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Group chasing tactics: how to catch a faster prey

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Abstract

We propose a bio-inspired, agent-based approach to describe the natural phenomenon of group chasing in both two and three dimensions. Using a set of local interaction rules we created a continuous-space and discrete-time model with time delay, external noise and limited acceleration. We implemented a unique collective chasing strategy, optimized its parameters and studied its properties when chasing a much faster, erratic escaper. We show that collective chasing strategies can significantly enhance the chasers' success rate. Our realistic approach handles group chasing within closed, soft boundaries—in contrast with the periodic ones in most published literature—and resembles several properties of pursuits observed in nature, such as emergent encircling or the escaper's zigzag motion.

1. Introduction

The animal kingdom is full of fascinating phenomena on every level. An essential part of this diverse biosphere is the complex biological interaction network between different species and within the same species, in which interactions are categorized based on the benefits and harms to the interacting partners. An important type of driving force in these situations is the prey–predator interaction, which is also a very exciting example of collective behaviour in nature [1].

Natural prey–predator systems have already been studied many times, including long-term observations of population dynamics and a large number of field studies about animals' typical behaviour. One factor governing these tendencies is the group hunting of large carnivores, such as lions of the Serengeti, wild chimpanzees in the Tai National Park, and coyotes in Yellowstone National Park [2–4]. The results of these investigations revealed many interesting behavioural patterns of the animals, e.g. special hunting tactics and the size of packs.
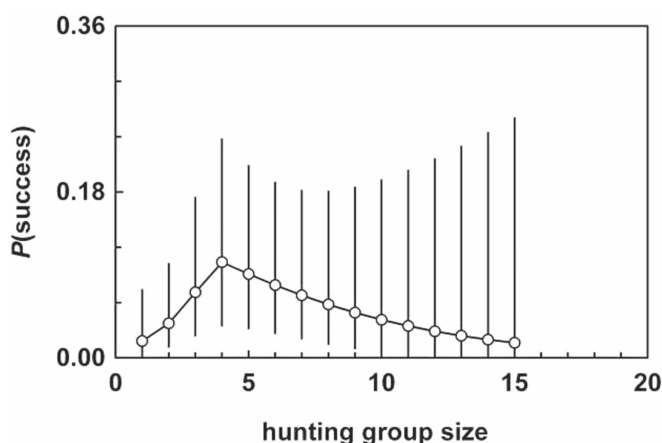
Prey–predator systems have also aroused the interest of theorists, who have constructed models to describe the behaviour of competing populations since Lotka and Volterra. As the field developed, the commonly used model schemes shifted from continuous ones based on a differential equation towards discrete models, due to advances in computational technology [5–7]. In the past few years, agent-based modelling has also become popular, using the concept of self-propelled particles in the spirit of the model by Vicsek *et al* [8].

In this work we propose a bio-inspired, continuous-space and discrete-time agent-based model of group chasing for the rarely studied scenario in which the evader is significantly faster than the pursuers. This realistic chasing approach overcomes many weaknesses of previously published models. It combines many environmental factors such as time delay, finite acceleration (inertia), external noise and closed boundaries (while most models in the literature still use periodic boundary conditions). Moreover, it includes special collective chasing tactics, the chasers' prediction of their target's future position and erratic tactics of the escaper as well [9–14]. Significantly, our model operates universally in both two and three dimensions.

1.1. Ethological background—chase and escape in nature
1.1.1. Chasing in nature
Group chasing is one of the most important forms of collective behaviour. Its significance arises from the fact that cooperation among predators can notably increase their chances of catching even hard-to-catch prey, which

Figure 1. The overall probability of success for a certain hunting pack of wolves encountering an elk, depending on the size of the pack [25].

makes these collaborative species much more successful predators. Packs in which the cooperation is more efficient have better chances of survival. This puts evolutionary pressure on the animals to optimize their strategies [15–18].

Previous field studies have reported approximately 50 different species in which increases in group size above a certain point reduce their success rate per capita [15]. A biologically logical explanation is that the group becomes too large and not all the predators were able to feed even if the hunt was successful; therefore the size of chaser groups generally does not grow past a specific threshold [19].

The variety of predator–prey systems is extraordinarily rich within birds, mammals, fish and even insects [3, 17, 20–23]. A surprising finding is that even cheetahs, the fastest animals in the world, show an affinity for hunting in pairs [15, 22]. Additionally, wolves tend to hunt elks, while coyotes have been studied hunting for pronghorns in, e.g., migration corridors using landmarks as a strategic tool (reported in Yellowstone National Park). In both cases the prey is faster than the predator [17, 24]. We can also conclude that even wolves, one of the most unwavering examples in the animal kingdom, give up their pursuit after roughly one or two kilometres (which takes barely two minutes at their top speed).

Cooperation between hunters has different levels. For example, group hunting within bats just emerges completely unintentionally from the similar hunting methods of the individuals, while the study of large carnivores led to the finding that certain predators, while hazing their prey, tend to surround it collectively [26, 27]. This so-called encircling was reported mostly regarding wolves and lions, but even bottlenose dolphins have been observed to encircle their prey [15, 20, 28].
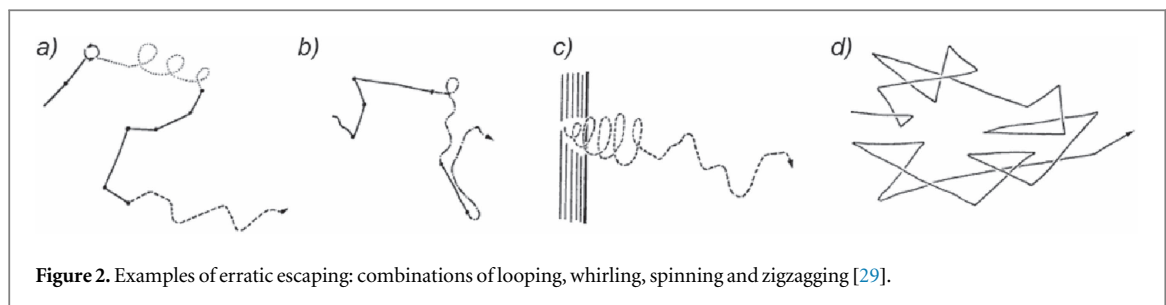
Despite the limited available data, it is clear that for many predator species group hunting has proved to be more beneficial than solitary hunting, even if not every member of the group participates in the pursuit. Evolution seems to have optimized the size of these hunting packs, because in the majority of cases, size of a hunting pack falls within the range 3–10 (figure 1).
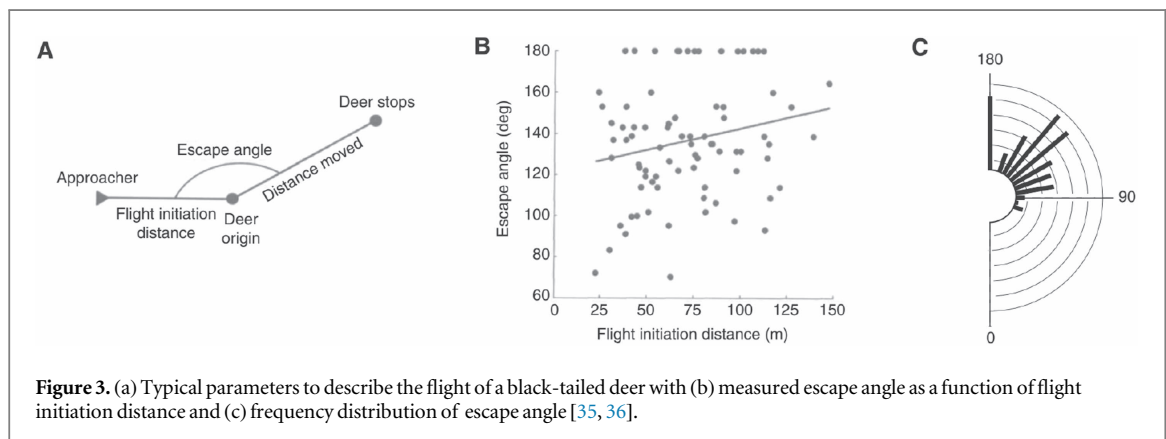
1.1.2. Natural escaping strategies

Fleeing is the most common response from animals to their chasers. First intuition would suggest that the only possible strategy for escape is to rush away from the chaser(s) as fast as possible. However, in real biological systems surprisingly different escaping strategies can occur. Based on a concept proposed by Domenici *et al* we can differentiate between direct escaping and erratic escaping as separate strategies, although other kinds of strange actions such as freezing or retaliating can also occur [29–32].

Direct escaping means that the prey runs straight in the opposite direction from its chaser(s) and relies on its speed and endurance to survive. In other words, under ideal conditions the escaper can outrun its chaser(s), but the prey can be caught if it is slower, if it encounters unexpected obstacles or if the chasers' strategies are more advanced.

When the escaping is erratic, the prey can use a mixture of direct escaping and other, stochastic patterns of motion. This can be zigzagging, a series of sudden changes in direction, or some even more advanced movements such as spinning, looping and whirling (figure 2) [29, 31]. For example, deers use a particular distribution of escaping angles, which is also slightly dependent on the distance from their chaser (figure 3). The effectiveness of these quick and unexpected changes in the escaper's direction relies mostly on the animals' inertia (and the difference between inertia of the prey and the predator) and the different time delays within the

Figure 2. Examples of erratic escaping: combinations of looping, whirling, spinning and zigzagging [29].

Figure 3. (a) Typical parameters to describe the flight of a black-tailed deer with (b) measured escape angle as a function of flight initiation distance and (c) frequency distribution of escape angle [35, 36].

Table 1. The escaping distance of several typical prey animals of large carnivores [34].

Species	Escaping distance(m)
Pronghorn	235
Mule deer	149–250
Elk	85–201
Bison	101

animals' sensory and motor systems, even if their reaction time may be very short (of the order of magnitude of 50 ms) in chase and escape situations [33].

In conclusion, we can say that evaders do not always escape directly from their chaser but are likely to combine direct escaping with some sort of random motion in order to trick their chasers and prevent their tactics (e.g. zigzagging) being learned. The directions of these random segments of their trajectory vary significantly among different species. The prey have typical escaping distances of usually around a few hundred metres and they take into account all the chasers within that range when determining the direction and strategy of the escape (table 1) [34, 35, 37].

1.2. Previous models of prey–predator systems

The latest paradigm of prey–predator modelling is the agent-based approach, in which the main objective for chasers is to locate and catch the escapers as quickly as possible, and for escapers it is to flee and avoid getting caught. The first agent-based theories were completely analytical, using the tools of different branches of mathematics from game theory to geometry but lacking many real-life, biologically relevant attributes (e.g. noise) [38, 39].

Later on, researchers began to study the scenario of many chasers versus an escaper on a finite lattice with periodic boundary conditions, random spatial distribution of the agents, different sight ranges and uniform speed for all agents [40]. In the first models there was no interaction between the chasers and they were performing e.g. nearest-neighbour random walks to find the prey.

The rarely studied case of a faster escaper appeared in the article of Jin and Qu, in which they were studying how a group of pursuers can catch a faster evader in infinite open space when the finite sight range of the chasers

is greater than that of the escaper [12]. They give geometric solutions to the question of how the chasers can catch the prey by blocking its escape routes—a solution very sensitive to the initial spatial distribution.

An agent-based group chasing model with many chasers and escapers was published by Kamimura *et al* [11, 41]. Here the group of chasers is pursuing the escapers on a two-dimensional lattice with periodic boundary conditions. Because the chasers and the escapers have similar speed, the chasers can only catch an evader if they encircle it, which depends on their initial positions. They also defined a cost function to quantify the pursuit, with which they determined the optimal number of chasers for a given number of escapers.

Angelani's model has gone further than many previous ones because instead of a cell automaton he constructed a model based on self-propelled agents according to the Vicsek model [8, 9]. The interactions between agents are formulated as physical forces in this two-dimensional, continuous model with periodic boundary conditions, where the groups have similar speed. The agents' velocity vectors are calculated at each time step according to an alignment rule, a short-range collision-avoidance force within the same groups, some noise and the rules for chasing and escaping. This escaping tactics had only one parameter, which also had an optimum with regard to the escapers.

2. Model description

2.1. Simulation framework

For studying group chasing we used a simulation framework developed in our research group, which was designed to model real-life agents and study their collective motion [42, 43]. Because of their importance and generality in various prey–predator systems we added the following features of the framework to the group chasing model:

- **Inertia**—A restricted manoeuvrability and finite acceleration (a_{max}) is a fundamental property of every moving object of finite size and mass. Therefore, it is crucial to include it in the model (note that the previously published chasing models lacked this feature). In our framework it is assumed that the agents reach their desired velocity exponentially with a characteristic time τ_{CTRL}.

- **Time delay**—In both biological and mechanical systems various types of time delays 0 are an unavoidable consequence of the limited speed of data transmission and processing (either via nerve cells and axons or via electric wires and circuits). The simplest approach to describe this is to consider the value of a general time delay to be constant (t_{del}).

- **Noise**—Natural systems are usually biased by some kind of noise. To test our model's tolerance against such effects, a delta-correlated (Gaussian) external noise term $\eta(t)$ was added with standard deviation σ.

Therefore, the general parameter-set describing a realistic agent (without model-specific parameters) is

$$\{\tau_{CTRL}, a_{max}, t_{del}, \sigma\}. \tag{1}$$

We are using velocity-based dynamic equations that are specified by the individual models. Such a velocity term, the desired velocity $\mathbf{v}^d$ of the ith agent, can be expressed in general by using the agent's position $\mathbf{r}_i$ and velocity $\mathbf{v}_i$ as follows:

$$\mathbf{v}_i^d(t) = \mathbf{f}_i(\{\mathbf{r}_j\}_{j=1}^N, \{\mathbf{v}_j\}_{j=1}^N, \boldsymbol{\eta}(t)). \tag{2}$$

From this, the equation of motion is

$$\mathbf{a}_i = \boldsymbol{\eta}(t) + \frac{\mathbf{f}_i(...) - \mathbf{v}_i(t)}{|\mathbf{f}_i(...) - \mathbf{v}_i(t)|} \min\left\{\frac{\mathbf{f}_i(...) - \mathbf{v}_i(t)}{\tau_{CTRL}}, a_{max}\right\}, \tag{3}$$

$$\mathbf{f}_i(...) = \mathbf{f}_i(\{\mathbf{r}_j(t - t_{del})\}_{j\neq i}, \mathbf{r}_i(t), \{\mathbf{v}_j(t - t_{del})\}_{j\neq i}, \mathbf{v}_i(t)). \tag{4}$$

Equation (3) describes the acceleration characteristics of the ith agent reaching its desired velocity, assuming finite acceleration, inertia and external noise. Equation (4) incorporates the assumption that the information from agent j reaching agent i is delayed by the given time parameter t_{del}.

2.2. The realistic group chasing model

2.2.1. General properties of the model

Agents. In our model there are N_c chasers and N_e escapers with different top speeds ($v_{max,c}$ $v_{max,e}$) but a similar top acceleration (a_{max}). Let $\mathbf{r}_{c,i}$, $\mathbf{v}_{c,i}$ and $\mathbf{r}_{e,j}$, $\mathbf{v}_{e,j}$ be the positions and velocities of the ith chaser and jth escaper. An actively escaping prey will become inactive (out of the game) if the distance between it and the nearest chaser decreases below the catching distance (r_{cd}); otherwise the agent remains active. In this model the agents are

represented by a circular/spherical object of radius $r_{cd}/2$. The experiment is terminated when all of the escapers are caught.

Arena. We aimed to build a bio-inspired model, and therefore we study group chasing within finite boundaries, because pursuits in nature have boundaries in both space and time. However, many previously published models use either periodic boundary conditions or infinite space. Although both can be very useful, e.g. in statistical physics, in the modelling of group chasing they can lead to very strange and unrealistic situations (for example, a prey 'coming back' from the other side of the cell 'falling into the arms' of chasers wandering at the edge of the cell). For the sake of simplicity and to avoid edge-effects as much as possible, our simulation runs within a circular arena of radius r_a. We focus on the pursuit, and therefore we assume that each and every agent can see all the other agents—we do not examine (group) foraging methods. In this constellation, the origin is the center of the arena.

The arena is surrounded by a soft wall [44]. In this construction if any of the agents gets outside the arena, a virtual agent starts to repulse it towards the center of the arena:

$$\mathbf{v}_i^a = s(r_i, r_a, r_{wall}) \left(v_{\max,k} \frac{\mathbf{r}_i}{r_i} + \mathbf{v}_i \right) \qquad (k = e, \ c), \tag{5}$$

where

$$s(r_i, r_a, r_{wall}) = \begin{cases} 0 & \text{if } r_i \in [0, r_a], \\ -\dfrac{1}{2} \sin\left(\dfrac{\pi}{r_{wall}}(r_i - r_a) - \dfrac{\pi}{2} \right) - \dfrac{1}{2} & \text{if } r_i \in [r_a, r_a + r_{wall}], \\ -1 & \text{if } r_i > r_a + r_{wall} \end{cases} \tag{6}$$

where r_{wall} is the width of the wall and $r_i = |\mathbf{r}_i|$.

Collision avoidance. Between each pair of agents of the same type there is a short-range repulsive interaction term to avoid collisions:

$$\mathbf{v}_{k,i}^{coll} = v_{\max,k} \, \mathcal{N} \left[\sum_j^{N_k} \frac{|\mathbf{d}_{ij}| - r_{cd}}{|\mathbf{d}_{ij}|} \, \mathbf{d}_{ij} \, \Theta(r_{cd} - |\mathbf{d}_{ij}|) \right], \quad \text{where} \tag{7}$$

$$\mathbf{d}_{ij} = \mathbf{r}_{k,i} - \mathbf{r}_{k,j} \qquad (k = e, \ c), \tag{8}$$

r_{cd} is the catching distance, defined as twice the radius of the agents, Θ is the Heaviside step function, $\mathbf{d}_{ij}$ is the displacement vector between the ith and jth agents, and the operator $\mathcal{N}[.]$ normalizes its argument and returns it as a dimensionless vector.

Viscous friction-like interaction. To simulate realistic motion, we introduced viscous friction-like interaction terms [45], parametrized with a specific friction coefficient C_f, with the general form

$$\mathbf{v}_{ij} = C_f \frac{\mathbf{v}_j - \mathbf{v}_i}{(\max\{r_{cd}, |\mathbf{d}_{ij}|\})^2}. \tag{9}$$

Additionally, viscous friction-like damping is important because it minimizes unwanted oscillations in any delayed system [42].
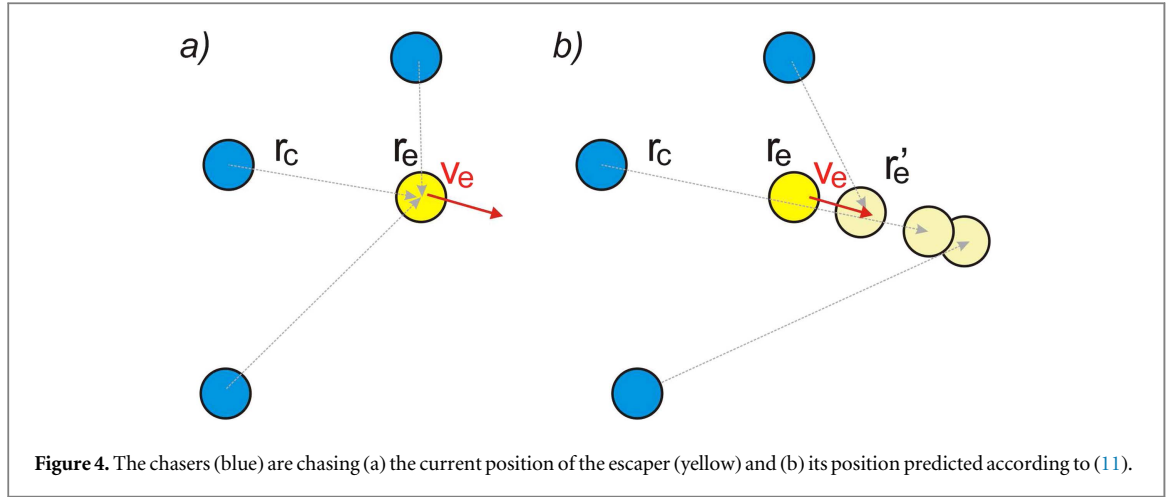
2.2.2. Chasers

Chasing rule. Each chaser chases the closest escaper (chasing term). The collective chasing strategy includes a soft repulsion between the chasers and the prediction of their target's position.

Chasing term. The chasing is represented by an attractive interaction between the ith chaser and its target escaper toward the escaper and a viscous friction-like velocity alignment term in the following way:

$$\mathbf{v}_{c,i}^{ch} = v_{\max,c} \, \mathcal{N} \left[\frac{\mathbf{r}_{c,i} - \mathbf{r}_e}{|\mathbf{r}_{c,i} - \mathbf{r}_e|} - C_f' \frac{\mathbf{v}_{c,i} - \mathbf{v}_e}{|\mathbf{r}_{c,i} - \mathbf{r}_e|^2} \right], \tag{10}$$

where C_f' is the coefficient of the velocity alignment term relative to the attraction.

Prediction. A part of the chasers' strategy is the cognitive prediction of their prey's future position. This means that the chasers are heading to the point $\mathbf{r}_e'$ (the estimated future position of the escaper) instead of the escaper's current position $\mathbf{r}_e$ (figure 4). Here we use only a simple linear approximation to determine the value of $\mathbf{r}_e'$, which is the point at which the chaser could catch the escaper if the time needed for this is below a certain threshold time (τ_{pred}); if this is not the case, then it is the point that the chaser can reach during time τ_{pred}. Then the value of $\mathbf{r}_e'$ is the numeric solution of the following equation:

Figure 4. The chasers (blue) are chasing (a) the current position of the escaper (yellow) and (b) its position predicted according to (11).

$$\mathbf{r}'_{\mathrm{e}} = \mathbf{r}_{\mathrm{e}} + \frac{\mathbf{v}_{\mathrm{e}}}{|\mathbf{v}_{\mathrm{e}}|} \, v_{\mathrm{max,e}} \, \min\!\left[\frac{\mathbf{r}'_{\mathrm{e}} - \mathbf{r}_{\mathrm{c}}}{v_{\mathrm{max,e}}}, \tau_{\mathrm{pred}}\right] \tag{11}$$

Interaction between chasers. Let us assume that a group of chasers is chasing the same escaper. If there is no interaction between the chasers they will eventually get too close to each other because their driving forces are similar. This results in a tail of chasers behind the escaper. This is neither a logical predatory behaviour nor one observable in nature. What we can see in nature, though, is that chasers do not get too close to each other as they pursue their prey, but the distance between them decreases as they get closer to (and finally catch) the escaper. We modelled this with a repulsive interaction term that has a characteristic length r_{inter}, a magnitude factor C_{inter} and a magnitude $C_{\mathrm{inter}} \, v_{\mathrm{max,c}}$. Consequently, $C_{\mathrm{inter}} = 0$ means that there is no interaction and $C_{\mathrm{inter}} = 1$ means that the repulsion between chasers is just as strong as their attraction towards the escaper. The mathematical definition of this interaction is

$$\mathbf{v}^{\mathrm{inter}}_{\mathrm{c},i} = C_{\mathrm{inter}} v_{\mathrm{max,\,c}} \, \mathcal{N}\!\left[\sum_{j}\!\left(\mathbf{d}_{ij}\frac{|\mathbf{d}_{ij}| - r_{\mathrm{inter}}}{|\mathbf{d}_{ij}|} - C''_{\mathrm{f}} \frac{\mathbf{v}_{\mathrm{c},i} - \mathbf{v}_{\mathrm{c},j}}{|\mathbf{d}_{ij}|^2}\right)\right], \tag{12}$$

$$\mathbf{d}_{ij} = \mathbf{r}_{\mathrm{c},i} - \mathbf{r}_{\mathrm{c},j}, \tag{13}$$

where C''_{f} is the coefficient of the viscous friction-like term.

The driving force of the *i*th chaser is the sum of the previously introduced terms (interaction with the wall of the arena, collision-avoiding short-term repulsion, direct chasing force and the long-term repulsion between chasers):

$$\mathbf{f}_{\mathrm{c},i} = \mathbf{v}^{\mathrm{a}}_{i} + \mathbf{v}^{\mathrm{coll}}_{\mathrm{c},i} + \mathbf{v}^{\mathrm{ch}}_{\mathrm{c},i} + \mathbf{v}^{\mathrm{inter}}_{\mathrm{c},i}. \tag{14}$$

2.2.3. Escapers

Escaping rule. The escaper moves in the free direction that is furthest away from all the chasers within its sensitivity range. At the wall, the escaper aligns its velocity to the wall. If the escaper can slip away between the nearest two chasers, then it returns to the field. We defined a panic parameter that depends on the distance between the escaper and its nearest chaser and controls the erratic behaviour.

Direct escaping. An escaping agent takes into account every chaser within its range of sensitivity (r_{sens}), while it weights this effect by the distance of each chaser. This represents the biological observation that the prey is concerned about all the chasers that are too close, and the closer a predator is, the more dangerous it is. This interaction term for the *i*th escaper is

$$\mathbf{v}^{\mathrm{esc}}_{\mathrm{e},i} = v_{\mathrm{max,e}} \, \mathcal{N}\!\left[\sum_{j}\!\left(\frac{\mathbf{r}_{\mathrm{e},i} - \mathbf{r}_{\mathrm{c},j}}{|\mathbf{r}_{\mathrm{e},i} - \mathbf{r}_{\mathrm{c},j}|^2} - C'''_{\mathrm{f}} \frac{\mathbf{v}_{\mathrm{e},i} - \mathbf{v}_{\mathrm{c},j}}{|\mathbf{r}_{\mathrm{e},i} - \mathbf{r}_{\mathrm{c},j}|^2}\right)\Theta(r_{\mathrm{sens}} - |\mathbf{r}_i - \mathbf{r}_j|)\right], \tag{15}$$

where C'''_{f} is the coefficient of the velocity alignment term.

Erratic escaping. In nature many species tend to use certain kinds of erratic escaping strategies in which they combine direct escaping with some more advanced patterns of motion. Here we implemented the most basic one called zigzagging [29, 31]. During zigzagging, the escaper tries to trick its chaser(s) with a set of sudden and unexpected changes in direction. For this we introduced a so-called panic parameter (p_{panic}), which is an exponential function of the distance between the escaper and the nearest chaser (d_{min}), with the value of 0 if the

chaser is outside the escaper's range of sensitivity and 1 when the escaper gets caught:

$$p_{\text{panic}} = \frac{1}{e-1}\,[\mathrm{e}^{-d_{\min}/r_{\text{sens}}+1} - 1]. \tag{16}$$

The escaper starts zigzagging when the panic parameter reaches a certain threshold (p_{thres}) and it is not closer to the wall than a certain distance (r_{zigzag}):

$$p_{\text{panic}} < p_{\text{thres}}, \tag{17}$$

$$r_{\text{e}} < r_{\text{a}} - r_{\text{zigzag}}, \tag{18}$$

where r_{e} is the absolute value of $\mathbf{r}_{\text{e}}$. If these conditions are true, the escaper starts moving in a certain direction for a given amount of time. Afterwards, the prey zigzags in another direction for a period of time if the zigzag conditions are still true, otherwise it continues to escape directly. The zigzagging gets interrupted when the distance between the chaser and the escaper decreases below r_{zigzag}. We determine the direction of a zigzag segment in the following way:

$$\mathbf{v}_{\text{e},i}^{\text{zigzag}} = v_{\max,\text{e}}\,\mathcal{N}\left\{\mathcal{R}\left[\sum_{j}\left(\frac{\mathbf{r}_{\text{e},i} - \mathbf{r}_{\text{c},j}}{|\mathbf{r}_{\text{e},i} - \mathbf{r}_{\text{c},j}|^2}\right)\Theta(r_{\text{sens}} - |\mathbf{r}_i - \mathbf{r}_j|)\right]\right\}, \tag{19}$$

where $\mathcal{R}$ is a rotating operator that rotates its argument vector by an angle in two dimensions randomly chosen from the interval $[-\pi, \pi]$ and by two random angles (one azimuth and one polar) in three dimensions from the intervals $[0, 2\pi]$ and $[0, \pi]$. The duration of a zigzag segment is also a random parameter, which we chose from a power-law distribution with an exponent of -2, a lower limit of $r_{\text{zigzag}}/v_{\max,\text{e}}$, and an upper limit of $r_{\text{a}}/v_{\max,\text{e}}$.

Behaviour at the wall. Confronting the wall would significantly decrease the escaper's speed; therefore, the escaper should avoid getting too close to the wall. This is ensured by cutting off the radial component of the escaper's velocity vector depending on how close to the wall the agent is:

$$\mathbf{v}_{\text{e}}^{\text{final}} = \mathbf{v}_{\text{e}} - C_{\text{wall}}(r_{\text{e}}, r_{\text{a}}, r_{\text{wall}})\,\frac{\mathbf{r}_{\text{e}}}{r_{\text{e}}}\left(\frac{\mathbf{r}_{\text{e}}^{\mathrm{T}}}{r_{\text{e}}}\cdot\mathbf{v}_{\text{e}}\right) = \hat{\mathbf{W}}\mathbf{v}_{\text{e}}, \tag{20}$$

where C_{wall} is defined as

$$C_{\text{wall}} = \begin{cases} 1 & \text{if } r_{\text{e}} > r_{\text{a}} - 2r_{\text{wall}}, \\ \dfrac{1}{2}\left[1 - \sin\left(\pi\,\dfrac{r_{\text{e}} - r_{\text{a}} + 2r_{\text{wall}}}{r_{\text{zigzag}}} - \dfrac{\pi}{2}\right)\right] & \text{if } r_{\text{e}} > r_{\text{a}} - 2r_{\text{wall}} - r_{\text{zigzag}}, \\ 0 & \text{otherwise.} \end{cases} \tag{21}$$

Applying this method exclusively would mean that once the escaper reaches the wall it is stuck there forever, which would be unrealistic. Thus, we extended this rule: if the escaper is close to the wall ($C_{\text{wall}} > 0.5$) and it can slip through the gap between the two closest chasers, it does, and it returns to the central part of the arena. In order to determine whether or not jumping back to the arena means a successful escape, the prey routinely calculates how long it would take for itself and the two nearest chasers to reach certain points. These points are the ones we get when we project the difference vectors pointing from the prey to the chasers onto the line defined by the sum of these two vectors (equation (22), figure 5):

$$\mathbf{e} = \frac{(\mathbf{r}_{\text{c},1} - \mathbf{r}_{\text{e}}) + (\mathbf{r}_{\text{c},2} - \mathbf{r}_{\text{e}})}{|(\mathbf{r}_{\text{c},1} - \mathbf{r}_{\text{e}}) + (\mathbf{r}_{\text{c},2} - \mathbf{r}_{\text{e}})|}, \tag{22}$$

$$\mathbf{r}_{\text{p},k} = \mathbf{e}[\mathbf{e}^{\mathrm{T}}\cdot(\mathbf{r}_{\text{c},k} - \mathbf{r}_{\text{e}})], \tag{23}$$

$$\tau_{\text{e},k} = \frac{r_{\text{p},k}}{v_{\max,\text{e}}}, \tag{24}$$

$$\tau_{\text{c},k} = \frac{|\mathbf{r}_{\text{p},k} - \mathbf{r}_{\text{c},k} + \mathbf{r}_{\text{e}}| - r_{\text{cd}}}{v_{\max,\text{c}}}, \tag{25}$$
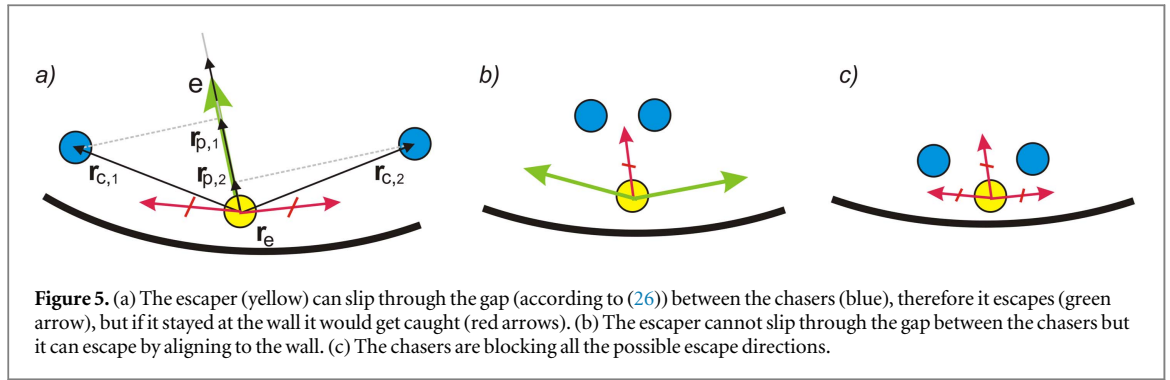
$$\tau_{\text{e},k} \overset{?}{<} \tau_{\text{c},k}, \tag{26}$$

where $k = 1, 2$ are the indices of the two nearest chasers (see figure 5). If condition (26) is true, the escaper can run back to the arena without getting caught; otherwise it stays at the wall where it will either be caught or chased.

The driving force of the ith escaper will be the sum of the interaction with the wall, collision-avoiding repulsion and either the direct or the zigzagging escaping term, finally transformed by the $\hat{\mathbf{W}}$ operator (20):

$$\mathbf{f}_{\text{e},i} = \hat{\mathbf{W}}(\mathbf{v}_i^{\text{a}} + \mathbf{v}_{\text{e},i}^{\text{coll}} + (\mathbf{v}_{\text{e},i}^{\text{esc}} \vee \mathbf{v}_{\text{e},i}^{\text{zigzag}})). \tag{27}$$

Figure 5. (a) The escaper (yellow) can slip through the gap (according to (26)) between the chasers (blue), therefore it escapes (green arrow), but if it stayed at the wall it would get caught (red arrows). (b) The escaper cannot slip through the gap between the chasers but it can escape by aligning to the wall. (c) The chasers are blocking all the possible escape directions.

Table 2. The environmental and tactical parameters of the model.

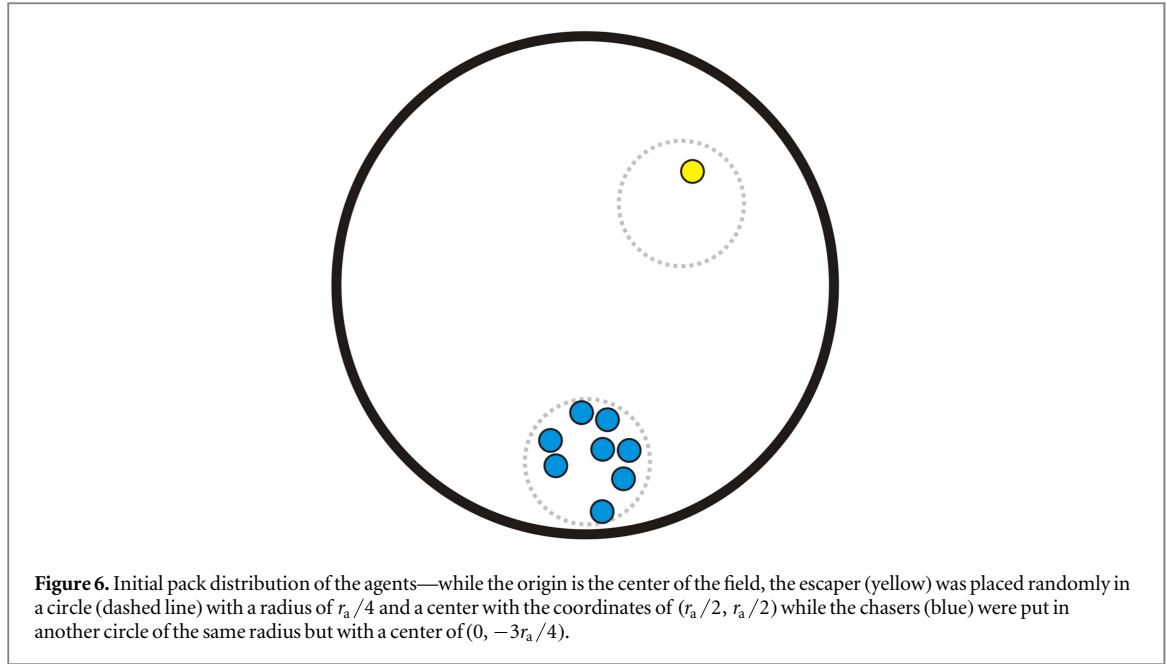| Environmental parameters	Typical range	Dimension	Definition
a_{max}	6	$m\,s^{-2}$	Maximum acceleration of the agent
σ	0.0–1.0	$m^2\,s^{-3}$	Standard deviation of the Gaussian noise
τ_{CTRL}	0.06	s	Characteristic time of the acceleration
t_{del}	0–6	s	Delay time
C_f'	1.1	ms	Friction coefficient in the direct chasing term
C_f''	1.1	$m^2\,s$	Friction coefficient in the velocity alignment between chasers
C_f'''	1.1	s	Friction coefficient in the direct escaping term
r_a	150	m	Radius of the arena
r_{cd}	1	m	Catching distance
r_{wall}	5	m	Width of the wall
Parameters of chasers' tactics	Typical range	Dimension	Definition
$v_{max,c}$	6	$m\,s^{-1}$	Maximum velocity of the chasers
τ_{pred}	0–6	s	Upper limit of the chaser's prediction
C_{inter}	0–1	1	Strength of interaction between chasers
r_{inter}	0–300	m	Interaction distance between chasers
Parameters of escapers' tactics	Typical range	Dimension	Definition
$v_{max,e}$	8	m/s	Maximum velocity of the escapers
p_{thresh}	0–1	1	Escaper's panic threshold
r_{sens}	0–120	m	Escaper's range of sensitivity
r_{zigzag}	0–80	m	Minimal length of a zigzag segment; the distance limit between an escaper and a chaser when the escaper stops zigzagging

2.2.4. Model parameters

Although in our model the number of expressions and parameters is significantly larger than in the simplest statistical mechanical models, these expressions and parameters are far from arbitrary; almost all of them are in a direct relation with the observed systems and originate from such trivial facts as the existence of time delays (e.g. reaction time). The parameters are 'freely' tunable from the point of the model, but most of them are experimentally measurable for an actual predator–prey system.

These parameters can be separated into two sets: environmental and tactical parameters (table 2). Except for t_{del}, all the environmental parameters had fixed values during the measurements: for instance, $a_{max} = 6\,m\,s^{-2}$, $r_a = 150\,m$ and $r_{wall} = 5\,m$. On the other hand, all the tactical parameters except the fixed velocities ($v_{max,c} = 6\,m\,s^{-1}$, $v_{max,e} = 8\,m\,s^{-1}$) can be adjusted at the beginning of each run to create and study different chasing and escaping tactics. We studied most cases in both 2D and 3D.

3. Results and discussions

We use a finite and fixed simulation length ($\tau_{max} = 600\,s$), which is comparable to the observed length of pursuits in nature, and also practical for the simulations because of the limited computation time. This means that when counting the average results of the runs we have to handle properly those cases in which the escaper was not caught. Therefore we assume that the uncaught prey's lifetime was the maximum, so if the escaper's average lifetime is τ_{esc} out of n runs when it was caught, the average time is

Figure 6. Initial pack distribution of the agents—while the origin is the center of the field, the escaper (yellow) was placed randomly in a circle (dashed line) with a radius of $r_a/4$ and a center with the coordinates of $(r_a/2, r_a/2)$ while the chasers (blue) were put in another circle of the same radius but with a center of $(0, -3r_a/4)$.

$$\overline{\tau}_{esc} = \frac{n\,\tau_{esc} + (n_{tot} - n)\,\tau_{max}}{n_{tot}}. \tag{28}$$

We defined the following effectiveness functions to quantify the pursuit with regard to the chasers:

$$\text{Effectiveness}_c = \frac{n/n_{tot}}{(\overline{\tau}_{esc}/\tau_{max})N_c}, \tag{29}$$

which means that the group of chasers is most effective if it catches the escaper the greatest number of times out of n_{tot} similar runs, gets the prey as fast as possible, and needs the smallest number of chasers to do so. The division by N_c refers to the observation that the greater the number of chasers that catch the same prey, the less food per capita they get. On the other hand, we defined an effectiveness function for escapers as well:

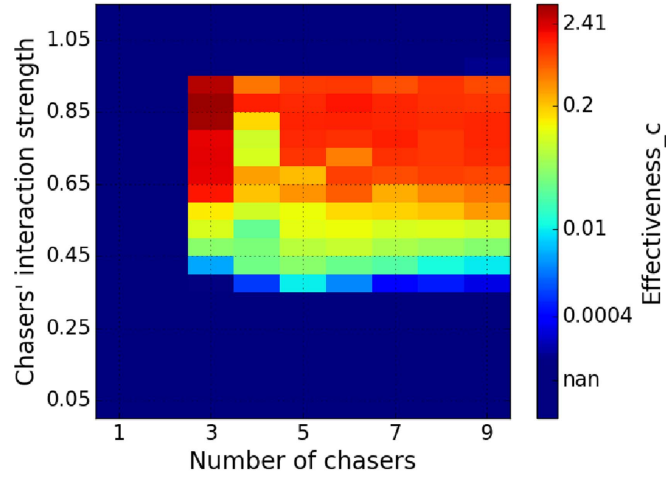$$\text{Effectiveness}_e = \frac{\overline{\tau}_{esc}}{\tau_{max}}. \tag{30}$$

The escaper's effectiveness is the ratio of the average lifetime to the maximum time allowed, and those who are not caught are taken into account with Effectiveness$_e$ of 1.

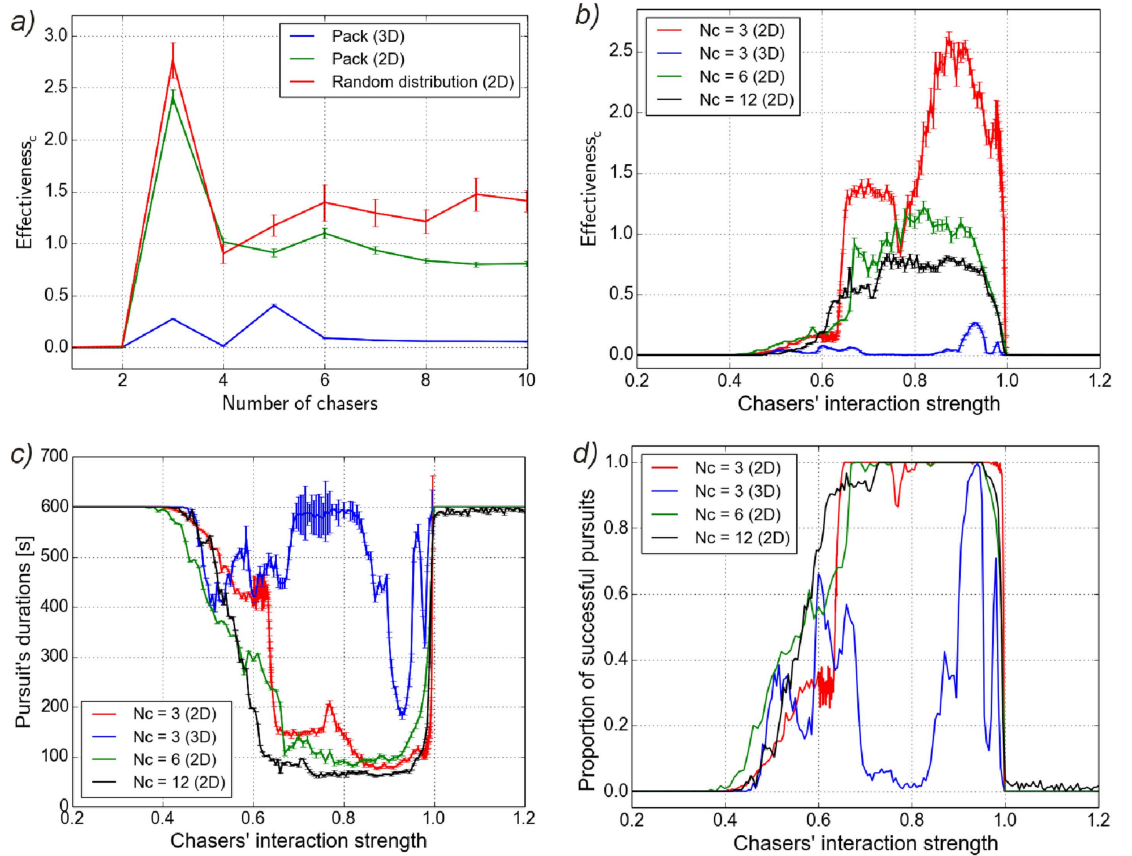### 3.1. A group of chasers versus a single escaper

3.1.1. Strength of the interaction and the number of chasers

At first we studied the effect of the interaction between the chasers as a function of N_c with two different spatial distributions of the agents and the interaction range fixed ($r_{inter} = 300\,\text{m}$). In the first distribution, all the agents were spaced randomly on the field with no regard to their type. In the second one, the escaper was placed randomly in a circle with a radius of $r_a/4$ and a center with coordinates $(r_a/2, r_a/2)$ while the chasers were put in another circle of the same radius but with a center of $(0, -3r_a/4)$, where the center of the field is the origin (figure 6). In 3D the method is the same but using spheres. The completely random starting position is widely used in the literature, but in reality it is more common that the chasers are closer to each other when they start the pursuit (it is also not logical for the prey to wander into a place where the predators are scattered all around).

For the random distribution, the chasers sometimes happened to be initially around the escaper, which leads to an immediate encircling and a very quick (and unrealistic) pursuit. However, with the pack distribution the chasers have to build up their chasing formation to catch the prey, which produces a well-defined regime of the parameter space in which the chasers are successful. Despite this, there is no big difference in the maximal Effectiveness$_c$ values in these two cases, as figure 7 demonstrates. For the case of the pack distribution, the chasers' effectiveness can be seen in figure 7 as a function of the number of chasers and the interaction strength between them. It is important to point out that these results are the solid proof of the fact that in these scenarios (i.e. where the escaper is faster) a single chaser is not able to catch the prey and multiple agents only have a chance to do so if there is a strong tactical interaction between them. As an example, we took a closer look on certain cross sections around the optimum of figure 7, which are presented in figure 8. figure 8 illustrates that chasing in three dimensions is a lot harder than in two dimensions, and while three chasers can form an optimal group for 2D, five is more advantageous for 3D.
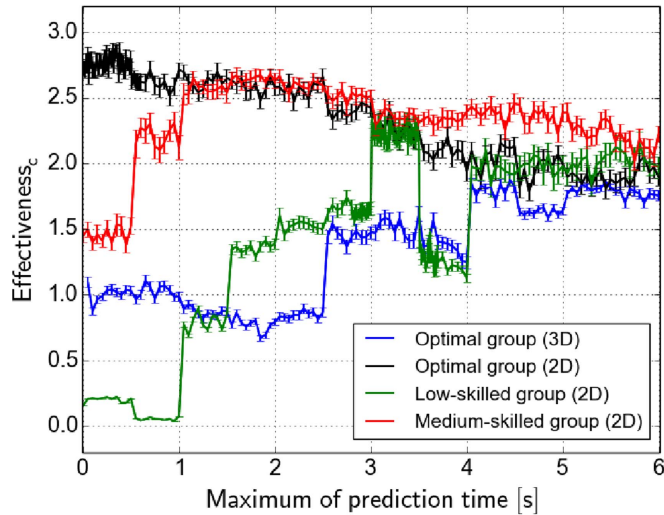
Figure 7. The effectiveness of the group of chasers in the case of an initial pack distribution in 2D as a function of the number of chasers and the strength of the interaction between them. In the dark blue regime the chasers never catch the prey.

Figure 8. Cross sections of figure 8: the Effectiveness$_c$ as a function of (a) N_c when $C_{inter} = 0.9$, (b) C_{inter} when $r_{inter} = 300$ m for various cases, (c) the pursuit's duration and (d) the proportion of successful pursuits (which ended in catching the escaper). We can see on the graphs that cooperative hunting is effective with well-tuned interaction between the chasers, and optimal when $N_c = 3$ for 2D or $N_c = 5$ for 3D. There are two well-defined regimes in (b): one in which the chasers are successful and one in which they are not. The narrow boundaries between the regimes are the results of the fixed geometric assumptions. The quick breakdown at $C_{inter} = 1$ means that at that point the chasers align into a regular grid formation, which cannot be changed by a single (driver) escaper.

On one hand, we can see that the effectiveness decreases monotonically above $N_c = 6$, which happens because of the division by N_c in (28); on the other hand, one and two chasers have no chance to ever catch the faster prey. Between these two regimes the tendency is not monotonic. This happens for geometric reasons (symmetric arrangements), which will be averaged out for larger N_c values: an odd number of chasers have a

Figure 9. The effectiveness of a previously optimized group of three chasers, a group with medium-level efficiency (about half as effective as the optimized one) and a group with low-level efficiency (less effective than 10% of the optimized one) as a function of the maximum of the prediction time. These results show that if the prediction time is large enough, it significantly enhances the effectiveness of the least effective group. On the other hand, in the case of the optimized group, a longer prediction time lengthens the pursuit's duration, which (because of the 100% success rate via optimization) decreases the group's effectiveness.

much bigger chance to block all the escape directions, but it is much easier for a gap to remain when the number of chasers is even (see figure 5).

3.1.2. Prediction and delay

In this subsection we study a chaser's cognitive prediction regarding the escaper's path, how the time delay can affect the outcome of the pursuit and how the prediction can compensate for the delay. As it was introduced in section 2, the prediction has an upper time limit, the maximum time of prediction (τ_{pred}), which is studied in this subsection. This quantity is proportional to how far ahead the chasers forecast their prey's position. If we add the prediction (figure 9) to the previously optimized chasers, their effectiveness increases a little (with a maximum at $\tau_{pred} \approx 0.38$ s), but after that it starts to decrease. This happens because the optimized chasers are already hunting with a 100% success rate ($n = n_{tot}$ in (29)), while a long prediction time extends the pursuit's duration because the chasers do not rush immediately towards to the escaper but extrapolate and chase the escaper's future position, which is always further away, and this longer duration leads to lower efficiency, while in 3D even the efficiency of an optimized (with regard to the interaction between the chasers) group can be significantly increased by the prediction. However, if we take a look at chasing packs with non-optimized interaction parameters (in 2D), we can see that prediction improves their efficiency to near the level of the optimized group.
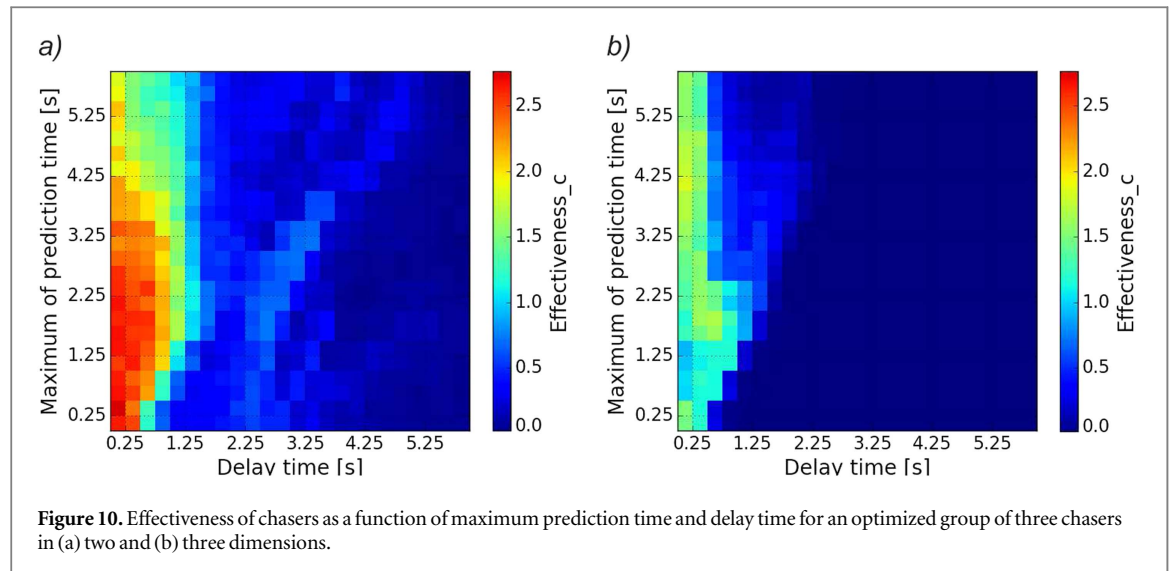
We tested the tolerance of the Effectiveness$_c$ against delay with different prediction times for different groups of chasers (figure 10). These experiments led to the conclusion that if the prediction time is large enough in comparison to the delay (but still of the same order of magnitude), prediction will compensate for the delay and the pursuit remains successful. However, a very large delay (e.g. 5 s) with a small prediction can completely prevent the success of the pursuit. Based on these results, the optimal values of the chasers' tactical parameters can be found in table 3 if the system has a delay of 1 s.

3.1.3. The effect of external noise

We examined the effect of external, Gaussian noise within the range $\sigma = 0$–2 m^2 s^{-3}, where 0.2 m^2 s^{-3} is equivalent to, e.g., the wind blowing with medium strength. The values of Effectiveness$_c$ proved to be quite robust and stable against this perturbation, which just slightly increased the deviation of the statistical results. The standard deviation of the noise amplitude–Effectiveness$_c$ dataset was about 2% in two dimensions, and 2.4% in three dimensions, and it stayed fairly constant.

3.1.4. Emergent phenomena in the model

Despite our model's simplicity, while studying it in real time we can observe very interesting, life-like patterns of motion emerging. These can be categorized as follows:
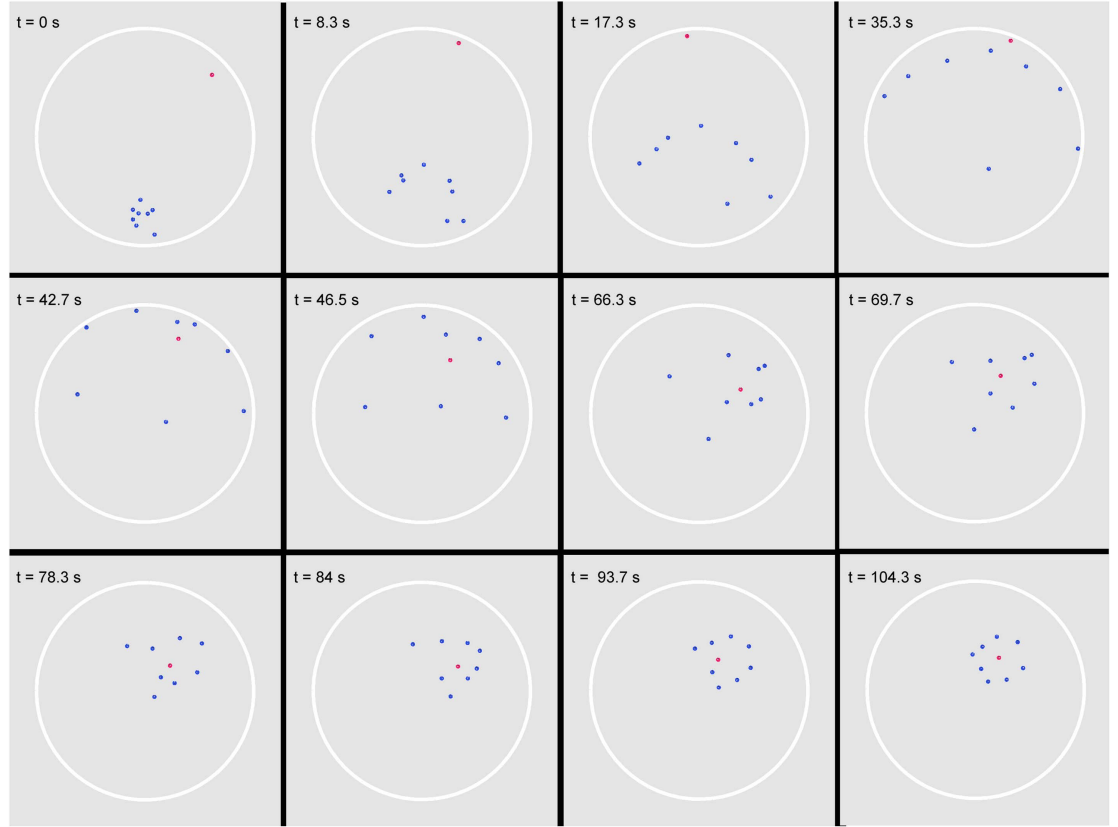
Figure 10. Effectiveness of chasers as a function of maximum prediction time and delay time for an optimized group of three chasers in (a) two and (b) three dimensions.

Table 3. The optimal chasing parameters in two and three dimensions with prediction and delay (1 s).

	N_c	C_{inter}	r_{inter}	τ_{pred}
2D	3	0.86	155 m	1.75 s
3D	3	0.9	135 m	2 s

- The optimal group of chasers catches the prey very quickly: they rush towards the escaper on the right trajectories to block all its possible escape routes. This can also happen (with a lower frequency) in three dimensions. This sometimes results in line formation, too.

- If the chasing parameters are moderately efficient, 'on-the-field' pursuit often happens: the agents cross the field several times, the escaper moves along the wall, and hops back to the center of the field several times. In these situations the classical encircling (observed, e.g., in lions) can also happen completely emergently (figure 11). With significantly more chasers, this phenomenon (sometimes called as caging) can be observed in three dimensions as well.

3.1.5. Summary: chasers

In this section we have demonstrated that those chasers that are unable to catch the prey alone can successfully pursue it if there is a certain, well-parametrized interaction between them, which is their collective chasing tactics. For this we studied and optimized the parameters of the group of chasers by scanning their parameter space. We have found that even in three dimensions three chasers can efficiently catch the prey if the strength and characteristic distance of the interaction are set properly. We have shown that the prediction method enhances the capabilities of the chasers (even if their interaction parameters are sub-optimal), and that prediction can suppress the negative effects of time delay. We pointed out that these optimal chasing tactics are robust against external noise and we have found interesting, emergent behaviour patterns, such as life-like encircling. The data also implies that chasing in three dimensions is a lot more difficult task than in two dimensions, which is consistent with the fact that truly three-dimensional pursuits are very rare in nature. What is more common in three dimensions is to restrict the degrees of freedom in some way. Flying and swimming animals frequently use the natural borders of their open 3D space (water–air or air–ground boundaries) to drive their prey into a corner. It has also been reported for dolphins hunting in groups that certain individuals tend to have different roles during the hunt, for example they create artificial blockades to restrict the possible escaping routes of schools of fish and catch them more efficiently [47, 48]. Finally, certain species, such as fish-hunting cone snails or all kinds of web spiders use various 'sit-and-wait' strategies—they hide, and attack abruptly only when the prey is close enough [23, 46].

Figure 11. Nine chasers can quickly encircle the evader.

Figure 12. Effectiveness$_e$ as a function of p_{thresh} in (a) two and (b) three dimensions with and without delay. This shows that the escaper can optimize its tactics with a well-chosen panic threshold parameter, and therefore increase its lifespan.
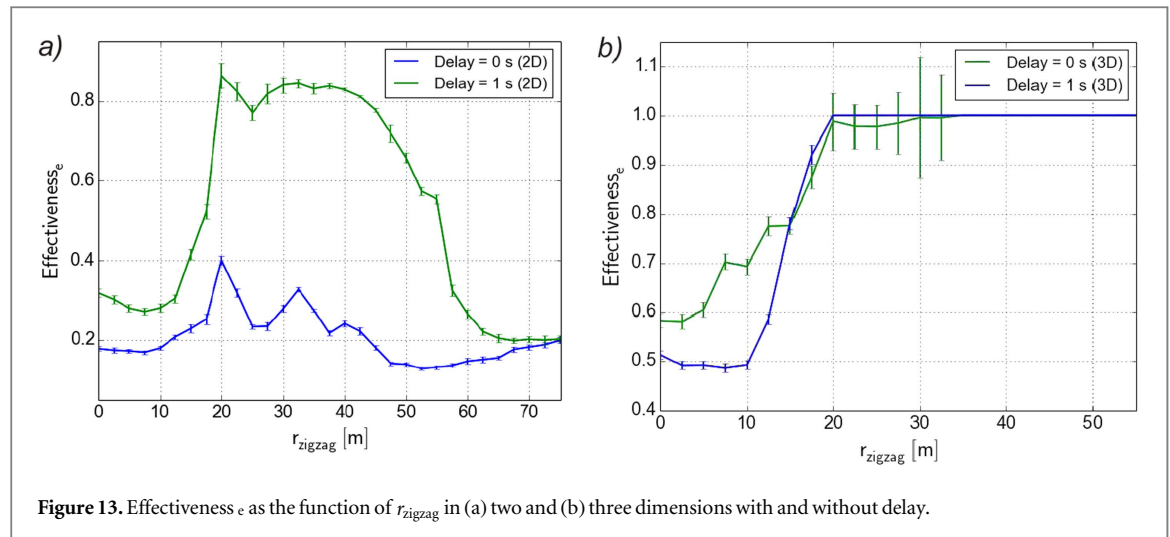
3.2. Erratic escaper

We study the panic threshold (p_{thresh}), which is the parameter controlling the zigzag pattern of motion, and seek the optimum of r_{zigzag} and r_{sens}. In this section $n_{tot} = 1000$ for each data point.

3.2.1. Zigzag motion: the panic threshold

The panic parameter of the zigzag motion was defined in (16) as a real number between 0 and 1 that depends on the distance between the escaper and its nearest chaser. If this value reaches the panic threshold, the escaper begins a zigzag motion. At first we examined the Effectiveness$_e$ values as a function of p_{thresh} to study the zigzag's effect on the pursuit's outcome. The results are presented in figure 12 with and without delay, in two and three dimensions. These figures tell us that zigzagging can significantly improve the escaper's efficiency in all the cases studied; moreover, p_{thresh} does have optimal values.

Figure 13. Effectiveness $_e$ as the function of r_{zigzag} in (a) two and (b) three dimensions with and without delay.

3.2.2. Zigzag motion: not too close

The zigzagging has another parameter: r_{zigzag}, which is the critical distance at which the escaper ceases zigzagging and returns to direct escape to avoid dangerous situations due to the closeness of the chaser(s). figure 13 implies that in 2D $r_{zigzag} = 20$ m is a universal optimum, while in 3D, if $r_{zigzag} > 20$ m, the chasers cannot catch the escaper. In other words, (i) zigzagging too close to chasers is disadvantageous in both two and three dimensions, (ii) in two dimensions there is an advantageous regime with an optimal parameter for the zigzagging, and (iii) in three dimensions the Effectiveness$_e$ gets saturated at $r_{zigzag} = r_{sens}$, which means that the evader successfully escapes even without the zigzag tactics.

4. Conclusion

Based on the corresponding ethological literature we built up a bio-inspired realistic agent-based approach to model collective chasing in continuous space and discrete time within closed boundaries for the case when the escaper is significantly faster than the chasers—a situation in which the chasers have no chance to catch the prey alone or without collaboration. Examining the model, we have found the following:

- An optimal group of chasers, which can catch a faster prey, exists in both two and three dimensions when there is a soft, repulsive interaction force between them. This would be impossible without the interaction between the chasers. The optimal group size found here is also comparable to sizes observed in nature when using realistic model parameters.

- Emergent behaviour occurs—with certain parameters the chasers have the chance to encircle (encage) their prey. These patterns emerge directly from the implemented chasing rules and reflect similar phenomena observed in real biological systems.

- If the chasers are using the prediction method to forecast their targets' position, their effectiveness increases.

- Great delay can completely suppress the chasers' success, but with a long enough prediction time, this can be overcome.

- We demonstrated that the zigzag pattern of motion of erratic escapers can be advantageous, especially when there is delay in the system.

- Chasing in three dimensions is a much more difficult task for chasers, therefore the evader is more likely to survive.

- Both the chasers' and the escaper's optimal set of parameters seems to be robust against external noise.

5. Outlook

Even though our model supersedes those previously proposed in many respects (e.g. two and three dimensions, delay, erratic escaper, prediction), it leaves many directions of the topic to be studied and extended, such as: (i) many chasers versus many escapers is just as interesting, or even more escapers versus a small group of

chasers; (ii) applying evolutionary optimization methods to the species; (iii) finding real-life applications; (iv) equipping agents with machine learning or real-time adaptive algorithms.

Acknowledgments

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