

## RESEARCH ARTICLE

# Numerical Modeling of the Collective Behavior of Scarab Beetles Transporting Dung Balls and Competing for Them on Complex Terrain

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To avoid competition for the same food resource, scarab beetles form dung ball and roll it away from the dung pile. They randomly choose direction which they strictly follow. According to previous results, the dynamic behavior of the beetle rolling dung ball is essentially defined by the complexity of the surface. The typical real surface is combined from a universal scale invariant (fractal) component and another component having a well-defined characteristic scale. If the transported dung ball has a size comparable with the dimensions of peculiarities of the surface, it strongly influences the motion trajectory. On the flat terrain and at the absence of competitors, beetles manage to roll the ball along a nearly perfect straight path. However, even if the beetle is alone, on a more realistic terrain, the motion is more complex. The motion becomes much more complicated in the realistic situation, when the beetles compete for the balls. In this study, a numerical model is developed which combines 1) attraction of the beetles to the dung, 2) production of the balls of different sizes depending on the size/fitness of the animals, 3) the ball transportation on complex terrains, and 4) the competition between the beetles for already existing balls. A strong correlation between typical radius of the ball and the size of the relief minimums and the results of the competitions, as well as possible optimal strategies of the beetle behavior are found.

dung in warmer climates makes it crucial to quickly use or bury the ephemeral dung, because it quickly becomes unsuitable for most dung feeding insects. While most of the dung beetles (Scarabaeoidea) live in or underneath the dung pile and compete for burial space, telecoprid dung beetles have evolved a unique technique to avoid the competition at the dung pile by forming a dung ball and rolling it away from the hot spot of strong competition.<sup>[4]</sup> This dung balls weigh on average about 5–20 times the body weight of the dung beetle<sup>[5]</sup> and can vary in diameter (1–3 cm) depending on the dung beetle species. Those dung balls have to be transported away from the dung pile as fast as possible, to reduce the risk of losing the accurately molded dung ball in fights with competitors. It is generally assumed that, in order to quickly increase distance to the dung pad, dung beetles randomly choose an arbitrary direction<sup>[6]</sup> which they strictly seem to follow. On the flat terrain, they manage to almost roll the dung ball along a nearly perfect straight path.<sup>[7]</sup> Even

confronted with an obstacle, they will try to go over the obstacle rather than go around it.<sup>[8]</sup>

Although research has previously addressed the transport mechanism of balls by dung beetles<sup>[8,9]</sup> and several engineering studies have looked into the impact of substrates on the motion of a sphere on different substrates,<sup>[10–12]</sup> to the best of our knowledge, no research has been done to consider the impact of terrain characteristics on the performance of the dung beetles during dung ball transportation.

Like many other soil dwelling organisms, dung beetles show strong habitat association with preference for specific substrate and vegetation cover.<sup>[13,14]</sup> While ball rolling is most effective in open terrains, such as steppes, savannahs, and deserts, telecoprid dung beetle species are native to habitats showing great variability in the soil surface characteristics. Even in tropical rain forests with challenging terrains, telecoprid dung beetles are capable of efficient transport of dung balls.<sup>[15,16]</sup>


By decoupling the motion of the ball from the complex and irregular external force produced by the dung beetle, we can simplify the problem to the stage, at which one can handle it for the numerical simulation. In such an approach, we become able to exclusively study the rolling pattern of the ball in relation to

## 1. Introduction

Many dung-feeding insect species compete for the same food resource. This leads to an intense inter- and intraspecific competition at the dung pile.<sup>[1–4]</sup> In addition, quick dehydration of

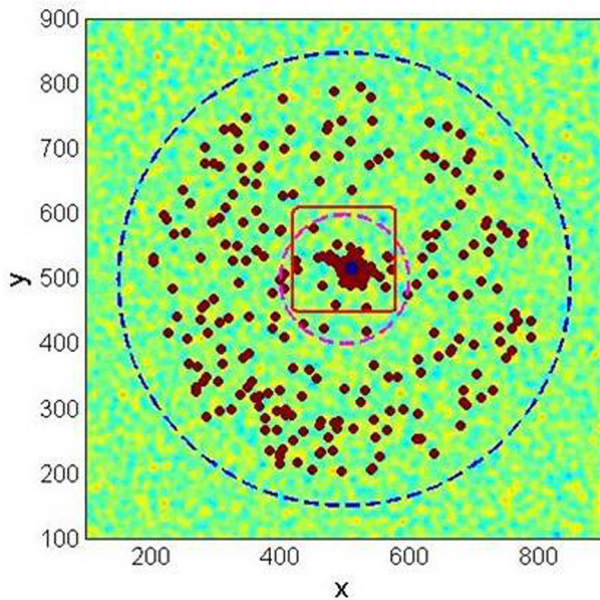
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**Figure 1.** Early stage of the process. The beetles having a ball of the maximal size preferable for a given animal are marked by the blue color. Large blue dashed circumference outlines originally populated area. Small dashed circumference qualitatively restricts a region with sufficiently high density of food. Rectangle marks small region magnified in Figure 2 below. Relief of the terrain is plotted by the “jet” color scheme of MatLab with strongly reduced contrast to make all the circles and dots visible.

varying surface characteristics, while keeping the mass of the ball as well as the speed and direction of the externally applied force constant.

Qualitatively presented configurations of the terrains in field situations with different relations between the characteristic scales of the structures and the radius of the transported ball are schematically presented in the conceptual picture of **Figure 1**.

As natural molded dung balls are never perfectly round and intense competition at the dung pad even forces dung beetles to decrease the time spend to shape the dung ball, we additionally include the effect of some random perturbations to the rolling trajectories. The results of this study aid in prediction of the energy amount spent for dung transportation depending on particular terrain and in turn to predict preferable habitats for telecoprid dung beetle species.

## 2. Numerical Model

### 2.1. Random Walk of Solitary Beetle on Combined Surface

In this section, we briefly reproduce approach and basic results of the recent work,<sup>[17]</sup> which underlies the present study. To perform a numerical simulation of the mechanical motion on a complex surface, we create numerically a potentially unlimited number of such numerically generated surfaces. The majority of real surfaces have semifractal structure with a well-defined Fourier spectrum and amplitude of roughness.<sup>[18]</sup> It is widely accepted in the current literature<sup>[19]</sup> that, such surfaces are

the self-affine fractal given by the real part of the following function

$$Z(x, y) = A \iint dq_x dq_y C(q) \exp(iq_x x + iq_y y + \zeta(x, y)) \quad (1)$$

with a scaling spectral density  $C(q)$ . Here  $A$  is an amplitude of the surface roughness,  $i$  is an imaginary unit,  $q_{x,y}$  are the Fourier components along the  $x$  and  $y$  directions with an absolute value of  $q = \sqrt{q_x^2 + q_y^2}$ , and  $\zeta(x, y)$

$$\langle \zeta(x, y) \rangle = 0; \quad \langle \zeta(x, y) \zeta(x', y') \rangle = D \delta(x - x') \delta(y - y') \quad (2)$$

is  $\delta$ -correlated random phase. The wave-vectors vary from minimum  $q_{\min} = 0.03\pi$  to  $q_{\max}$  defining an interval of the scales, where the semifractal structure of the surface may take place (e.g., refs. [19, 20]). In the current literature,<sup>[18]</sup> it is accepted that for the majority of such physical surfaces, the expansion Equation (1) has a scale-invariant spectral density  $C(q) = 1/q^\beta$  with an exponent  $\beta \approx 0.9$ . However, here the surface is not so simple and “general.” It has some characteristic scale of the peculiarities with at least one selected wave-vector  $q_0$ .<sup>[17,18,19]</sup> It leads to the combined spectral density with two terms

$$C(q) = \mu C_1(q) + \nu C_2(q) \quad (3)$$

reproducing both different impacts onto the surface. The scaling part  $C_1(q) = 1/q^\beta$  and the second one  $C_2(q) = \exp\{-(q - q_0)/\Delta q\}^2\}$ , which causes minimums randomly distributed around the wave-vector  $q_0$  with the width  $\Delta q$ . The coefficients  $\mu$  and  $\nu$  determine different weights of the corresponding substructures in the total surface  $Z(x, y; q_0)$ . Below according to the previous studies,<sup>[21]</sup> we apply:  $\Delta q = 3q_{\min}$ ,  $\mu = 0.2$ , and  $\nu = 1$ .

At every fixed value of  $q_0$ , the numerical procedure generates a new function  $Z(x, y; q_0)$  distributed between the particular global minimum  $Z_{\min}$  and maximum  $Z_{\max}$ . To describe all the realizations in the regular manner, we normalize it by a scalar factor  $U_0 : U(x, y; q_0; U_0) = U_0 Z(x, y; q_0) / (Z_{\max} - Z_{\min})$ , which defines the actual amplitude of roughness. The final combination  $U(x, y; q_0; U_0)$  plays a role in an effective potential in the equations of motion depending on the amplitude  $U_0 (1 \leq U_0 \leq 11)$  and the wave-vector  $q_0$

$$dx/dt = -\partial U(x, y; q_0; U_0) / \partial x + f_x^{\text{ext}} \quad (4)$$

$$dy/dt = -\partial U(x, y; q_0; U_0) / \partial y + f_y^{\text{ext}} \quad (5)$$

Considering the small mass of the ball, one can neglect the inertial terms and simplify them to the over-damped form. However, the factor  $U_0 \sim M$  here is proportional to the mass of the ball  $M = 4\pi\rho R^3/3$  calculated using its density  $\rho$  and the volume  $V = 4\pi R^3/3$ . The larger the ball, the more food can be transported at the individual trip. However, the bigger is the ball, the deeper are the valleys of the effective potential  $U_0 \sim M$  and the harder the transportation process is. Besides, the ball attracts attention of other beetles, who can potentially take it away. As a result, the radius  $R$  can appear important for specific terrains and

conditions of the competition for the food. It causes a wide number of optimization strategies, which can appear in the course of biological evolution.

The values  $f_x^{\text{ext}}$  and  $f_y^{\text{ext}}$  in Equation (5) formally define  $x$ - and  $y$ -components of the external force. Previously, we studied an idealized case of one beetle, which tries to move in a randomly chosen, but fixed direction.<sup>[6,21]</sup> The numerical procedure in this idealized case is regular, because one can associate one of the axes of coordinates with the preferable direction of motion:  $f_x^{\text{ext}} = \text{const} \neq 0$ ;  $f_y^{\text{ext}} = 0$ . However, a randomness and corresponding statistics still exists here, because each time the procedure specified in Equations (1)–(4) randomly generates a new realization of the potential  $U(x, y; q_0; U_0)$ . For a fixed stripe of variables  $\{x, y\}$  (with  $L_x = 256$ ;  $L_y = 64$ ) studied in our numerical experiments:  $x = [0 \dots L_x]$ ;  $y = [0 \dots L_y]$ , we always used the same pair of initial coordinates  $\{x_0, y_0\}$ .

From Equation (5), the typical dynamic scenario will depend on the relationship between the potential  $\{-\partial U/\partial x, -\partial U/\partial y\}$  and external  $\{f_x^{\text{ext}}, f_y^{\text{ext}}\}$  forces. If they are comparable, the ball will move meeting from time to time proximities of local potential minimums. Formally, if the time is unlimited, the ball will be trapped sooner or later by a sufficiently deep minimum and stopped. However, the length of the stripe  $L_x$  is limited and the ball can pass all space completely before it is trapped. From a biological point of view, it means that the beetle will successfully transport the ball to the target site. If the characteristic width of the surface minimums is very large, the surface becomes very smooth and despite the deepness of the valleys, the ball will practically ignore them. In an opposite case with very narrow valleys, the ball with a fixed radius  $R$  should ignore them as well. To include this effect into consideration, we averaged the interactions in Equation (5) with the size of the ball by Gaussian convolution of the local potential  $U(x, y) \rightarrow U(x, y) \iint dx' dy' G(x - x', y - y'; R) U(x', y')$  in every point  $\{x', y'\}$  with the smoothing function  $G(x - x', y - y'; R) = \exp\{-[(x - x')^2 + (y - y')^2]/R^2\}$ .

As already mentioned above, the large ball is generally preferable from a biological point of view, because it contains more food for the beetle offspring. However, the large ball is also heavier and makes the valleys of the effective potential deeper. At the same time, the interaction with a large number of points in the proximity effectively smoothens the potential. However, for the specific terrain with relatively wide valleys, which could be ignored by the small ball, the bigger one can match their size perfectly and be stronger resisted by them.

All the mentioned factors cause a wide spectrum of possibilities, and many of them are closely related to the reality. We studied different combinations of the factors both numerically and experimentally in the situation with solitary beetles.<sup>[17,22]</sup> However, the real biological situation in the field is much richer, because many beetles act simultaneously and interact. Below we develop a model, which potentially allows describing such a complexity.

## 2.2. Collective Behavior of the Interacting Beetles

The model of collective behavior is organized as follows. It conserves all the steps, which were used to describe motion of the

solitary beetle. Further, we simulate the beetles group as an array of the discrete “objects,” which interact one with another according to natural rules. The interaction includes strong short-range repulsion between the animals. Mathematically, short-range repulsion means that one animal cannot penetrate inside some “private” area surrounding another animal. Normally, such repulsion takes place at relatively short distances corresponding to the radius  $R^{\text{repuls}}$ , where despite the complex terrain, the beetle can observe other ones and treat the area with radius  $R \leq R^{\text{repuls}}$  as its “private” territory.

Besides, there is mutual attraction at longer distances  $R^{\text{attract}} > R^{\text{repuls}}$ . In the majority of cases, such an attraction has an important biological meaning of a tendency to aggregation.<sup>[23]</sup> The tendency to aggregation often gives some competitive advantage due to possible collective reactions, e.g., on the attacks of the predator and on the other external challenges, or due to the “collective” search of the places, where a portion of the dung is disposed. However, for the system under consideration, the general impact to the attraction is probably not very specific. The most important part of the attraction in animals which do not have their own balls yet could be an attraction to the animals with the balls. We will include such a specific interaction into the model below.

The simplest way to simulate any kind of interaction with regulated characteristic distance is to use Gaussian effective potential with some characteristic radius  $R_0$ . Repulsion force in this case looks as follows

$$f_j^{\text{rep}} = A_0(\vec{r} - \vec{r}_j) \exp \left[ -\left( \frac{\vec{r} - \vec{r}_j}{R_0} \right)^2 \right] \quad (6)$$

where the factor  $A_0 < 0$  defines an amplitude of the attraction, vector  $\vec{r} = \{x, y\}$  describes a position of some particular animal, and the array of the vectors  $\vec{r}_j = \{x_j, y_j\}$  describes the positions of all other animals numerated by the index  $j = 1, \dots, N - 1$  with total number of them in the population  $N$ . Let us note also that the animals generally have different size and strength, which can be modeled with the repulsion forces amplitude  $B_{0j}$  and radius  $R_{0j}$

$$f_{jk}^{\text{repuls}}(\vec{r}_j, \vec{r}_k) = B_{jk}^{\text{repuls}}(\vec{r}_j - \vec{r}_k) \exp \left[ -\left( \frac{\vec{r}_j - \vec{r}_k}{R_{jk}^{\text{repuls}}} \right)^2 \right] \quad (7)$$

In general case, the parameters of this interaction and their dispersion can vary from one population to another around some mean value typical for the particular species.

The force of mutual attraction can be written in the analogous form

$$f_{jk}^{\text{attract}}(\vec{r}_j, \vec{r}_k) = B_{jk}^{\text{attract}}(\vec{r}_j - \vec{r}_k) \exp \left[ -\left( \frac{\vec{r}_j - \vec{r}_k}{R_{jk}^{\text{attract}}} \right)^2 \right] \quad (8)$$

where the coefficient  $B_{jk}^{\text{attract}}$ , situated before the exponent, regulates the attraction strength, and  $R_{jk}^{\text{attract}}$  characterizes the effective distance of the attraction. In the case of aggregation studied earlier,<sup>[23]</sup> the attraction is normally weaker than the repulsion and acts at relatively long distances. However, for the case



discussed here, the attraction of the beetle without the ball to the one already having it appears at the distance, comparable to the same for repulsion. It is possible at least inside an “observation horizon,” where the animals can see one another on complex terrain. Below, for definiteness, we use  $R_{jk}^{\text{attract}} = R_{jk}^{\text{repuls}}$ . However, we simulated the behavior of system at different relations between them. For the comparable ones  $R_{jk}^{\text{attract}} \approx R_{jk}^{\text{repuls}}$ , the model demonstrates more or less the same behavior. The only difference is in the probability, with which an offensive animal reaches proximity of the defensive one (where it can provoke a fight for the ball).

If the area  $\{[0, Lx], [0, Ly]\}$  is limited, the equations of motion must be supplied by appropriate boundary conditions, which do not allow the animals to leave it. The simplest way to introduce the boundary conditions is to apply mathematically “soft,” but extremely high and narrow walls around the system, which repulse the animals back to the internal space with exponentially growing force  $f_j^{\text{bound}} = B_j^{\text{bound}} \exp[-|\frac{\vec{r}_j - \vec{r}_{\text{bound}}}{R_{\text{bound}}}|]$  acting in the direction opposite to that, in which the animal occasionally crosses any of the boundaries.

The “extremely high” means that the amplitude of this force should be supplied by the prefactor  $B_j^{\text{bound}}$  which is much bigger than the amplitude of the repulsion force between the animals (regulated by the amplitude  $B_{jk}^{\text{repuls}}$ ) to be able to overpower their mutual repulsion  $B_j^{\text{bound}} \gg B_{jk}^{\text{repuls}}$  pushing them out the boundaries. Therefore also the characteristic distance of the repulsion from the wall should be much shorter than the typical distance between the animals  $R^{\text{bound}} \ll R^{\text{min}}$ . In other words, the boundary should be as narrow as possible.

One can expect that mean density of the population is not extremely high and does not force the animals to stay exactly at the minimal distance  $R^{\text{min}}$  between them. In this case, total combination of the attracting and repulsing interactions combined with the rejecting boundary conditions normally leads to the specific patterns, where relatively dense groups of the animals spread on the mutual distances close to the equilibrium ones are accompanied by almost empty voids between them.<sup>[20]</sup> We have checked this hypothesis numerically many times. It allows (maximally as possible) excluding an effect of the boundary conditions. In particular, instead of the boundary, one can apply appropriate initial conditions.

Let us suppose that we have an isotropic area of some initial radius  $R_0$  randomly, but uniformly on average, occupied by  $N$  animals and separated from all other populated “circles,” by the empty “voids” with negligible interaction either with the animals living in other regions or their attraction to the food, placed inside other such “circles.” We will return to more general picture of many dung spots disposed randomly on the wide area and population of the beetles which can choose between different ones somewhere else, but here, to perform transparent regular study, we restrict ourselves to the relatively simple model situation.

When a portion of the food falls onto the surface, the animals which occasionally appear relatively close to it are attracted to it and start to “build” their balls with some characteristic rate. Generally speaking, the food can fall into random position  $\vec{r}_n$  inside the area. In our previous studies of qualitatively close problems,<sup>[21]</sup> the food was supposed to be randomly deposited in-

side populated area. The attraction to the portion of food was simulated by the following term in the attraction force

$$f_{jn}^{\text{food}}(\vec{r}_j, \vec{r}_n) = B_{jn}^{\text{food}}(\vec{r}_j - \vec{r}_n) \exp \left[ - \left( \frac{|\vec{r}_j - \vec{r}_n|}{R_j^{\text{food}}} \right)^2 \right] \quad (9)$$

According to the interactions introduced above, the animals compete for the food. However, an additional “channel” of the competition appears due to different speed of the reaction on the food deposition. The faster animal reaches the goal quicker. Attraction force  $f_{jk}^{\text{food}}(\vec{r}_j, \vec{r}_k)$ , generally speaking, is different for different individuals. That is why we apply here the nonuniform coefficient  $B_{jk}^{\text{food}}$  which depends on the index  $j$  and in fact on some power of mass  $B_{jk}^{\text{food}} \sim m_j^\alpha$  with some exponent  $\alpha$ . Scaling estimation gives the value of the exponent  $\alpha \approx 5/3$ .<sup>[21]</sup>

Another form of the competition relates to their simultaneous production of the balls with different rate depending on the size of different individuals. A final size of the ball, which is treated by an animal as large enough to start its escape, also monotonously depends on the size (and strength) of an individual. Below, for definiteness and simplicity we suppose that the size of an individual is proportional to its mass:  $\partial m_j / \partial t = \mu m_j$ . Let us remind that the accumulation of the food ball is possible only when the animal is close enough to a food portion. In other words, one more characteristic distance  $|\vec{r}_j - \vec{r}_n| \simeq R_{\text{ball}}^{\text{food}}$  has to be incorporated into the model. It seems natural to simulate distribution of the dung around a center of every deposited portion by an additional Gaussian

$$P = B_{jn}^{\text{ball}}(t; \vec{r}_j - \vec{r}_n) \exp \left[ - \left( \frac{|\vec{r}_j - \vec{r}_n|}{R_{\text{ball}}^{\text{food}}} \right)^2 \right] \quad (10)$$

The coefficient  $B_{jn}^{\text{ball}}(t - t_n; \vec{r}_j - \vec{r}_n)$  here decreases with a time  $t - t_n$  elapsed from the deposition moment  $t_n$ . It reflects shrinking of the portion due to its integral consumption by the beetles altogether. To simulate the shrinking, one can either extract from the pile an amount extracted by every beetle during each time step of the simulation and integrate them, or postulate, for the sake of simplicity, some smooth time-dependence integrated over the ensemble of beetles.

Last simplification is convenient for the regular study as well as for the further experimental validation of the model. Analogous regularity can be achieved, if we suppose that the local group of the beetles spatially isolated from the other ones operates with the only one food portion originally disposed in the center of its symmetrically distributed population. In this case, index  $n$  in Equations (9) and (10) simply disappears and the simulation routine can start directly from the moment  $t_n = 0$ .

Even being simplified in this manner, the model still consists of nonlinear dynamic equations of motion, described above. It involves also additional numerical procedures, which work in parallel with dynamic equations and cannot be written satisfactorily in analytical form, but essentially affect dynamic behavior and the results. The most important complication comes from direct physical competition between the beetles for the balls. It obviously exists in nature and can be qualitatively described.

However, in contrast to other interactions, it should be implemented into the model only as a logical procedure. The main aspects of modeling of such competition process are briefly described below.

- 1) It is natural to suppose that on the nonflat terrain one beetle can catch another one starting from some minimal distance, which plays a role of the “threshold” for such an interaction between the animals. In principle, this distance depends on the individual capabilities (size, maturity, experience, etc.). In order to do not make the model too complicated, we apply some randomized condition. If two beetles (one with the ball and another one without it) appear at distance smaller than a critical one, they compete for the ball. This distance in reality is comparable to the size of the animals and characteristic scale of the surface peculiarities (introduced in Equation (7) and corresponding discussion). At each meeting of the animals, such critical distance is randomized, and result of the competition is randomized as well. To simulate it, the program generates a random number  $0 < \xi_k < 1$  at each time step and for every pair of the beetles  $k = 1, 2, \dots, N_{\text{pairs}}$  with and without the ball which enter the critical proximity  $|\vec{r}_j - \vec{r}_k| < R_{\text{threshold}}$  and compares it with a threshold  $\Psi_{\text{thres}} \ll 1$ . If the condition  $\xi_n \leq \Psi_{\text{thres}}$  is satisfied, the ball continues to belong to its previous owner. In opposite case  $\xi_n > \Psi_{\text{thres}}$ , the ball is moved to another one.
- 2) Besides, the result of the bout depends on the relation between the animal sizes. The simplest variant to account this is to make the threshold proportional to the relation of the masses of the beetles
 
$$\Psi_{\text{thres}} \rightarrow [M_j/M_{j'}]\Psi_{\text{thres}}^*, \text{ where } \Psi_{\text{thres}}^* = \text{const.} \quad (11)$$
- 3) Immediately after the “transfer” of the ball, new owner starts to push it in a new direction, which is personally “prescribed” by randomly distributed angle of the preferable directions assigned to each animal. This direction does not coincide with the previous one and, as a rule, is quite far from it. At the same time, old owner after losing the ball immediately “reminds” its attraction back to the food location. This force, however, competes with the attraction to all the ball owners. Sometimes this beetle goes to the proximity of the new owner again, and the bout resumes. Sometimes, it occasionally finds another beetle with the ball in vicinity, and attempts to attack it. Sometimes, it simply turns back to the common pile.
- 4) This complexity causes a number of different scenarios leading to very complicated dynamics. This behavior is additionally complicated because of the complex relief of combined terrain. As it was shown already for the solitary beetle, the running along complex terrain<sup>[17]</sup> causes additional forces changing the trajectories of the ball by itself. Now, the trajectories depend on combination of all the forces acting from the surface and from the other interacting animals moving simultaneously with each beetle under observation.
- 5) In particular, all the animals demonstrate common tendency to follow the same valleys of the potential. If the surface has sufficiently deep minima and maxima, the trajectories concentrate near the same “big roads” and probability for the animals to meet one another increases. The number of the bouts

between them including the “successful robberies” grows correspondingly. One can predict strongly structured dendrite pattern of the both probabilities: to find an animal in a particular place of the area around the food position and to find a place, where the owner change happened.

Now formally written equations of motion, which accumulate all the above mentioned forces of the problem

$$\partial \vec{r}_j / \partial t = \sum_k \left[ f_{jk}^{\text{repuls}}(\vec{r}_j, \vec{r}_k) + f_{jk}^{\text{attract}}(\vec{r}_j, \vec{r}_k) \right] + \sum_n f_{jn}^{\text{food}}(\vec{r}_j, \vec{r}_n) + \sum_{\text{Boundaries}} f_j^{\text{bound}} \quad (12)$$

must be combined with the procedures described above counting on the competition. This combination makes the solution nontrivial, especially due to varied sizes and forces of the participants. Nevertheless, possible scenarios can be predicted and verified by the large set of numerical experiments performed at different combinations of the parameters.

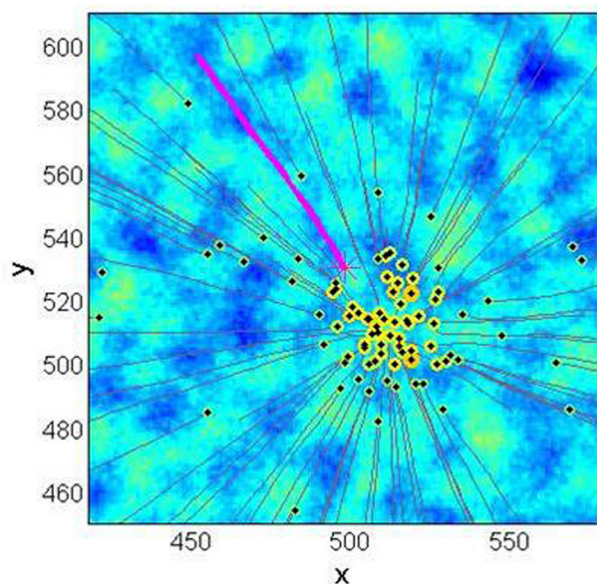
### 2.3. Results of the Numerical Simulations

Typical scenario of the behavior in the frames of model is consequently reproduced in the sequence of Figures 1–16 below. For definiteness, the following intermediate values of the parameters were used:  $\Delta q = 3q_{\text{min}}$ ,  $\mu = 0.2$ ,  $\nu = 1$ ,  $U_0 = 1$ ,  $R_0^{\text{food}} = 112$ ,  $R_0^{\text{ball}} = 32$ ,  $R_{jk}^{\text{attract}} = 10$ ,  $B_{jk}^{\text{attract}} = 0.3$ ,  $R_{jk}^{\text{repuls}} = 9$ ,  $B_{jk}^{\text{repuls}} = 0.3$ ,  $B_j^{\text{bound}} = 100$ ,  $R_0^{\text{bound}} = 1$ ,  $r^{\text{bound}} = 1000$  time dependence of the food value  $B_0^{\text{food}}(t) = \exp(-0.001t)$ , and threshold  $\Psi_{\text{thres}} = 0.001$  at the time step  $dt = 0.025$ .

Early stage of the process is shown in Figure 1. This figure combines a colormap of numerically generated particular realization of the terrain with discrete colored circles presenting current positions of the beetles and theirs balls (if the balls already exist). Here and below, the beetles having a ball of the maximal size corresponding to the given animal are marked by the blue color. The size of the circles monotonously increases with the size of the ball. The minimal circles in the plot mark the beetles without balls. Large blue dashed circumference outlines originally populated area. Small magenta dashed circumference qualitatively restricts a region with density of food high enough to build a ball.

To show the dynamic scenarios in more details, it is convenient to choose arbitrary one of the beetles as a reference animal and enlarge its vicinity in following system of the coordinates in separate plot. Rectangle in the figures below always marks such a small region magnified in the figures directly following them corresponding detailed fragment of the global picture at every stage of the process. See Figure 2 which follows Figure 1, as an example.

The trajectories of the animals in the magnified images are shown by the gray curves. Instant positions of the animals here are marked by the black dots, which overlap the circles having different size and color corresponding to different sizes of the balls. The balls are also colored in MatLab “jet” color scheme. To enhance a color difference between the circles and terrain, their color scales are slightly shifted one from another. Instant position of the selected beetle (which is placed exactly in the center



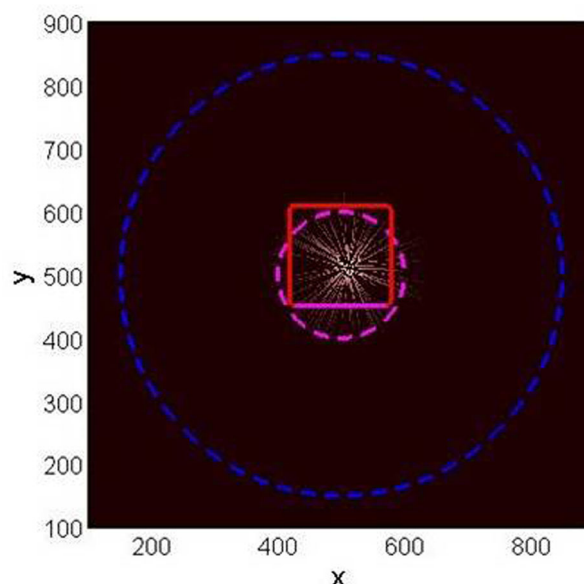
**Figure 2.** Magnified small region marked by the rectangle in global picture of Figure 1. The trajectories of the animals are shown by the gray lines. Instant positions of the animals are marked by the black dots. The circles of different size and color, which cover the dots, correspond to different sizes of the balls and colored, respectively, in MatLab “jet” color scheme. The size of each dot corresponds to the size of the ball (the smallest dots mark the beetles without balls). Instant position of the selected beetle in the center of the rectangle is plotted by the star. Bold magenta curve reproduces trajectory of the selected beetle.

of the rectangle) is plotted by the star. It is seen that the center of the pile slightly deviates from this center in the following system of coordinates. Bold magenta curve reproduces trajectory of the selected beetle from the beginning of routine to the current moment.

It is seen from Figure 2 how quickly at the early stage of the process, the beetles, situated relatively close to the center, are attracted to the food source (black dots without circles or with extremely small pale ones) and start to build their balls (shown by the larger and brighter circles). The selected animal also appears in this group, so the center of the distribution moves quite closely to the formal center of the following system of coordinates (Figure 2). The process is reproduced in dynamics in Movie *Beetles\_complexity.avi* in the Supporting Information.

Starting from the very beginning, we accumulate a time spent by each beetle in the particular cell of numerical grid under the numerically generated surface and perform a summation over the whole ensemble of the animals. Below, for brevity, we will call it “density of states.” To distinguish between this density and the map of the surface itself, it is convenient to plot it in a separate picture. In particular, such a density accumulated to the time moment shown in two previous figures is depicted below by “pink” colormap of MatLab.

The dashed circles and the rectangle in this figure have the same meaning as in Figure 1. The tracks left by the animals during their run to the center, as well as a brighter spot left by the “crowd” of the animals working on the production of their balls, are clearly seen in Figure 3. They can be treated as a global history of events, which leads to the configuration shown in Figure 1.



**Figure 3.** Density of states (total time spent by all the animals in each cell of the grid) accumulated starting from the beginning of the routine to the moment, shown in Figure 1. The colormap “pink” is applied here for the contrast. The dashed circles and the rectangle have the same meaning as in Figure 1.

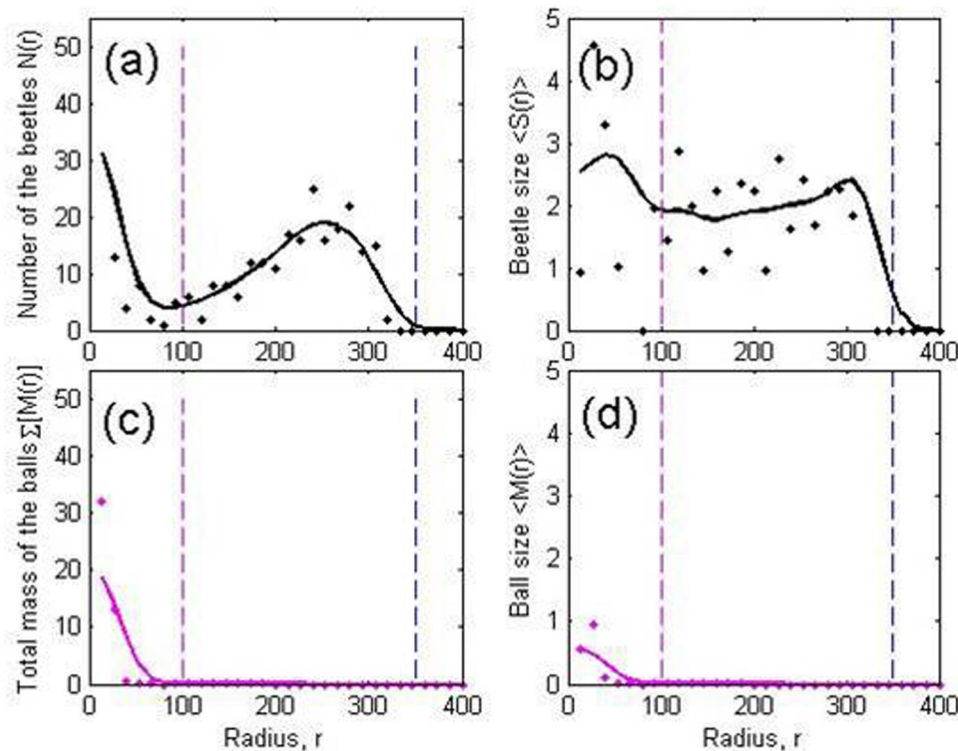
This presentation substantially complements the picture of the trajectories shown by the curves in Figure 2.

When the deposited spot of the dung is unique, the picture is expected to be generally isotropic for sufficiently large number of the realizations. For definiteness, we use ensemble of 300 animals. This number is sufficiently large to get good self-averaged statistics, but not too large to cause extremely time-consuming calculations. Counting on the symmetry, it is meaningful to integrate all the distribution over the angle and plot their radial dependencies. Corresponding results for the time moment, which is shown in Figures 1–3, are summarized in Figure 4.

Even for the group of 300 animals, instant distributions can fluctuate essentially (mainly because some of them quickly pass between different regions at some stages of the process). To get better static representation of the results, we filter them and plot by the smooth bold curves (which slowly evolve with the time) over instant histograms, shown by the small circles. Filtered histograms of the radius depending densities and averaged sizes of the beetles and balls, are shown together in Figure 4 by the black and magenta curves, respectively. Subplot a represents a number of the animals in narrow belt  $[r, r + dr]$  surrounding given radius  $r$ . Mean sizes of the beetles and their balls averaged inside the same belts are shown in the subplots b and d, respectively. Total mass of the balls inside the same region is plotted in subplot c. Vertical dashed magenta and black lines mark the radiuses of the circles plotted by the analogous lines in Figure 3, respectively.

With an increasing elapsed time, more beetles reach the pile-dung and start to create their balls. In the meantime, some of the other ones finish the building of the ball with the size, which corresponds to their personal fitness, and start rolling it away. Global process gets its intermediate stage. Such an intermediate stage (which follows exactly the same routine, as shown in





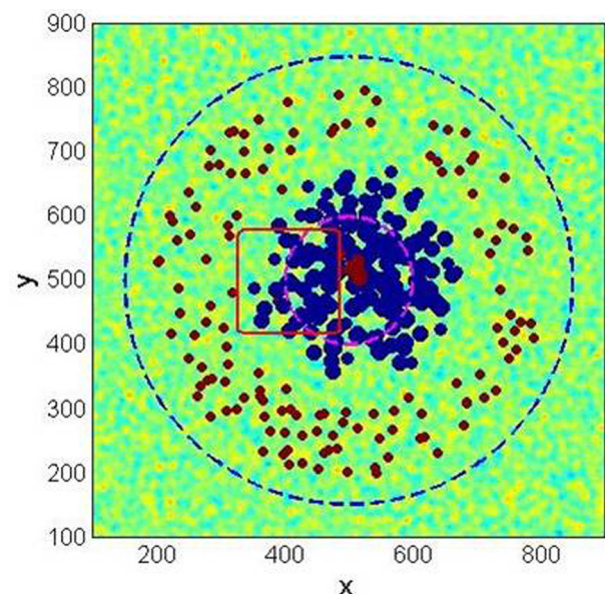
**Figure 4.** Filtered histograms of the radius depending densities and averaged sizes of the beetles and balls, shown by the black and magenta curves, respectively. Subplot a represents the number of animals in the narrow belt  $[r, r + dr]$  surrounding given radius  $r$ . Mean sizes of the beetles and their balls averaged inside the same belts are shown in the subplots b and d, respectively. Total mass of the balls inside the same region is shown in the subplot c. Vertical dashed magenta and black lines depict the radiuses of the circles plotted by the analogous lines in Figure 3, respectively.

previous figures) is illustrated in **Figure 5**. One can see that some of the beetles already reached the food, collected their own maximal balls and started to escape from the central area, while some others on a periphery are still almost unmovable and occupy approximately the same positions where they were at the very beginning. The red large circles near the center of this figure show the balls, which are not finished yet to the present moment.

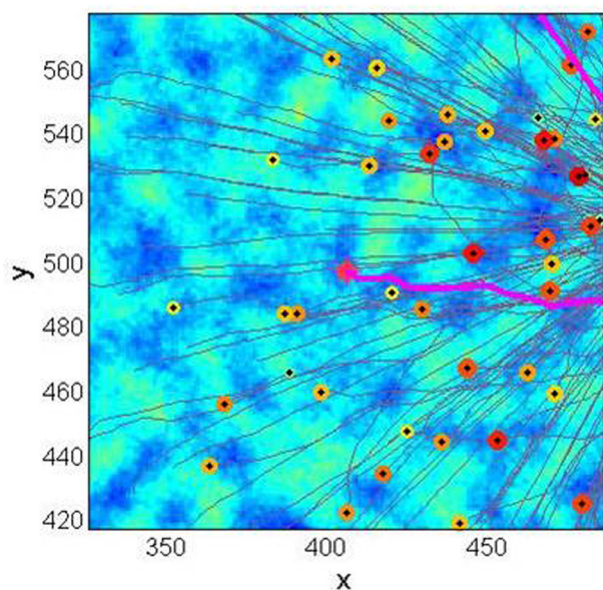
The colors and lines are the same as in Figure 1. In particular, one can note that the rectangle, which corresponds to a selected individual, shifts from the center of global distribution, because this beetle has also finished its own ball and drives it away.

One small fragment surrounding a selected animal at such intermediate stage of the process is magnified in **Figure 6**. It is directly illustrated here that this particular beetle has already finished building its own ball (large circle at the end of the magenta curve) and runs away inside of the group of others. So, one can really treat it as a representative example. Different colors and sizes of the circles here depict different sizes of the balls produced and carried by the animals, in the same manner as in Figure 2.

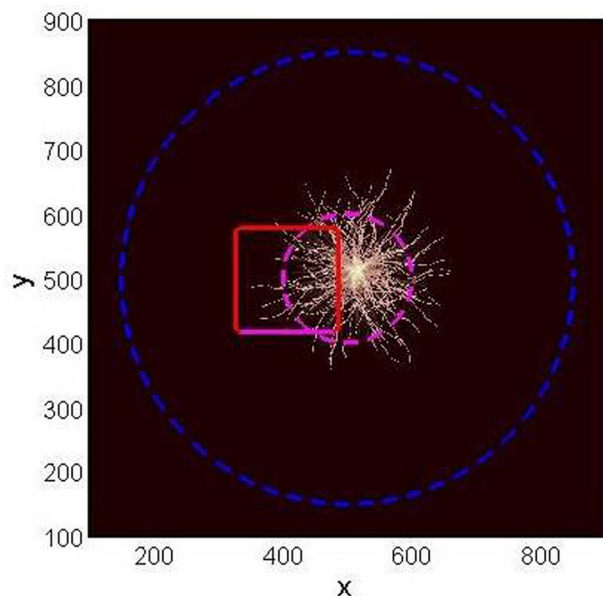
It is interesting to compare the density of states accumulated to this moment with the one presented in Figure 3. This density is reproduced in **Figure 7**. For the first time from the beginning of the process, one can notice here well-pronounced dendrite-like distribution of the density. Its structure reflects the terrain complexity, which makes some of the trajectories, mainly placed along the valleys of landscape, preferably visited by the animals,



**Figure 5.** The same process as in Figure 1 at its intermediate stage. Some of the beetles already reached the food, collected their balls (large blue circles), and started to escape from the central area, while some other ones on a periphery are still almost unmovable and occupy approximately the same positions, where they were at the very beginning. The red large circles near the center show the balls, which are not finished yet to the present moment. The colors and lines are the same as in Figure 1.



**Figure 6.** Small fragment of the modeling space surrounding a selected animal at the intermediate stage of the process. This beetle has already finished building its own ball and runs away. Different colors and sizes of the circles depict different sizes of the balls produced and carried by the animals.



**Figure 7.** Density of states accumulated to the moment presented in two previous figures. Dendrite structure of the density reflects the terrain complexity, which makes some of the trajectories inside the valleys of landscape preferably visited, whereas some places remain practically ignored (mainly near the tops of the hills).

while some of the other places remain practically ignored (mainly situated close to the tops of the hills).

As before, we calculated the histograms of the dependencies shown in Figure 4 at the intermediate stage of the process (Figure 8). From the comparison of the curves in different

subplots, one can see that many of the animals already finished building their balls and started to leave the central area. However, the local maximum of the number of beetles at large distances on the periphery is still conserved. It means that many of the large beetles almost do not react on the situation and remain quite far from the center. Small maximum of the size distribution testifies that remaining ones are mainly (statistically) slower larger animals. Additionally, one can see that both distributions in the subplots c and d did not get to the periphery of the beetle distribution to the moment and accordingly, smaller beetles already owing the balls, did not meet the larger ones without the balls yet.

The process is continued and the individuals with and without balls mix one with another. Such an advanced stage of the process is shown in Figure 9. This is the most representative stage of the process. Owners of the balls reach the region, where (statistically larger) slower beetles are waiting for them. In some cases, they fight for the balls one with another. Some of the balls shown in the figure already changed their owners. Normally, these balls are smaller than the maximal ones, as normally expected for the bigger new owners. As a result, these balls appear to be marked in the picture by the large red dots.

Small fragment of the same picture as in Figure 9 associated with the reference animal is reproduced in Figure 10. The places of the bouts, where the ball changed its owner, are marked in this picture by the contrast black-and-white dots. In fact, the pattern of these black-and-white dots records a history of the events in the system. It is seen directly that such places are concentrated near the “large roads” (mainly associated with the valleys of the surface), where the majority of beetles preferably move. In Figure 10, the gray lines of the trajectories are clearly correlated with the colored 3D profile of the surface.

Such a correlation becomes even more obvious in the next figure, which combines two different information of the same history together: the density of states plotted by the “pink” colormap and the history of beetle fights, which ended by the success of an offensive beetle, shown by the black-white circles. These sites are clearly attracted to the dendrite branches. This image is also accompanied by the image showing selected region around one selected individual (Figure 11).

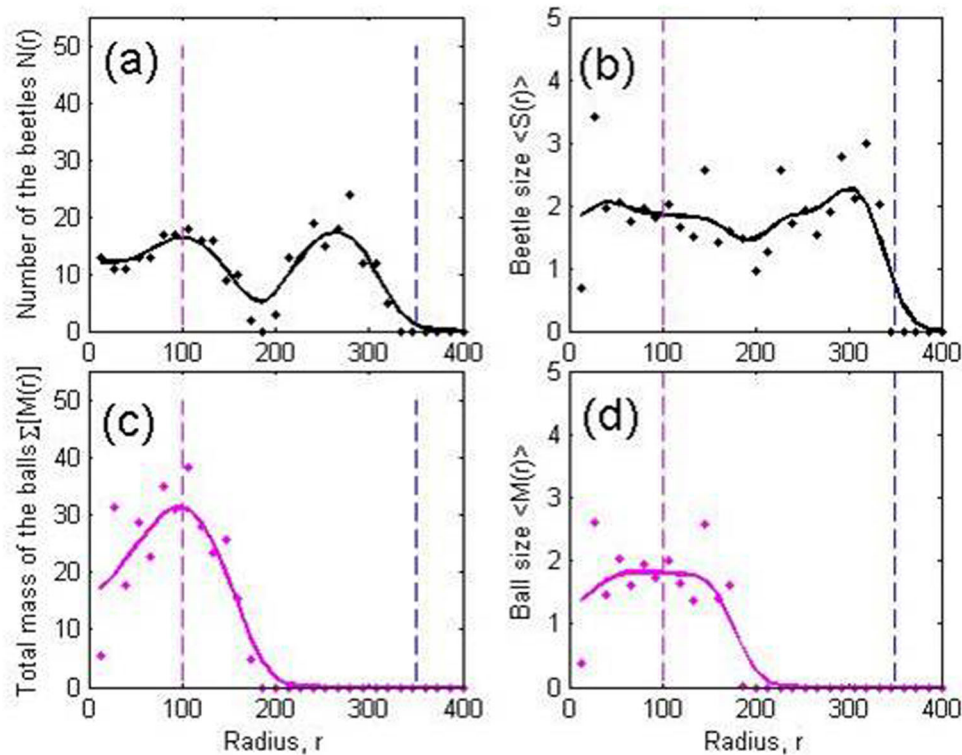
Statistical information about the same stage of the process is accumulated in Figure 12. One can see that at this stage of the process maximum of the states is already leaved central area. Outside it, the distribution of beetles tends to become uniform. As a result, the total number of animals and the total mass of carried balls inside every belt  $[r, r + dr]$  are practically proportional to its length. In turn, this length is proportional to the radius  $r$  by itself.

This fact is clearly verified by the additional inclined strait lines in the subplots a and c, which touch mentioned curves. Let us note also a small maximum corresponding to larger beetles, which still is concentrated at the periphery on the curve of averaged beetle size in subplot b.

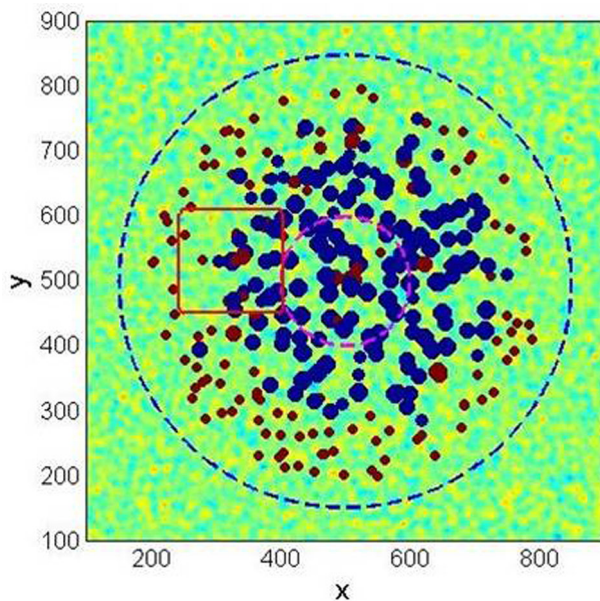
The process is continued and gradually reached its final stage. The final stage of the process can be associated with the following limits:

- 1) The majority of the beetles with their balls successfully reach the periphery of the population and together with the other ones, remaining inside the area, are redistributed into more

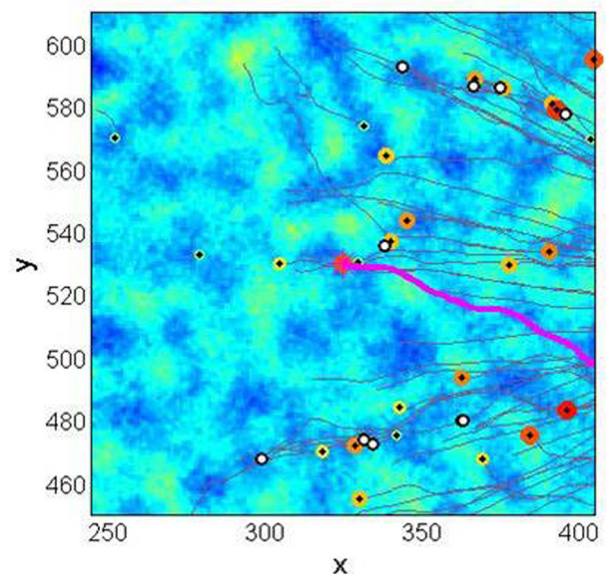




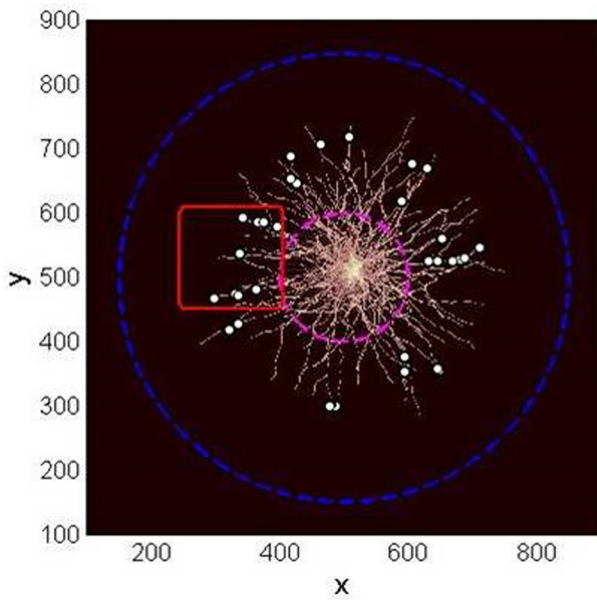
**Figure 8.** Histograms of the same radial dependencies as shown in Figure 4 at the intermediate stage of the process. Many animals already finished building their balls and started to leave the central area. At the same time, the local maximum of the number of beetles at large distances demonstrates that many animals remain rather far from the center. Small maximum of the size distribution testifies that majority of the animals remaining here are mainly (slower reacting) larger ones.



**Figure 9.** The advanced stage of the process. This is the mostly representative stage of the process. Owners of the balls reach the region, where (statistically larger) slower beetles are dwelling. Some of the balls already changed their owners. Normally they are smaller than the maximal ones for the new owners. They are depicted by the red large dots.



**Figure 10.** Small fragment of the same image as in Figure 9. The sites of the bouts, where a ball changed its owner are marked by the contrast black-and-white circles. It is seen that such places tend to concentrate near the “large roads,” where the majority of beetles preferably move.



**Figure 11.** The density of states accumulated to the moment shown in Figure 9. Global correlation between the preferable trajectories of motion and the concentration of changes of the ball owners is rather clear.

or less uniform configuration. This configuration provides a mean characteristic distance practically between all the individuals;

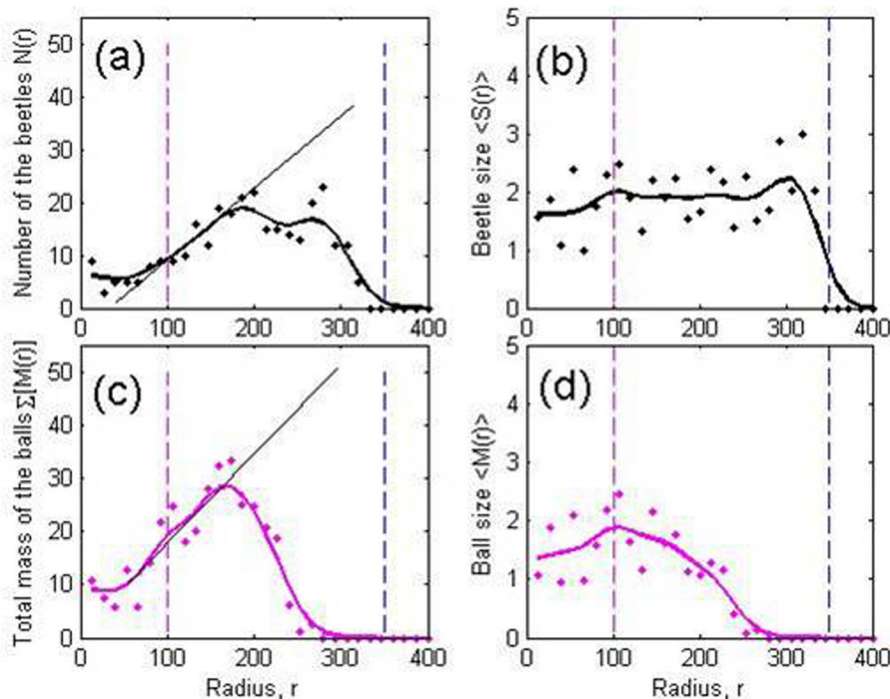
- 2) The disposed dung amount around the center becomes exhausted (either because of its consumption for the production and transportation of the balls, or due to other reasons, like drying, decreasing smell intensity, etc.).
- 3) Shrinking of the beetle population, or their leaving the area to other attractors, etc.

Mathematically it means that the routine stops, because the time is elapsed, force of the attraction to the center becomes weaker than some threshold, or by interruption, when the trajectories simply leave a grid, specified for the random surface generation and/or for the accumulation of all the densities.

Independently on the specific biological reason, one can preliminary run the program to the state close to any of the described configurations, define an appropriate time limit  $t_{\max}$  and forcibly interrupt it always at the same time  $t = t_{\max}$ . Below, we briefly name such a state as the “final stage.”

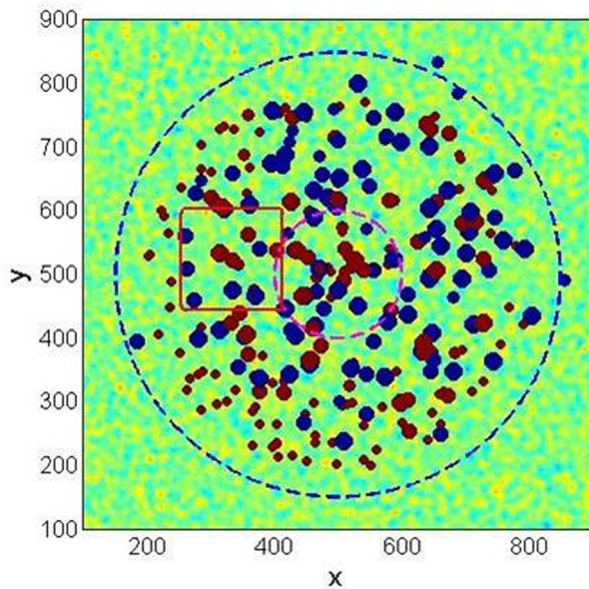
Typical results for the final stage (obtained from the same realization of the routine as for all the previous plots) are accumulated in Figures 13–16. One can see that to this stage some of the ball owners definitely reached a periphery of the population. Maximal and smaller balls (mainly taken by force) are mixed altogether.

The selected animal with a “typical” intermediate size was occasionally relatively “unlucky” in this realization of the process. It had lost its own ball, found another one, but was trapped inside a local valley for a while. It was still quite far from the periphery in the moment, when the routine has been finally interrupted.

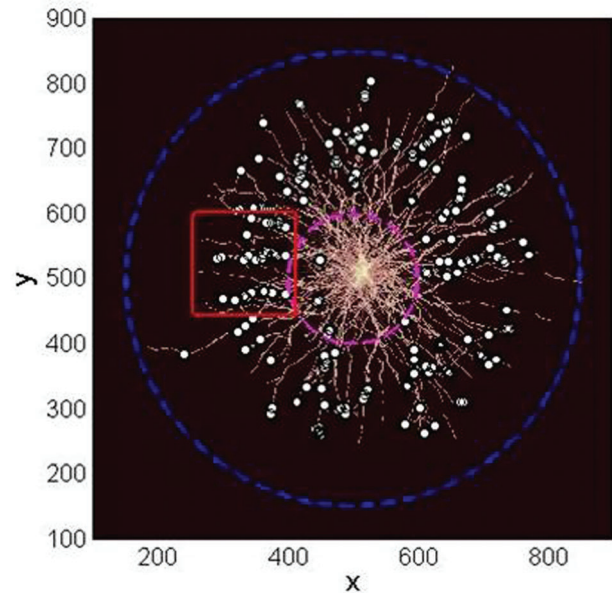


**Figure 12.** Radial dependencies at the intermediate stage of the process. Maximum of the states has already clearly left the central area. Outside this area, the distribution of beetles tends to become uniform. As a result, the total number of the animals and the total mass of carried balls inside every belt  $[r, r + dr]$  is practically proportional to its length and linearly increases with the radius  $r$ . This fact is confirmed by the inclined straight lines touching corresponding curves in the subplots a and c. Small maximum, corresponding to larger beetles remaining on the periphery, is still conserved on the curve of average beetle size in subplot b.

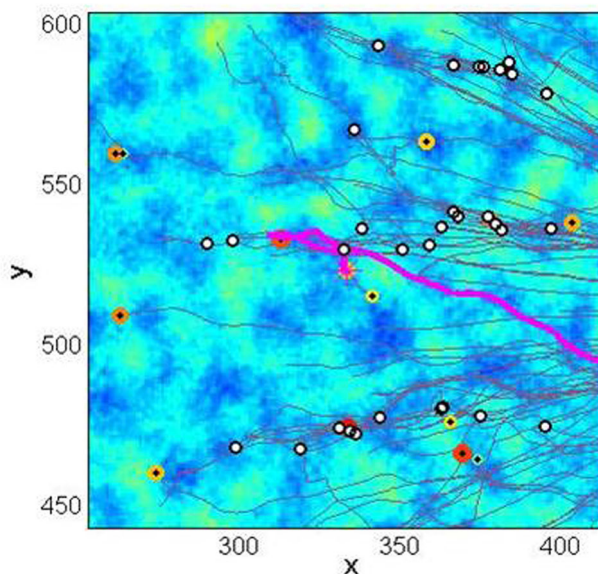




**Figure 13.** The final stage of the process. Some of the ball owners reach the periphery of population. Maximal and smaller (mainly taken by force) balls are mixed together.



**Figure 15.** Density of states and events accumulated at the final stage of the process.



**Figure 14.** Selected in this realization animal having a “typical” intermediate size appeared to be relatively “unlucky.” It had lost its own ball, found another one, but was trapped inside a local valley for a while. Some other animals successfully continue their run to the periphery (on the left side of this picture). High concentration of the trajectories and places of ball owner’s changes near the “large roads” is seen directly.

Some other animals successfully continued their run to the periphery. Their balls and trajectories are seen on the left side of Figure 14.

High concentration of the trajectories and places of changes of the ball owners near the “large roads” is seen directly in Fig-

ure 15, where the density of states and the history of events are accumulated to the final stage of the process.

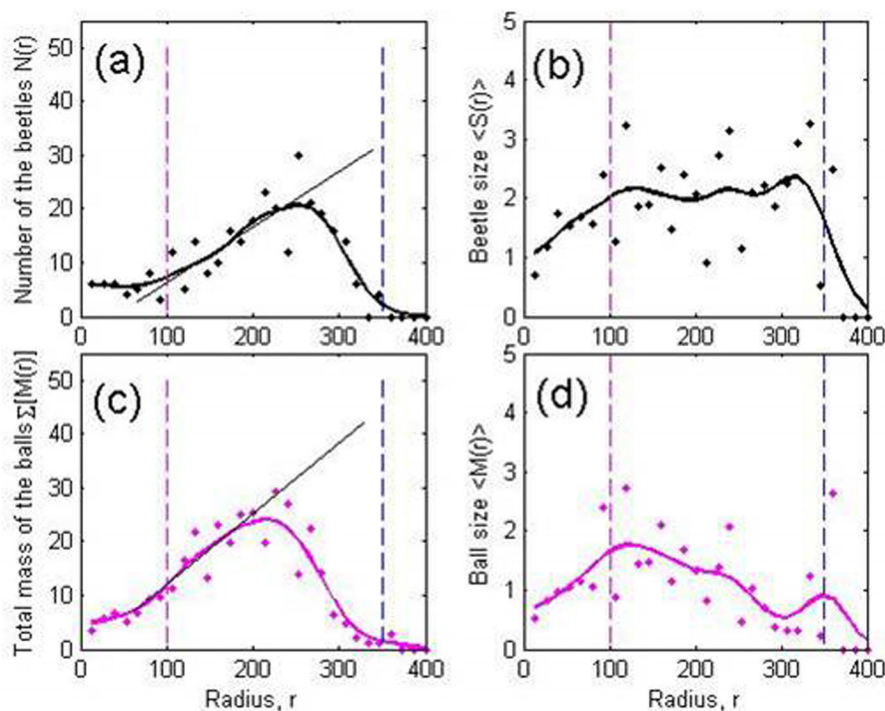
Radial distributions at the final stage of the process are accumulated in Figure 16. In contrast to all the previous cases, shown in Figures 4, 8, and 12, it is seen that all the distributions here started to deviate from zero at maximal radiuses, because some beetles with the balls reached the periphery of the initial distribution and continued to escape further. At the same time, the food pool in the center became exhausted. It almost does not attract the beetles and absolute majority of the animals (as well as produced by them balls) are outside of this region now.

Evolution of the scenarios with the competition for the balls raises an important question about possible behavioral strategies, which must give an advantage in such a competition. We plan to apply this model for further theoretical and experimental studies in this direction. However, brief announcement of its applicability to the related questions can be done right now.

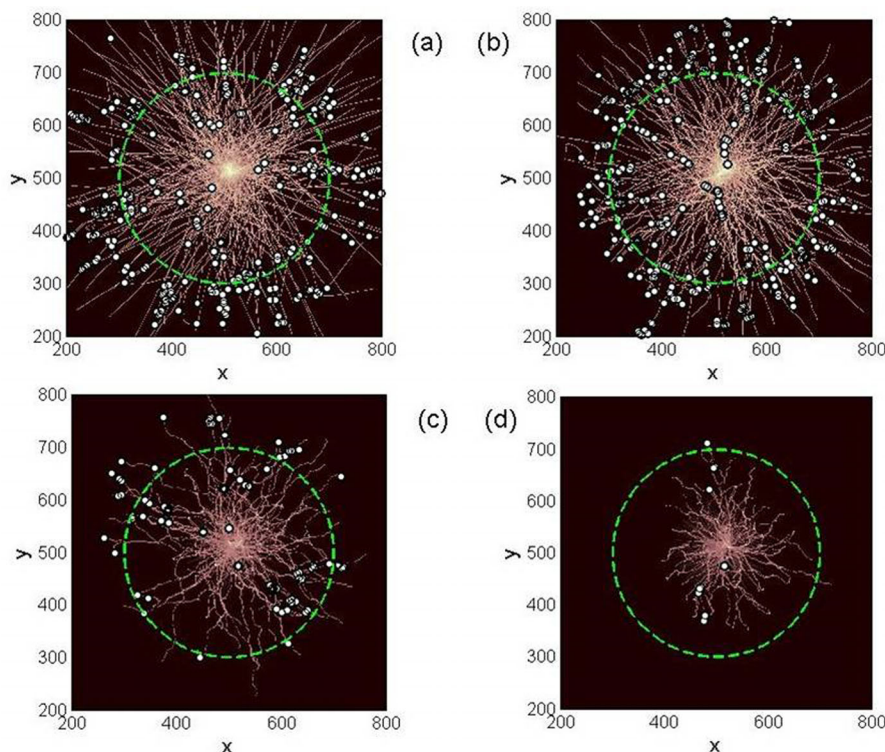
As we saw above, the ruggedness of the dendrite trajectories caused by its characteristic rate of the motion, as well as the probability for the beetles to meet one another (especially around “large roads”), strongly depends on the topography of terrain. It is expected that the animals living in particular regions of the specific terrain can potentially adapt their behavior to some extent to the local conditions.

To study the question more systematically, one can generate the random terrain profile at fixed other parameters and adjust time of the run (once for different terrain roughness) which a beetle can treat as a preferable one, in order to escape from the competition. Below, in **Figure 17**, we illustrate this using four different substrate profiles with the depth of valleys growing monotonously from the subplot a to the subplot d. As expected, deeper substrate peculiarities trap the ball (and beetle itself) with higher probability and make its way longer. As result, during the





**Figure 16.** Radial distributions at the final stage of the process. It is seen that (in contrast to all the previous cases shown in Figures 4, 8, and 12) all the distributions here deviate from zero at maximal radii, because some beetles with the balls reached the periphery of the initial distribution and continued to escape further. At the same time, the food pool in the center became exhausted and absolute majority of the animals (as well as balls produced by them) have left this region.



**Figure 17.** Comparison between the finally accumulated densities of states and events at different amplitudes of surface roughness. For the discussion of the preferable strategies for different cases, see the main text. The distributions shown in the subplots a–d are obtained at the same parameters as used for all previous figures with the only varied amplitude  $U_0 = 1$ ,  $U_0 = 5$ ,  $U_0 = 15$ , and  $U_0 = 20$ , respectively.

same run time, it statistically covers shorter distance (at all other parameters, including an interaction between the animals, fixed).

Generally, the strategy of escaping from the center immediately after creation of the ball seems to be an effective one. On relatively smooth (flat) surface, shown in subplot a, the trajectories are more or less straight and the “barrier” of the beetles without the balls on the periphery is rather transparent. Thus, the best strategy on such a terrain seems to be running away as far as possible out of the densely populated area.

It is very difficult to specify an optimal strategy on slightly rough (but not too much) terrain. The trajectories in the subplot b start to concentrate on the “large roads” and probability to meet a rival without the ball increases. However, if the height difference grows further (subplot c), strong concentration of the trajectories to the large roads opens wide windows between them. So, logical strategy here seems to try leaving a convenient “large road” as far as possible and wade through mechanically inconvenient, but relatively safe territory between the roads. It would be interesting to prove, if the beetles follow this strategies.

The last case of extremely deep height difference leads to maybe mostly paradoxical recommendation, which partially contradicts naively accepted hypothesis. Starting from some roughness, the “horizon of events” for the animals essentially shrinks. They do not see either deposited food from long distance and do not find one another over nearest hill. The “outer” animals can see the food only in the case, when some of the “inner” ones with already created ball, occasionally go near them. Original strategy of the beetles in close proximity of the dung spot is still valid, to avoid any confrontation with other animals, who also already came to central region, but did not finish its own ball yet. However, later when practically all such animals already produced their own balls and have no reason to fight one with another, it should be more advantageous to stop running. In this case, they remain invisible for the “outer” animals, which still stay on the periphery and do not see either owners of the ball or the dung pile. This strategy is well illustrated by the last subplot d, where only very few places of the contacts between animals can be found.

### 3. Conclusions

We numerically analyzed the impact of complex rough surfaces on the running trajectories of dung beetles pushing a ball along a straight path. The randomness and combined nature of real surfaces led to a wide spectrum of complex trajectories which are planned to be compared with future experimental studies in the field. The combined potential also caused interesting theoretical problems including the statistical analysis of the numerically found solutions. One can note that study of the motion in such a potential causes a number of interesting mathematical offshoots related in particular to quasi-1D trajectory with a fractal dimension  $1 < d < 2$ . This would presumably be a Weierstrass curve, a curve which from a mathematical viewpoint is everywhere continuous but nowhere differentiable.<sup>[24,25]</sup>

In particular, it has been found that, depending on the mutual relationship between the size of the ball and the distribution of the surface minimums, the actual trajectories form a number of dynamic patterns which result in qualitatively different sce-

narios of the ball transportation. Different patterns have been systematically studied in this paper and the results clearly show that a characteristic size of the surface irregularities comparable in size with the ball radius causes stronger difficulties for the ball transportation in comparison to surfaces with smaller or larger dimensions of the surface features. The study presented here can be extended to more advanced description of the corrugated surfaces (or, quasi-2D landscapes), where the trajectories represented by a random walk having a fractal dimension of  $(d+2)/3$ , with  $d$ —Euclidean dimension of the space. Under certain mechanical restrictions, this is also valid for a path composed of infinitely many micro-inclined planes over which the ball is rolling down over a corrugated nonflat landscape in gravity conditions.<sup>[24–27]</sup>

The motion of the beetles becomes much more complicated in realistic situation, when the beetles compete for the balls. In this study, we develop numerical model which combines attraction of the beetles to the dung, production of the balls of different sizes depending on the fitness of the animals, the ball transportation on terrains with different scales of the surface profile, and the competition between beetles for the already existing balls. A strong correlation between typical radius of the ball and the size of the relief minimums and the results of the competitions, as well as possible optimal strategies of the behavior is found.

Evolution of the distributions and the scenarios with the competition for the balls observed here raise important question about possible behavioral strategies which give an advantage in such a competition. We plan to apply this model for further theoretical and experimental studies in this direction.

### Supporting Information

Supporting Information is available from the Wiley Online Library or from the author.

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### Conflict of Interest

The authors declare no conflict of interest.

### Author Contributions

A.E.F.: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing—original draft; S.N.G.: Conceptualization, Formal analysis, Writing—review & editing.

### Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

## Keywords

characteristic scale, collective behavior, combined terrain, dung beetle, food competition, fractal surface, locomotion, random walk

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