Collective Predation and Escape Strategies

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The phenomenon of collective predation is analyzed by using a simple individual-based model reproducing spatial animal movements. Two groups of self-propelled organisms are simulated by using Vicseklike models including steric intragroup repulsion. Chase and escape are described by intergroups interactions, attraction (for predators) or repulsion (for preys) from nearest particles of the opposite group. The quantitative analysis of some relevant quantities (total catch time, lifetime distribution, predation rate) allows us to characterize many aspects of the predation phenomenon and gives insights into the study of efficient escape strategies. The reported findings could be of relevance for many basic and applied disciplines, from statistical physics, to ecology, and robotics.

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Introduction.—Chase and escape situations are widespread in animal behavior in very different contexts, ranging from a child's game of tag to predation events in species interactions. In many cases, a large amount of organisms are involved, resulting in nontrivial dynamic behaviors, such as the emergence of collective and coordinated motions [1,2]. The search for efficient strategies is usually of fundamental importance, being determinant in enhancing the survival chance of single organisms or entire populations. Animals adopt a large variety of escaping strategies, ranging from a straight line flight from a predator to more complex behavior, e.g., running in zigzags, performing intermittent locomotion, or jumping, just to cite a few [3]. Very often, the same animal can also adopt unpredictable escape behavior, choosing among different preferred trajectories in a random fashion (for a recent review on escape responses against predator attacks see Ref. [4]). While much effort has been devoted to the study of one-to-one predation [5], only recently has the role of multiple predators and/or preys been investigated [6–16]. In order to study collective effects emerging in predation phenomena, one can resort to individual-based numerical models, in which each organism is represented by a particle following a few simple dynamics rules, such as erratic free motion in a given space in addition to straight line escape from a near predator. Such simplified models can be useful to elucidate the emergence of some nontrivial behaviors and can be considered as a starting point for more realistic modeling. In a recent paper, Kamimura and Ohira [6] have introduced a lattice model (pointlike randomly walking particles following simple dynamical rules, increasing or decreasing the distance from nearest particle of the opposite group) to analyze group spatial chase and escape phenomena. Despite its simplicity, the model is able to reproduce rich and interesting behaviors [7].

In this Letter, I will address the question of characterizing the statistical properties of predation phenomena, focusing on the efficiency of escape strategies. I will introduce an individual-based off-lattice model, based on the modeling of self-propelled organisms by Vicsek *et al.* [17] and including chase-escape mechanisms through simple intergroup pairwise interactions and predation events through the elimination of preys once caught by predators. Unlike the Kamimura and Ohira model [6], the present study allows us in a simple way the investigation of various interesting situations, such as the presence of different escape strategies, the case of different groups speeds, and the role of alignment rules. By analyzing the statistics of predation events (lifetime distributions and total catch time), we provide evidence for the existence of two catch regimes with different scaling behaviors, in agreement with what was observed in lattice models [6]: a *fast-catch* regime at a high predator concentration and a *slow-catch* one at low concentration. The role of emerging collective catch is particularly evident by analyzing the predation rate. One observes "spike-like" events, corresponding to cage trapping of a preys group by many predators converging on it. The main new finding of the present Letter concerns the role of escape strategies in enhancing survival probability for the prey. The optimal strategy is obtained by considering a power-law weighted average of nearest predators, with the optimal power-law exponent around $w = 2$. A simplified mathematical model provides a simple explanation of this fact. The reported finding can be of interest in all the cases in which one has to find or explain escaping strategies, from robotics [16] to animal behaviors.

The model.—We consider the following model. There are two groups of organisms, predators or chasers (C), and preys or targets (T). The number of chasers is N_C (constant during simulations) and the number of initial targets is N_T, which can decrease over time due to catching events. Each organism is described by position and velocity vectors in a d-dimensional space (in the following, $d = 2$). Simulations will be performed in a box of length L with periodic boundary conditions. Particles move at constant speed v_0 and their positions and velocities are updated according to Ref. [18]

$$\mathbf{r}_i(t+\Delta t) = \mathbf{r}_i(t) + \mathbf{v}_i(t+\Delta t)\Delta t \tag{1}$$

$$\mathbf{v}_i(t+\Delta t) = v_0 \hat{\mathbf{v}}_i^{(\mathrm{int.})}(t), \tag{2}$$

where i is the particle label and $\hat{\mathbf{v}}^{(\mathrm{int.})}$ is a unit vector which is determined by various intra- and intergroups interacting terms:

$$\mathbf{v}_i^{(\mathrm{int.})} = \mathcal{R}_\eta[\hat{\mathbf{v}}_i^{(\mathrm{al.})}] + \beta \mathbf{f}_i^{(\mathrm{rep.})} + \gamma \hat{\mathbf{f}}_i^{(CT)}. \tag{3}$$

The first term describes the self-propulsion and alignment effect

$$\mathbf{v}_i^{(\mathrm{al.})} = \sum_{j \in \mathcal{S}_i^{(\mathrm{al.})}} \mathbf{v}_j, \tag{4}$$

where the sum is over the particles of the same group (including particle i) within a sphere of radius r_0 surrounding particle i. The effect of noise is described by the operator $\mathcal{R}_\eta$ which performs a rotation of $\hat{\mathbf{v}}_i^{(\mathrm{al.})}$ by a random angle uniformly distributed in the interval $[-\eta\pi, \eta\pi]$ with $\eta \in [0, 1]$ [20]. The second term

$$\mathbf{f}_i^{(\mathrm{rep.})} = \sum_{j \in \mathcal{S}_i^{(\mathrm{rep.})}} \mathbf{f}(\mathbf{r}_i - \mathbf{r}_j) \tag{5}$$

is a steric repulsive force preventing particle overlap, the sum is over particles of the same group within a sphere of radius r_e surrounding particle i, and $\mathbf{f}$ is a pair-repulsion force. In Eq. (3), β measures the relative strength of this repulsive term. The function $\mathbf{f}$ can be chosen in different ways, here we adopt the following [19]:

$$\mathbf{f}(\mathbf{r}) = \frac{\hat{\mathbf{r}}}{1 + \exp[(r - r_f)/\sigma]}, \tag{6}$$

where $r = |\mathbf{r}|$, r_f set the length scale of repulsion (particles size), and σ the steepness. The last term in Eq. (3) describes the chase or escape force (γ quantifies its strength). We choose the following form [6]

$$\hat{\mathbf{f}}_i^{(CT)} = p \hat{\mathbf{r}}_{ik_i}, \tag{7}$$

where k_i indicates the closest target (chaser) to any chaser (target) within a radius r_s (sighting radius) of organism i, $\mathbf{r}_{ik_i} = \mathbf{r}_i - \mathbf{r}_{k_i}$, $p = -1$ for chasers (pursuit of targets) and $p = +1$ for targets (escape from chasers). We also consider another form of the escape force for targets, obtained as a weighted average over particles within the sighting radius

$$\mathbf{f}_i^{(T)} = \sum_{k \in \mathcal{S}_i^{(\mathrm{sight.})}} h(r_{ik}) \hat{\mathbf{r}}_{ik}, \tag{8}$$

where the sum is over chasers within a sphere of radius r_s surrounding target i and $h(r)$ is a weight function. We will consider here two kinds of weight: power law $h_{pl}(r) = r^{-w}$ and exponential $h_e(r) = e^{-kr}$. The parameter w (or k) determines the escape strategy: for $w = 0$, all the particles equally contribute to the force, while for $w \gg 1$, only the nearest particle contributes and the original form [Eq. (7)] is recovered. The predation event is described by the elimination of target particles when they enter in the capture sphere (of diameter r_c) of a chaser. It is worth noting that we are interested, here, in chase-escape phenomena at time scales much shorter than the typical lifetime of single organisms, thus, we will not consider processes like reproduction or mortality [21–24].

The proposed simplified model describes organisms which randomly move in a given space at constant speed—avoiding overlap, Eq. (5), and potentially moving in a swarm, Eq. (4)—and interact with the opposite group through pairwise repulsive or attractive terms—Eqs. (7) and (8). In real life, this corresponds to cases in which predators chase the nearest prey, which responds to the attack in the most simple way, performing straight line escape from the nearest predator (or a weighted average of neighboring ones) [4]. Despite its simplicity, the model allows the study of a huge variety of possible situations, by considering group-dependent values of the different parameters. In this analysis, we will consider cases in which the only group-dependent parameters are the speed v_0 and alignment radius r_0. Simulations are performed, updating at each time step particle positions and velocities according to Eqs. (1) and (2), using the following parameters values: $\beta = 5$, $\gamma = 1.2$, $r_e = 5$, $r_f = 1$, $\sigma = 0.5$ (times are in the unit of Δt and length in the unit of r_c). The relative strength of the different terms in Eq. (3) has been chosen in such a way to ensure the correct relative dominance in the following order: nonoverlapping, chase or escape, and self-propulsion. The values of the other parameters will be indicated in the various analyzed cases. In the following, we mainly report results obtained for the unbounded sighting radius and the lack of alignment effect ($r_0 = 0$). See Fig. 1 for a snapshot taken from simulation runs.

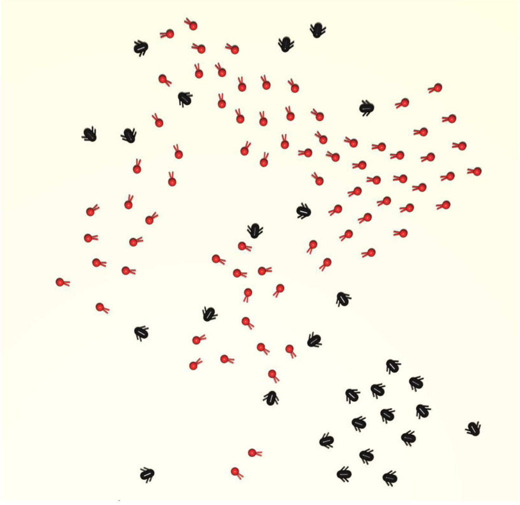

FIG. 1 (color online). Snapshot of a predator-prey configuration from a simulation run. Black organisms are the predators, red smaller ones are the preys.

Results.—We first analyze how the total catch time T, i.e., the time needed to catch all the preys, depends on the number of predators. We study the case in which the preys escape from the closest predators—Eq. (7)—and the preys and the predators have the same speed, $v_T = v_C$, for which, in the simple one-to-one chase situation, the predator is unable to end the catch. In Fig. 2, the quantity T is reported for different noise strengths (averaged over 10^4 independent runs). Contrary to the case of single predator, the many chasers are able to complete the catch, due to the cage trapping events (see below) and also to the waste of time by the targets in deciding the escape direction when chased by many predators [25]. As intuitively expected, the time T is a decreasing function of N_C, the more the chasers, the shorter the time needed to complete the catch. However, there is an interesting crossover between at least two power-law regimes: N_C^{-1} at high chasers concentration, while a more steep decrease, N_C^{-2}, at low concentration. The crossover is observed when the number of chasers is about 5 times that of the targets, indicating such a value is a lower bound to ensure a fast catch of all the targets. We also note that there is a crossover region in between, $N_C^{-\alpha}$ with $2 < \alpha < 5$, that is more pronounced when the noise is reduced. Similar results (two regimes with the same scaling exponents and possible quantitative differences only in the absolute T values or in the crossover region) are obtained with different parameter values, for example, considering alignment effects for targets ($r_0 = 5$), finite sighting radius for both species ($r_s = 10$), different targets number ($N_T = 10,\ 20$), or box length ($30 \leq L \leq 70$). We note that a crossover between two power-law regimes has been also observed in the case of lattice models [6], however, with different power-law exponents. These results seem to indicate that the presence of the two regimes is quite a general result, while quantitative details seem to be model-dependent. Analyzing the dynamics in the single runs, it is evident that the two regimes correspond to two different situations: when the chasers are numerous enough, they are able to conclude the task after few time steps (up to 100 or 200) from random initial starting configuration (*fast catch*) while, when they are few, some targets are able to escape from initial caged configurations and the chase process (typically a group of many predators chasing one or few targets [25]) lasts for a longer time (*slow catch*). This is also evident by looking at the distribution of a target's lifetime, shown in the inset (a) of Fig. 2 for $N_C/N_T = 7$ (left curve, *fast catch* regime) and $N_C/N_T = 1$ (right curve, *slow catch* regime). In the latter case, there is a double peak in the distribution, indicating the presence of two subgroups of targets, those which are captured after few steps and those which are able to fly off and are captured after a long chase. It is worth noting that the noise has the effect of decreasing the time T, disturbing more the escape process of the targets (the change in the velocity direction due to noise is fatal for the target chased by many predators).

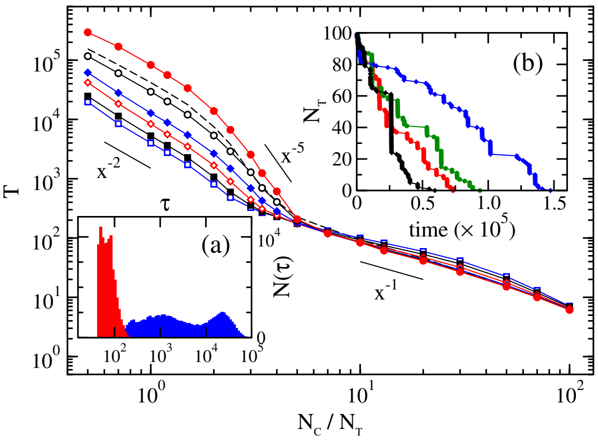

FIG. 2 (color online). Time of catch T as a function of chasers fraction N_C/N_T ($N_T = 10$, $L = 50$). Data correspond to different noise levels: from top to bottom $\eta = 0$ (absence of noise), 0.2, 0.4, 0.6, 0.8, 1 (maximum noise). Dashed line refers to the case $N_T = 20$, $L = 70$, and $\eta = 0.2$. Insets: (a) distribution of target lifetime for the cases $N_C/N_T = 7$ (left red curve) and $N_C/N_T = 1$ (right blue curve), both referring to the $\eta = 0.2$ case ($N_T = 10$, $L = 50$); (b) time dependence of the number of targets N_T obtained in four different simulation runs ($N_C = 50$, $L = 100$, $\eta = 0.0$, $v_T = 0.1$, $v_C = 0.06$).

We now investigate the role of escape strategies and their effect on the survival probability of the preys. In principle, one should expect that considering the position of many chasers, should give a better chance of finding the optimal escape trajectory, especially when there are many predators converging on the target. To quantify the effect, we have considered different escape strategies, based on the weighted average over close predators—Eq. (8). In particular, we have analyzed how the total catch time T depends on the parameter w or k in the considered weight function h_{pl} or h_e. In Fig. 3, the quantity T (averaged over 2×10^4 independent runs) is reported as a function of the target's velocity in the fast catch regime for different w values, compared to the original escape-from-the-nearest strategy. It appears that the targets that escape, considering the weighted average of predator directions, are able to survive for a longer time, and the effect is more pronounced for the faster targets. More specifically, the optimal strategy is observed around the value $w \simeq 2$, as it evident in the inset of Fig. 3, where data referring to the slow catch regime are also reported. A simple qualitative explanation of the peak is the following. When the preys escape from the closest predator (high w values), they are unable to efficiently avoid other coming predators from different directions, while considering unweighted average ($w = 0$), they are unable to escape from the most dangerous closest predator: the optimal strategy (w value) has to be in between. A quantitative argument can be given considering a simplified mathematical model describing one

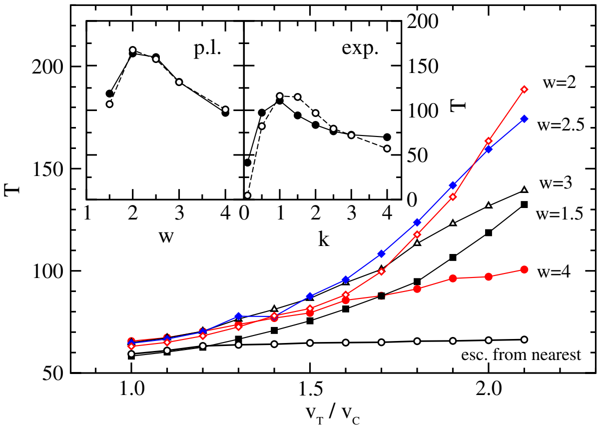

FIG. 3 (color online). Time of catch T as a function of the ratio of velocities v_T/v_C for $N_T = 10$, $N_C = 100$, $L = 40$, $\eta = 0.2$, $v_C = 0.1$ (fast catch regime). Data correspond to different escape strategies: escape from the nearest chaser (Eq. (7), open black circles) or from a weighted average of nearest chasers (Eq. (8) with h_{pl}) with $w = 1.5, 2.0, 2.5, 3.0, 4.0$. Insets: Time of catch T as a function of w (left panel) and k (right panel), respectively, for the power-law and exponential-law weights. The curves refer to the fast catch regimes ($N_T = 10$, $N_C = 100$, $L = 40$, $\eta = 0.2$, $v_T/v_C = 2$, full symbols linked by continuous line) and the slow catch ones ($N_T = 10$, $N_C = 30$, $L = 40$, $\eta = 0.2$, $v_T/v_C = 1$, open symbols linked by dashed line, in this case, the reported quantity is $T/50$).

prey chased by two predators (see discussion in Supplemental Material [25]). By considering an exponential weight h_e, one also observes a peak (around $k = 1$), although with T values lower than in the previous case, resulting in a less efficient escape (see right panel in the inset of Fig. 3).

As stated above, a crucial role in the predation events is played by a kind of coordination in the predators movements, particularly evident when considering the case of slow predators, for which there are no chances to succeed in the catching events until a kind of coordinated motion is achieved. In the inset (b) of Fig. 2, examples of time evolution of the targets number N_T are reported as obtained in four independent simulation runs, for the case $v_C = 0.6v_T$. Catching events are mainly "spike-like"; i.e., they are concentrated in very short time intervals, corresponding to coordinated trapping of targets due to many chasers which converge to the same spatial region from different directions [25].

By including alignment rules in prey-prey interactions, i.e., setting $r_0 > 0$ in Eq. (4), we do not observe relevant differences with respect to the case of no-alignment, at least for what concerns catch times and predation rates. This indicates that in our model there are no advantages in escaping together, even though the pattern dynamics is quite different due to the presence of swarms and flocking phenomena [25]. The cooperative escape strategies observed in nature may rely on other mechanisms not included in the present model, for example, some kind of confusing perception effect of predators when chasing many preys moving together [26].

Conclusions.—Predation phenomena and escape strategies have been analyzed through numerical simulations by using a simple Vicsek-like individual-based model. Two catch regimes are found (in agreement with previous lattice models [6]) characterized by different lifetime distribution of preys: a *fast* regime at a high predators to preys ratio and a *slow* one when the ratio is less than about 5, which then represents a lower bound to ensure a rapid and efficient catch. We also demonstrate that predation is often characterized by "spike-like" events, caused by cooperative cage trapping of preys. The main result concerns the efficacy of escape strategies: we find that the preys escape more efficiently by considering a weighted (power-law) average of neighboring predators, with an optimal weight exponent $w = 2$. The reported findings contribute to the enhancement of the theoretical knowledge of collective and predation phenomena in animal behavior, and could be also useful in applied disciplines, for example, to develop efficient strategies in collective robotics.

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