. The aggregation point does not follow the group moving direction and misleads prey to turn around toward the predators, as shown in video S4, available from stacks.iop.org/njp/16/083006/mmedia.

For the second strategy, \textit{aggregation toward the nearest neighbor prey} (NN), the aggregation point is the coordinate of the closest prey, as explained in figure 1. For the third strategy, \textit{aggregation is to minimize the distances to all the other live prey} (MD), prey \( i \) chooses the site among all possible sites which has the shortest distance to all other live prey, described as follows:

\[ U_a = \left\{ \vec{u} \in U_e \mid \min \left( \sum_{p=1}^{N} D\left(\vec{c}_i + \vec{u}, \vec{c}_p\right) \right) \right\} , \]  

(7)

where \( \vec{c}_p \) is the coordinate of live prey \( p \).

The procedure for choosing the direction with aggregation strategies is listed in the methods section.

**Methods**

Pseudocode for the prey to choose a direction using aggregation strategies.

1. Choose directions for evading the nearest predator.
   1.1 Calculate the distance from each predator.
   1.2 Find the nearest predator(s). If the number is more than one, select a random one as escaping target.
   1.3 Find the possible direction set \( U_e \) to get away from the escaping target.
2. Determine whether to aggregate with probability \( P \).
   2.1 If not to aggregate, randomly choose a direction among the possible directions in \( U_e \).
   2.2 If to aggregate, choose aggregation directions \( U_a \) among the possible directions in \( U_e \). If there are more than one element in \( U_a \), then choose one randomly.
3. If the site in the chosen direction is occupied, the prey stays. (This follows the rules in [12] for convenience to compare. We tested other alternatives and did not find significant differences.)

**Results**

For each aggregation strategy and parameter configuration, the system is run for \( \text{runtimes} = 10^4 \) times. The survival time of each prey is recorded. The survival time of the last prey is defined as the survival time of the group, denoted as \( T \).

We first analyzed the survival time \( T \), depending on the number of predators with full aggregation probability \( (P = 1) \) and a fixed prey number \( (N = 10) \). We present the analysis of \( T \) with the three strategies. We find that when \( M = 500 \), predators are dominant and the aggregation strategy has no effect, as shown by the square symbol lines in figures 2, 3 and 4,
Figure 2. Distribution of the prey’s group survival time, where $N = 10$ and $P = 1$. The black curves are the simulation results of strategy MC, compared with the gray curves with no aggregation strategy. Aggregation has no effect for $M = 500$, as the two curves overlap, and there is an identifiable improvement for $M = 100$, which shows a rightward shift of the aggregation curve. When $M = 10$, the distribution becomes bimodal. There are numerous prey with survival times around $10^2$ and $8 \times 10^2$ time steps, forming the first and the second peaks. However, there also exist some prey with very long survival times of over $10^6$ time steps.

Figure 3. Distribution of the prey’s group survival time, where $N = 10$ and $P = 1$. The black curves are the simulation results of strategy NN, compared with the gray curves with no aggregation strategy. Aggregation has no effect for $M = 500$ and $M = 100$, as each pair of curves overlaps. When $M = 10$, there are more prey with a shorter survival time of approximately $10^2$, as indicated by the leftward shift of the peak of the distribution. There is also a long tail which consists of scattered points. There are 4872 out of $10^4$ runs in which predators cannot finish the entire catch. These cases are truncated at the $10^7$th time step, shown as an outlier point in the upper right corner.
where the two curves (with and without aggregation strategies) overlap in each figure. For strategy MC and MD, when $M = 100$, there is an obvious increase of the average group survival time without changing the distribution pattern, as is demonstrated by a rightward shift of the curve shown in figures 2 and 4. For strategy NN, the two star symbol lines overlap in figure 3.

With the same numbers of predators and prey, $M = 10$, strategy MC changes the distribution into a bimodal one, while strategy NN and MD change the distribution to a single peak and an outlier point. The outlier point is because strategy MD uses the aggregation effect for the prey so that they can survive much longer. $T$ in such runs is truncated at the $10^7$th time step, considering the computational time consumption, and prey can be regarded as immortal for such a long survival time. Strategy NN produces the same result when $M = 10$, as is shown in figure 3. In strategy NN and MD, 48.72% and 58.68% of the runs, respectively, end with the predators unable to accomplish the entire catch. This makes a great contribution to the sharp increase of the survival time with the two strategies. In the rest of the runs, the peak of the survival time distribution (black dots) shifts to the left and reaches over 10 times more than that of the previous peak (gray dots). The distribution of NN has a long tail, while that of MD does not.

In contrast, strategy MC does not perform as well as the others. The maximum survival time $T$ is only extended to over $10^6$ time steps, as shown in figure 2, and it produces a bimodal distribution. A small portion of the runs with less survival time than the no-aggregation case has a relatively high frequency. At the same time, the long tail indicates that there are cases when the group survival time increases by one or two orders of magnitude.

Before the aggregation strategy is introduced, the prey’s survival time is relatively concentrated between $10^2$ and $10^4$ time steps. After each strategy is introduced, each first peak for $M = 10$ of $T$ moves to the left a little in figures 2–4. This shows that the proportion of prey

Figure 4. Distribution of the prey’s group survival time $T$, where $N = 10$ and $P = 1$. The black curves are the simulation results of strategy MD, compared with the gray curves with no aggregation strategy. Aggregation has no effect for $M = 500$, as the two curves overlap, and there is an identifiable improvement for $M = 100$, for which the aggregation curve shifts to the right. When $M = 10$, there are more prey with a shorter survival time of approximately $10^2$, as indicated by the leftward shift of the peak of the distribution. However, there are 5868 out of $10^4$ runs in which the predators cannot finish the entire catch. These cases are truncated at the $10^7$th time step, shown as an outlier point in the upper right corner.
with shorter survival time increases. This is because all the prey aggregate together and lead their chasers to complete encirclement, also called cage-trapping [14] and discussed in [15], as shown in video S1 clip 1 and video S2 clip 1, available from stacks.iop.org/njp/16/083006/mmedia.

The positive side for the prey, though, does compensate for the negative impact of aggregation strategies in the sense of increasing the survival time of the whole prey group. In some cases, there are some prey that attract all the predators together into a predator group, leaving the other prey out of the encirclement. After the sacrifice of these prey, the predator group chases the other prey, and this may lead to a very long survival time, as shown in video S1 clip 2 and video S2 clip 2. In some other cases that benefit the prey, the predators form a group without evidence of sacrificing some prey, and this, as expected, leads to a very long survival time, as demonstrated in figure S3, where all ten prey survived until the end (10^7 time steps) in nearly 4% of the runs. The critical factor that extends the prey’s survival time is that the prey form alignments. The definition of an alignment is given in the supplementary data, available from stacks.iop.org/njp/16/083006/mmedia. Once predators converge into a group, there is only one remaining chasing direction, and prey aggregate along this direction to form an alignment. The predators will never catch the rest of the prey if the prey do not slow down along that direction for some reason.

Next, we discuss how the aggregation probability affects the survival time. As mentioned above, there is no obvious increase in survival time even after introducing aggregation when the predators’ number is dominant. Thus, we only investigated the case of M = 10, N = 10 by focusing on the average entire catch time τ = T/runtimes.

We simulated the chase-and-escape behaviors with aggregation probability P ranging from 0 to 1, indicating from non to full aggregation. Figure 5 shows that τ changes insignificantly as P increases from 0 to 0.9. When P is set greater than 0.9, the average survival time increases steeply. We can perceive a power-law dependence of τ ∼ (1 − P)^−1 in the interval P ∈ [0, 0.997]. Because there are truncated runs when P = 0.998 and P = 0.999, shown in table 1, we do not take into account these values for the fitting of τ ∼ α(1 − P)^b for the interval P ∈ [0.9, 0.997]. We still keep the values with truncation at the 10^7th time step for reference, which are supposed to be greater without truncation. The slope b, which measures the effectiveness of τ along with P, is approximate to −1.

Next, we address the impact of changing the number of predators. Figure 6 shows that the phase transition critical point stays the same around M = 40 with or without the aggregation strategies when N = 10. While the region above the phase transition is the same with or without aggregation, the curves with aggregation are above the basic curve with no aggregation when there are relatively fewer predators. This means that aggregation effectively improves the survival time. When M ≤ 40, τ of NN and MD is clearly greater than that of non-aggregation, and there are some cases in which predators cannot catch all the prey. There is a drop when M = 10 because of the more percent of runs which is truncated at 10^7. For strategy MC, aggregation shows benefits only when M = 10.

Interestingly, as we mentioned above, we find that the two aggregation strategies NN and MD make the prey live more than 10^7 time steps (immortal) when M < 40. Table 2 shows the proportion of runs with immortal individual prey out of total runs. We present an explanation in the supplementary data. We modified the previous definition of alignment to be the vector sum of each prey’s velocity [7]. Video S1 and S2 show how prey form an alignment and escape in a fixed pattern.
However, when one prey is caught, aggregation may result in prey blocking each other, as shown in video S3, clip 2 and clip 4. The reason is that the remaining live prey and the predators need to recalculate their nearest escaping and chasing targets. It may happen that after one prey is caught, some of the predators lagging behind turn into chasing targets running in the front due to the periodic boundary condition. These predators will chase the prey in the opposite direction. The prey in the front will thus escape in the opposite direction. Still, the remaining predators are chasing along the original direction. Prey may compete for the same sites and block each other. It is not rarely observed when aggregation probability \( P \) is in the interval \((0.9, 1)\).

### Discussion and conclusion

Angelani stated that the alignment makes no difference with no-alignment cases [14]. Yamamoto et al stated that for the efficient escape, it is important for the targets not to form a
We did observe in some cases that prey died quickly because of the encirclement resulted from aggregation as stated in the Results section. However, by introducing proper aggregation strategies, the system can dramatically increase the group survival time by comparison with the no-aggregation case. There may even be immortal prey. There is still a phase transition as in [12], with the critical point unchanged. When the number of predators is less than the critical point value, the survival time increases much more than that without aggregation [12]. Power-law dependence between $\tau$ and $1 - P$ is found when $P \in [0.9, 0.997]$ with exponential approximate to $-1$, which enriches the popular studies on power-law distribution, e.g., the aggregate-size distribution [17].

The power-law distribution can be understood by recalling that $1/(1 - P)$ indicates the expected time steps between two consecutive hoppings of a prey following the original strategy without aggregation. Because the aggregate direction is among the possible escape directions, the time steps between two consecutive hoppings that a prey escapes without following the aggregation direction is proportional to $1/(1 - P)$. Considering our explanation that when the
prey form alignment, the same speed makes the prey never caught, the survival time $\tau$ should be proportional to $1/(1 - P)$.

Aggregation can have a strongly beneficial effect, allowing prey with the same speed as predators to survive much longer in a lattice model. There are strategies to maximize the total of the distance from their mates for both prey and predators in [15]. This current research studies only strategy for prey, which is easy to adopt and benefit themselves, while strategies for both prey and predators may involve gaming. We believe that aggregation can also benefit the prey in an off-lattice model as the Angelani’s mechanism does [14], which will be reported in our future work. References [12, 14, 15] and [16] all introduced noise as a parameter and analyzed its impacts. In order to show the explicit impact of the aggregation probability exerts on group survival time, we did not introduce noise in the current research, which can be a task in the next step.

The benefits to the prey gained from aggregation may be viewed as the prey sharing evasion information with each other to form set the correct escape direction for the whole group. To escape to the pro-aggregation direction is a breaking of symmetry to all the possible escaping directions in the absence of aggregation.

In the three aggregation strategies proposed, the NN and MD strategies perform better, while NN may be more suitable for biological creatures and simple robots that do not have global sighting range. This is because finding the nearest mate as an aggregation target is easier to understand and implement among these agent groups in practical use. The MC strategy performs more poorly because the aggregation point may not be the prey group MC due to the periodical boundary, as explained in the supplementary data. This strategy leads the prey to form the alignment with keeping a distance from their mates as shown in video S4. Most importantly, the alignment with MC strategy is not so steady as NN and MD.

Couzin’s work also demonstrated from another perspective that one agent from the prey group may be more easily attacked by fish [22].

These studies may promote the understanding of aggregation in prey animals [19, 20] by providing an alternative explanation for the fact that, although animals may not understand why they aggregate, aggregation does let them live longer.

**Acknowledgments**

This research is supported by China National Natural Science Foundation grants 61374165, 31261160495, and the Fundamental Research Funds for the Central Universities of China as well as the project by State Key Laboratory of Earth Surface Processes and Resource Ecology of Beijing Normal University. The authors would like to thank Professor Shlomo Havlin from Bar-Ilan University, Israel and Dr Yangqing Hu from Beijing Normal University.

**References**

[1] Halloy J et al 2007 Science 318 1155
[2] Nagy M, Ákos Z, Biro D and Vicsek T 2010 Nature 464 890
[3] Beckers R, Deneubourg J L and Goss S 1992 J. Theor. Biol. 159 195
[4] Buhl J et al 2006 Science 312 1402
[5] Ward A et al 2008 Proc. Natl Acad. Sci. USA 105 6948
[6] Shklarsh A, Ariel G, Schneidman E and Ben-Jacob E 2011 PLoS Comput. Biol. 7 e1002177
[7] Vicsek T et al 1995 Phys. Rev. Lett. 75 1226
[8] Reynolds C W 1995 Flocks, herds and schools: a distributed behavioral model Proc. of the 14th Annual Conf. on Computer Graphics and Interactive Techniques (New York, USA) pp 25–34
[9] Couzin I D, Krause J, Franks N R and Levin S A 2005 Nature 433 513
[10] Oshanin G, Vasilyev O, Krapivsky P L and Klafter J 2009 Proc. Natl Acad. Sci. USA 106 13696
[11] Nahin P J 2007 Chases and Escapes: The Mathematics of Pursuit and Evasion (Princeton, NJ: Princeton University Press)
[12] Kamimura A and Ohira T 2010 New J. Phys. 12 053013
[13] Vicsek T et al 2010 Nature 466 43
[14] Angelani L 2012 Phys. Rev. Lett. 109 118104
[15] Yamamoto K and Yamamoto S 2013 SICE Annual Conf.
[16] Lin Y and Abaid N 2013 Phys. Rev. E 88 06272
[17] Convertino M, Simini F, Catani F, Linkov I and Kiker G A 2013 arXiv:1303.1610v1[q-bio.QM]
[18] Hamilton W D 1971 J. Theor. Biol. 31 295
[19] Elgar M A 1989 Biol. Rev. 64 13
[20] Burger J, Safina C and Gochfeld M 2000 Acta Ethologica 2 97
[21] Brown C and Warburton K 1999 Environ. Biol. Fishes 56 455
[22] Ioannou C C, Guttal V and Couzin I D 2012 Science 337 1212