Collective Motion due to Individual Escape and Pursuit Response

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Recent studies suggest that noncooperative behavior such as cannibalism may be a driving mechanism of collective motion. Motivated by these novel results we introduce a simple model of Brownian particles interacting by biologically motivated pursuit and escape interactions. We show the onset of collective motion for both interaction types and analyze their impact on the global dynamics. We demonstrate a strong dependence of experimentally accessible macroscopic observables on the relative strength of escape and pursuit and determine the scaling of the migration speed with model parameters.

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The emergence of collective motion of living organisms, such as exhibited by flocks of birds, bacterial colonies or insect swarms is an ubiquitous and fascinating self-organization phenomenon in nature, which still bears many open questions. A common explanation for the emergence of collective motion in a wide range of animals is that it serves as a protection mechanisms against predators. Recent experimental results suggest a novel mechanism driven by cannibalism which may, surprisingly, facilitate collective motion in mass migrating insects [1,2].

The phenomenon of swarming in general has attracted scientists from a wide range of disciplines with different scopes and perspectives [3]. In recent years it also became the focus of an increasing number of publications in the field of statistical physics, nonlinear dynamics and pattern formation. These contributions enhanced significantly our understanding of collective motion in systems of self-propelled particles (SPP) and by discovering universal scaling laws and phase-transitionlike behavior, have offered new stimuli to the theory of nonequilibrium systems [4–12]. Recent examples of the ongoing research are a special journal issue dedicated to active motion and swarming [13] or the work by Grossman *et al.* [14], where the authors demonstrate the emergence of collective motion of SPP interacting via inelastic collisions.

In this Letter we investigate a simple but generic model of individuals with escape and pursuit behavior which may be associated with cannibalism. We show how these selective repulsion or attraction interactions lead to collective motion of individuals with highly fluctuating speed and analyze the dependence of the model dynamics on the relative strength of individual escape and pursuit response. Directed translational motion in our model is a strictly collective (but not cooperative) behavior and may be therefore termed group propulsion. Our model offers a novel perspective on possible mechanisms of onset and persistence of collective motion and the resulting migration patterns in nature and represents a biologically-motivated example of pattern formation and phase-transitions in nonequilibrium systems.

We model an individual organism as an active Brownian particle in two dimensions ($d = 2$) with an internal energy depot (see [15] for details). This additional degree of freedom describes the internal energy budget of individuals determined by their uptake of nutrients, internal dissipation to maintain body processes and conversion of internal energy into energy of motion. It allows individuals in our model to increase their speed in reaction to external stimuli by conversion of internal energy into kinetic energy. For simplicity we assume throughout this work that at all times there is a surplus of internal energy which allows us to neglect the explicit treatment of the energy balance and focus on the spatial dynamics only.

Each individual (particle) obeys the following Langevin dynamics:

$$\dot{\mathbf{r}}_i = \mathbf{v}_i, \qquad \dot{\mathbf{v}}_i = -\gamma v_i^{\alpha-1}\mathbf{v}_i + \mathbf{F}_i^s + \sqrt{2D_v}\boldsymbol{\xi}_i. \qquad (1)$$

The first term on the left-hand side of the velocity equation (1) is a friction term with friction coefficient γ and an arbitrary power dependence on velocity represented by $\alpha = 1, 2, 3, \ldots$. The response of individual i to other individuals is described by an effective social force $\mathbf{F}_i^s$. The last term is a noncorrelated Gaussian random force with intensity D_v. A solitary individual ($\mathbf{F}_i^s = 0$) explores its environment by a continuous random walk, where the individual velocity statistics are determined by γ, α and D_v. The parameters are given in arbitrary time and space units T and X: $[\gamma] = X^{1-\alpha}T^{\alpha-2}$, $[D_v] = X^2T^{-3}$.

The finite size of individuals is taken into account by elastic hard core collisions with a particle radius R_{hc} [16].

Motivated by experimental observation [2], we introduce the following social response: If approached from behind by another individual j, the focal individual i increases its velocity away from it in order to prevent being attacked from behind. We refer to this behavior as *escape* (e). If the focal individual "sees" another individual up-front moving away, it increases its velocity in the direction of the escaping individual. We refer to this behavior as *pursuit* (p). No response in all other cases. The response of an individual is determined the following decision algorithm: (A) Is there another individual within my sensory range $l_s > R_{\mathrm{hc}}$; (B) If yes, is it in front or behind me, and (C) does it come closer or does it move away.

Thus we write $\mathbf{F}_i^s = \mathbf{f}_i^e + \mathbf{f}_i^p$ as a sum of an effective escape (e) and an effective pursuit (p) force

$$\mathbf{f}\,_i^k = \frac{\chi_k}{N_k}\sum_j \Delta\mathbf{v}_{ji}\theta(l_s - r_{ji})\theta(s_k\mathbf{v}_i\hat{\mathbf{r}}_{ji})\theta(s_k\mathbf{v}_{ji}\hat{\mathbf{r}}_{ji}) \qquad (2)$$

with $k = e$, p. Here $\chi_{p,e} \geq 0$ are the corresponding interaction strengths and $\Delta\mathbf{v}_{ji} = (\mathbf{v}_{ji}\hat{\mathbf{r}}_{ji})\hat{\mathbf{r}}_{ji}$ is the relative velocity of particle j with respect to particle i, with $\mathbf{v}_{ji} = \mathbf{v}_j - \mathbf{v}_i$ and $\hat{\mathbf{r}}_{ji} = (\mathbf{r}_j - \mathbf{r}_i)/|\mathbf{r}_j - \mathbf{r}_i|$. The Heaviside functions θ reflect the conditions for the escape and the pursuit response with $s_e = -1$ and $s_p = 1$. Both forces are normalized by the respective number of individuals the i-th individual interacts with (N_e, N_p).

The symmetry of the interactions is broken in several ways: the interactions act only on one of the interacting particles (action ≠ reaction); the interactions are direction selective - the particles distinguish between their front ($\mathbf{v}_i \cdot \mathbf{r}_{ji} > 0$) and their back ($\mathbf{v}_i \cdot \mathbf{r}_{ji} < 0$) and between approach ($\mathbf{v}_{ji} \cdot \mathbf{r}_{ji} < 0$) and escape ($\mathbf{v}_{ji} \cdot \mathbf{r}_{ji} > 0$); the strength of interaction to the front and back may be different ($\chi_e \neq \chi_p$). The most important property of the interactions is their antidissipative nature with respect to kinetic energy. Note that $\mathbf{F}_i^s$ leads only to acceleration of individuals and is analogous to the autocatalytic mechanism proposed in Bazazi *et al.* [2].

Throughout this Letter we will discuss our numerical results in terms of the rescaled density $\rho_s = Nl_s^2/L^2$, where N is the total particle number, l_s the interaction range and L the size of the simulation domain. All simulation results were obtained with periodic boundary condition. We will restrict here to the case of moderate noise intensity $D_v < 1$ and focus on the system behavior with changing density ρ_s, which may be controlled in experiments. For increasing noise D_v the system shows global behavior related to dynamics of SPP [4,7,11].

Numerical simulation reveal that irrespective of the detailed model parameters, the pursuit and escape interactions lead to global collective motion at high particle densities ρ_s and moderate noise intensities D_v (Fig. 1). At low ρ_s however we observe a very different behavior in dependence on the microscopic details of the model, where the velocity statistics and spatial migration patterns depend strongly on the relative strength of escape χ_e and pursuit χ_p. For $\chi_e > 0$ and $\chi_p \rightarrow 0$ with increasing ρ_s a transition between a disordered state, with vanishing mean migration speed $\langle U\rangle = |\sum_i \mathbf{v}_i|/N = 0$ and an ordered state with $\langle U\rangle > 0$ takes place. This resembles similar transitions reported for SPP with velocity alignment (Fig. 1 and 2) [4]. With increasing χ_p the transition shifts to lower ρ_s until it vanishes. For $\chi_p > 0$ and $\chi_e \rightarrow 0$ there is no dependence of $\langle U\rangle$ on ρ_s.

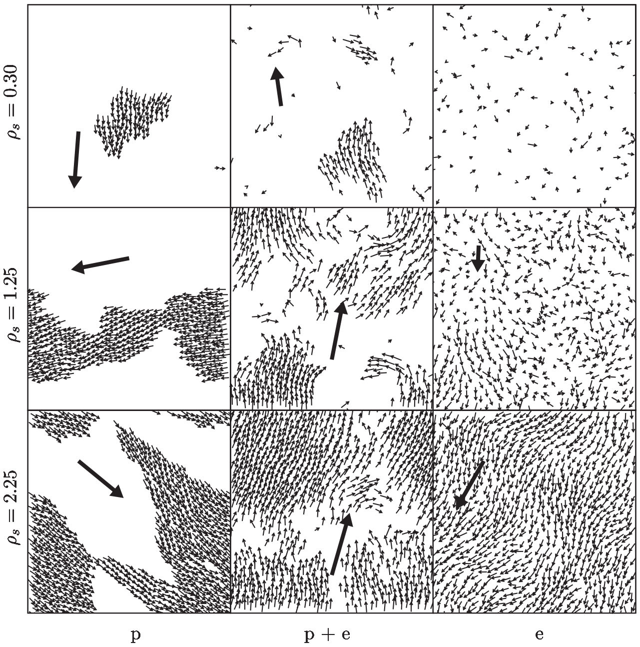

FIG. 1. Typical spatial configurations and particle velocities (small arrows) for pursuit-only (p), pursuit + escape ($p + e$) and escape only (e) cases at different particle densities $\rho_s = 0.30$, 1.25, 2.25. Mean migration direction and speed U is indicated by large arrows ($U \approx 0$ for escape only and $\rho_s \ll 1$).

In order to understand the dynamics we investigate the influence of escape and pursuit interactions independently, by analyzing the extreme cases: $\chi_p = 0$, $\chi_e > 0$ (only escape) and $\chi_e = 0$, $\chi_p > 0$ (only pursuit).

In the escape-only case the particles try to keep their distance with respect to individuals approaching from behind. To the front only interactions via the hard core collisions take place. At low ρ_s after an escape response the probability of interaction within the characteristic time of velocity relaxation vanishes and the particles are able to reorient themselves (disordered state). With increasing ρ_s the frequency of escape interactions increases and the particles are able to correlate their velocities on several interaction length scales but subensembles may still move in different directions. We observe a transition to the ordered state via an active fluidlike state [$\rho_s \approx 1.25$; Fig. 2(a)]. In the ordered state all particles are able to correlate their direction of motion. At all ρ_s we obtain spatially homogeneous distribution of particles. The transition is also reflected in the particle speed distribution $P(v)$. At low densities $P(v)$ corresponds to the analytical result obtained for noninteracting particles [Fig. 2(b)], whereas at high ρ_s the maximum of the distribution shifts to higher speeds indicating a transition from pure random walk to directed translational motion [Fig. 2(c)].

In the pursuit-only case already at low ρ_s a highly inhomogeneous state evolves, initiated by formation of

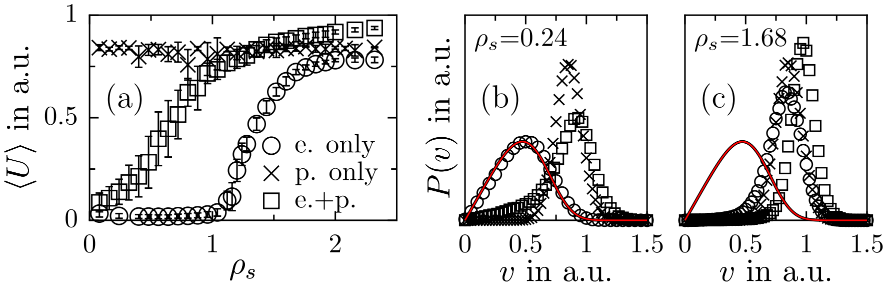

FIG. 2 (color online). (a) Mean velocity $\langle U\rangle$ for escape-only (○) $\chi_e = 10$, $\chi_p = 0$, pursuit-only (×) $\chi_e = 0$, $\chi_p = 10$ and symmetric escape + pursuit (□) $\chi_e = \chi_p = 10$ vs ρ_s obtained from numerical simulations with periodic boundary conditions ($\gamma = 1$, $D_v = 0.05$, $\alpha = 3$, $R_{\mathrm{hc}} = 1$, $l_s = 4$; only translational solutions were considered; error bars represent one standard deviation). Particle speed distribution $P(v)$ for the different interaction types in comparison with the analytical solution for noninteracting Brownian particles (solid line) at $\rho_s = 0.24$, 1.68 (b,c).

small compact particle clusters, performing coherent translational motion. As there is no escape interaction the density of the clusters is only limited by the hard core radius. At moderate noise intensities the clusters are highly stable and a process of cluster fusion can be observed where larger clusters absorb smaller clusters and solitary particles. The dominant stationary configuration with periodic boundary conditions, and moderate noise, is a single large cluster performing translational motion (Fig. 1). The migration speed $\langle U\rangle$ in Fig. 2(a) is given by the mean speed of a single cluster $\langle u\rangle = |\sum_{i\in\mathrm{cluster}} \mathbf{v}_i|/N_{\mathrm{cluster}}$, which for large clusters becomes independent of the cluster size and therefore independent of ρ_s. The same holds for $P(v)$ as shown in Figs. 2(b) and 2(c). An intriguing feature of pursuit-only is the possibility of the formation of large scale vortices out of random initial conditions due to collisions of clusters moving in opposite directions. After nucleation, a vortex may grow by absorbing smaller clusters leading to a single rotating structure [Fig. 3(a)] with lifetimes exceeding 10^3 time units. Preliminary results on vortex-stability indicate a monotonic increase of stability (i.e., lifetime) with size (not shown). The emergence of vortices in our model is, in particular, remarkable because so far they have only been reported for systems of SPP with confinement, or attracting potentials, respectively [17]. Here the pursuit interaction acts in a sense as both: a propulsion mechanism and an asymmetric attraction.

The analysis of the dynamics shows that both interactions—escape and pursuit—lead to collective motion but have an opposite impact on the density distribution. Whereas escape leads in general to a homogenization of density within the system, pursuit facilitates the formation of density inhomogeneities (clusters). This leads us to the insight that the actual escape + pursuit dynamics where χ_p, $\chi_e > 0$ is a competition of the two opposite effects with respect on the impact on the particle density. The stability of moving clusters in this simple model is determined by the relative ratio of the interaction strengths. In general for the escape + pursuit case at low ρ_s we observe fast formation of actively moving particle clusters with complex behavior: fusion and break up of clusters due to cluster collisions as well as spontaneous break up of clusters due to fluctuations. The weak dependence of the particle speed distribution $P(v)$ on ρ_s combined with the clear deviation from the noninteracting case at low ρ_s [Figs. 2(b) and 2(c)] shows that the increase of $\langle U\rangle$ with ρ_s for escape + pursuit originates from alignment of individual cluster velocities.

In order to determine the scaling of $\langle U\rangle$ with model parameters, we consider the smallest cluster which shows directed translational motion: a particle pair (1, 2). We assume particle 1 being in the front of particle 2, $\chi_e = \chi_p = \chi$ and $|\mathbf{r}_{12}| < l_s$ at all times. Through a transformation of Eq. (1) into polar coordinates with $\mathbf{v}_i = (v_i \cos\varphi_i, v_i \sin\varphi_i)$, where φ_i is defined as the angle between $\mathbf{v}_i$ and $\hat{\mathbf{r}}_{12}$, it can be shown that for $-\pi/2 < \varphi_i < \pi/2$ ($i = 1, 2$) the escape and pursuit interaction lead to an increase of either v_1 or v_2 in order to harmonize the speed of the slower particle with the faster one. The acceleration is counterbalanced by the frictional force and results in a nonvanishing translational velocity of

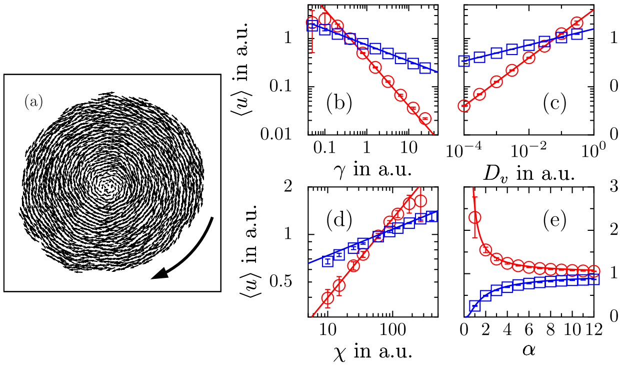

FIG. 3 (color online). (a) A single large vortex formed from random initial conditions for the pursuit-only case. The arrow indicates the rotational direction. Comparison of numerically obtained average pair velocities $\langle u\rangle$ for $\alpha = 1$ (○) and $\alpha = 3$ (□) with the result of Eq. (4) (solid lines): (b) $\langle u\rangle$ over friction coefficient γ, (c) noise intensity D_v, (d) and interaction strength χ. (e) $\langle u\rangle$ vs friction function exponent α. Here we distinguish two cases $A > 1$ (○) and $A < 1$ (□), with $A = \sqrt{D_v\chi/\pi}/\gamma$.

the particle pair. In addition the interaction stabilizes the translational motion along $\hat{\mathbf{r}}_{12}$, i.e., $\langle \varphi_i \rangle \rightarrow 0$. After the system relaxes to a stationary state ($\hat{\mathbf{r}}_{12}$ varies slowly in time) we end up with effectively one-dimensional translational motion of the particle pair.

The evolution of the mean speed of a particle pair in this one-dimensional situation $u_{1d} = (v_1 + v_2)/2$ with $v_1 \approx v_2$ can be approximated as

$$\frac{\Delta u_{1d}}{\Delta t} \approx -\gamma u_{1d}^{\alpha} + \frac{1}{2}\chi \langle |\delta v_i| \rangle_{1d}. \tag{3}$$

The second term on the right-hand side of Eq. (3) accounts for the acceleration of the particle pair due to the escape + pursuit interaction with $\delta v_i = u - v_i$. The factor $1/2$ takes into account that at a given time only one of the particles accelerates.

The deviations of individual particle speed from the mean speed result from the action of the random forces. We approximate the expectation value of the speed deviations $\langle |\delta v| \rangle_{1d}$, by considering the speed deviations as discrete increments taken from a Gaussian distribution with zero mean and variance $\sigma_{1d}^2 = 2D_v\tau$ (Wiener process). Replacing τ by the relaxation time of the interaction $1/\chi$ yields: $\langle |\delta v| \rangle_{1d} = 2\sqrt{D_v/\pi\chi}$. The stationary velocity of a particle pair can be calculated from (3) to:

$$u_{1d}^{s} = \left(\frac{1}{\gamma}\sqrt{\frac{\chi D_v}{\pi}}\right)^{1/\alpha}. \tag{4}$$

This result is in excellent agreement with numerical simulations of individual particle pairs (Fig. 3) for wide parameter ranges. The scaling in Eq. (4) agrees at moderate D_v with the measurements of the average speed of large clusters and the ordered phase for the escape-only case.

In summary, we have presented an individual based model for the kinematic description of large groups of individuals, where each individual responses to others in its local neighborhood by escape and pursuit behavior. The response is described by an effective social force motivated by recent experimental results on mass migrating insects. Our model shows the onset of collective motion due to the escape and pursuit interaction for wide range of parameters. The analysis of the model dynamics shows that the macroscopic behavior, which can be observed in experiments, such as migration speed vs density and the spatial migration patterns, depends strongly on the relative strength of the escape and the pursuit behavior of individuals. Furthermore we were able to obtain the right scaling of the migration speed with model parameters which is confirmed by numerical simulations.

The relevance of different possible swarming interactions in real systems is still an open question, but recent experiments on marching insects suggest that escape dominates their marching behavior [2]. In this case our model predicts a phase transitionlike behavior of the mean migration speed $\langle U \rangle$ in dependence on the density ρ, which is supported by previous results [18]. On the other hand, the coherently moving clusters and vortex structures emerging for the pursuit-only case resemble observations of fish schools [19] and suggest the relevance of our model to a wide range of swarming phenomena in nature: Escape dominated behavior offers a possible explanation for collective motion in species with high levels of intragroup aggression (cannibalism), whereas pursuit-only behavior might represent an effective mechanism for onset of collective motion in groups of nonaggressive individuals with limited sensory and cognitive abilities.

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