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Abstract. We study a simple model of a foraging animal that modifies the substrate on which it moves. This substrate provides its only resource, and the forager manages it by taking a limited portion at each visited site. The resource recovers its value after the visit following a relaxation law. We study different scenarios to analyze the efficiency of the managing strategy, corresponding to control the bite size. We observe the non trivial emergence of a home range, that is visited in a periodic way. The duration of the corresponding cycles and the transient until it emerges is affected by the bite size. Our results show that the most efficient use of the resource, measured as the balance between gathering and traveled distance, corresponds to foragers that take larger portions but without exhausting the resource. We also analyze the use of space determining the number of attractors of the dynamics, and we observe that it depends on the bite size and the recovery time of the resource.

1 Introduction

Complex patterns of animal movement arise from the interaction between the individual and the environment [1]. Despite usual assumptions of randomness made for the sake of mathematical tractability, these patterns are in general not random, and their characterization and dynamics is currently a subject of study of biologists, mathematicians and physicists. Complementary tools are used in this context: reaction-diffusion mechanisms [2–4] and simulation of individuals walks [5–7].

Of particular interest are the mechanisms underlying the formation of patterns in foraging walks. Many animals move around their habitats collecting food from patches of renewable resources such as fruit, nectar, pollen, leaves, seeds, etc. Often these animals play an important role, through mutualistic interactions, in the pollination, seeds dispersal and spread of the plants that provide their resource [8–12]. For these reasons their trajectories arise from an interweaving of the rules of movement, the spatial distribution of the substrate [12,13], and the interaction between both [14,15]. All of them are decisive for the emerging phenomenology and thus a complete characterization of the observed patterns requires an integral approach.

Foraging on renewable resources has been studied with a focus on finding optimal search strategies under different assumptions of animal perception and memory [16–18]. Some animals, for example, are able to find profitable routes without much computational power [19,20]. Also,

much discussion has been devoted to animals' search paths and whether Lévy walks or flights are predominant in nature [6,21–24]. While these examples focus on the cognitive abilities of the foragers, another approach considers the study of emerging patterns in the use of space as a result of the interaction between the behavior of the animal and the spatial structure of the environment, i.e. as a feedback mechanism.

In this regard, it is a fact that animals do not use all available space but prefer to stay in a limited region, their home range. It remains of particular interest to understand which characteristics of the system contribute to the formation of these ranges [25]. In our previous study [14] a similar model to the one presented in this work was analyzed, showing that two simple rules (preference of nearest plants and relaxation of the consumed resource), are enough to produce bounded home ranges. Such finite ranges arise even in the absence of any kind of memory of the walker or of a cost involved in movement. The situation resembles that of the *tourist walk* [26], where the walker has a finite memory that prevents them to revisit previously visited cities. In the formalism of [14] the memory is effectively stored in the landscape, and is “lost” gradually as the resource relaxes after its consumption. In the present work we generalize that model assigning to the spatially distributed resource a more specific role in the promotion of the emergence of a home range.

Among several aspects associated to the benefits of establishing a home range, we want to consider the availability of the resource and the efficacy of its sustainable exploitation. In this regard the harvesting strategy is crucial, as a non efficient activity can lead to the exhaustion

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of the available food. As recognized by Lima et al. [26] in the motivation for the tourist walk, local optimization strategies may be more appropriate for foraging than the minimization of global costs.

In particular, bite size drives harvesting rates because large bites require less handling (cropping time) per unit of ingested food than do small bites [27]. Since cropping and chewing are competing activities [28–30], if not mutually exclusive [27], cropping slows down the intake of food. Animals are also able to recognize the energetic value of harvesting larger bites, and select bites based on trade-offs between rapid harvesting and rapid and thorough digestion [31].

As a consequence of these mechanisms, there is a compromise between bite size and cropping rate, with the two usually inversely related, though there are at least two interpretations of this effect. Some authors [32–34] consider that this relationship responds to the need of grazing herbivores to balance small bite sizes with a higher cropping rate. However, since large bites can be chewed more efficiently than smaller ones [29], other authors [35] attribute the relation between bite size and cropping rate to anatomic limitations associated to body mechanics and a competition between chewing and cropping. In such a context, bite size influences harvesting rates, affecting the amount of time a herbivore spends foraging each day, and also influences short-term decisions made by animals and the corresponding responses of plants.

The effect of bite size on cropping rate goes beyond the locality of a single patch of vegetation, and when the distribution of the resource is very heterogeneous in space it also affects the profile of foraging across patches. At the same time, the topological properties of the distribution of the resource can impose additional constraints on the intake rate. When the forager travels without availability limitations among patches, the intake rate is defined by the bite size and the rate at which it can be processed in the mouth. But when the search time is longer than the time needed to chewing and/or swallowing food acquired from the last bite, the effect of the landscape on the foraging dynamics starts to be important [36]. Consequently, bite size/intake rate relationships are frequently included in foraging models designed to predict behavior, intake, and productivity of animals across landscapes [37–40].

In the present paper we consider three parameters of relevance for the interplay between real foragers and their environment: bite size (the amount of resource gathered at each foraging site), cost of movement and cost of stay. We show that these factors affect the ability to use the resource more or less efficiently or, in any case, the self organized optimization of the resource. At the same time, we find that foraging patterns that are usually attributed to memory skills of the foragers can emerge even in the absence of it.

2 Model definition and dynamics

The model consists of a walker that moves on a substrate modifying it, representing a forager moving from plant to

plant in order to collect food. The walker follows simple rules of movement, to be described below, and the substrate recovers from the depletion produced by the visits. Let us describe these basic rules in some detail.

The substrate consists of N sites distributed uniformly at random positions in the unit square. Each site represents a patch of vegetation that the animal can visit to collect food, and will be referred to as “plants” below. Each site is endowed with a crop size (a load of fruit, for example) $f_i(t) \in (0, f_i(0))$, with $f_i(0)$ initially assigned at random with uniform distribution between 0 and 1.

The walker visits the sites following a rule that mimics that of a feeding animal. At each visit of the walker the crop is reduced by an amount b , the *bite size* that characterizes the behavior of foragers [9,10,31]. We assume that the determinant factor of the movement is the proximity of the food. This is in fact the case with many foraging species, particularly if the distribution of the resource is not extremely heterogeneous. Nevertheless, since each visit consumes the resource, we assume that a site i will not be chosen if $f_i(t) - b < 0$. If the nearest plant does not have enough food, the walker chooses the next nearest that does so.

Finally, the vegetation substrate is subject to a replenishment of the crop of each plant: after a visit and a reduction b of its crop, the plant recovers that amount τ time steps later, until it saturates to its initial value $f_i(0)$. This simple relaxation dynamics can represent a ripening process, for example, in such a way that the crop size available to the animal is only the ripe fruit.

As mentioned above, the model just described is similar to the one analyzed by reference [14]. In this work we generalize that analysis, studying the dependence of the walks (and, in particular, of their cycles) on three magnitudes of relevance for real foragers: bite size, cost of movement and cost of stay. The present model does not ultimately explore all the aspects of a real foraging dynamics in detail, but isolates some very relevant factors that allow us to obtain interesting new results. For the sake of understanding the basic interplay between the walker and the environment, we have not taken into account several details, such as satiation, rest, return to the burrow or nest, or other activities related to intra- or interspecific interactions.

3 Results

Let us consider a single animal in the system. After a transient that depends on initial conditions, the walk settles on a periodic trajectory, a cycle. This is the same behavior observed by reference [14], where it was argued that this cycles are analog to home ranges of animals. It is also similar to the cyclic attractors exhaustively studied by Lima et al. [26]. We emphasize that these ranges arise in a very simple model, where the walker has no memory of the positions of the resource.

We studied the dependence of the properties of this cycles on the size of the bite, b . Relevant results are shown

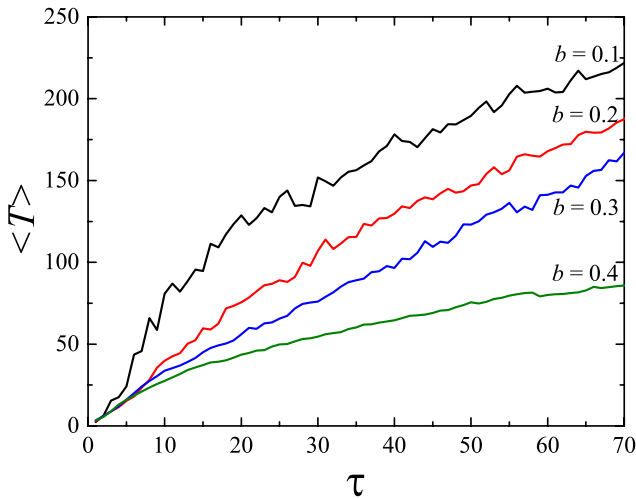


Fig. 1. Average period vs. relaxation time τ , averaged over 1000 realizations for different values of the bite size b , as shown in the legend. $N = 250$.

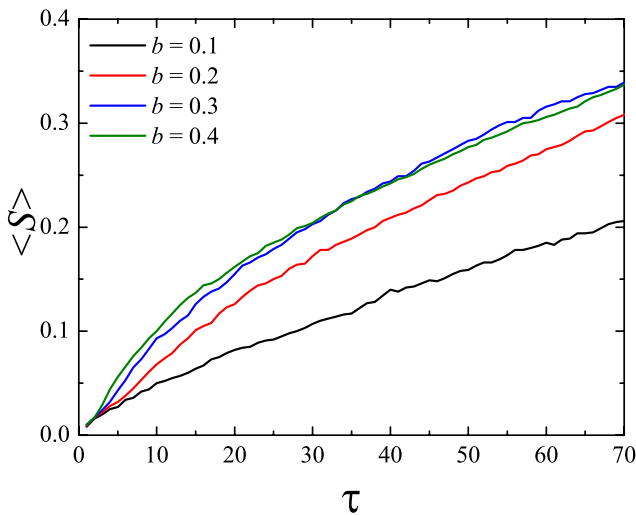


Fig. 2. Average fraction of visited sites, $\langle S \rangle$, vs. relaxation time τ , averaged over 1000 realizations for different values of the bite size b , as shown in the legend. $N = 250$.

in Figures 1 and 2 where we plot, as a function of τ , the period of the cycles, $\langle T \rangle$, and the habitat usage measured as the fraction of sites visited during the cycle with respect to the size of the system, $\langle S \rangle$. Both magnitudes are averaged over 1000 realizations of the walk with different random distribution of the sites for each simulation. The different curves correspond to values of the bite size $b = 0.1, 0.2, 0.3$ and 0.4 . As expected, and as in reference [14], both magnitudes grow with τ , since a slower relaxation time of the resource requires that the walker explores farther in order to find food.

It is worth mentioning that, to some extent, these results depend on the total time of simulation. The longest period observed cannot be longer than half of it, since at least one repetition is necessary for the detection of a cy-

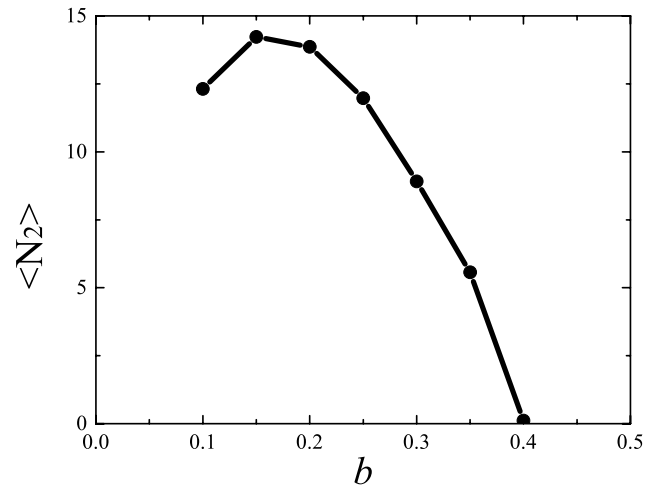


Fig. 3. Average number of two-steps sub-cycles per cycle, N_2 , vs. bite size b . $N = 250$, $\tau = 30$, 1000 realizations.

cle. For this reason we have repeated the analysis shown in Figures 1 and 2 for progressively longer simulation times. The result is exactly as the one observed in reference [14]: longer periods are detected, with corresponding larger values of their average $\langle T \rangle$ but, most importantly, the average space usage *does not* increase with total time. This indicates the existence of well defined ranges for the walker.

The dependence of $\langle T \rangle$ and $\langle S \rangle$ on b is also not obvious. On the one hand we observe that, the larger the bite size, the larger the use of space (Fig. 2). This is understandable: more plants are visited if the bite size is larger, since the crop of each plant is consumed faster. Observe, however, that the period of the cycles *decreases* with the growth of the bite size (Fig. 1). That is, animals that harvest less resource require *less* space (as argued above), but it takes them *longer* to complete their trajectories. The reason for this could be the fact that small bites allow the walker to oscillate back and forth between nearby plants while $f_i - b > 0$, effectively producing sub-cycles inside the home range. Animals with larger b , on the other hand, would find it more difficult to return to recently visited sites, because they are probably depleted.

If such is the case, it could be possible to see how the number of sub-cycles increases as the bite size decreases, for a fixed value of τ . Figure 3 shows this dependence: the number of two-step sub-cycles per cycle, N_2 , averaged over 1000 realizations. It can be seen that it has a maximum around $b \approx 0.15$, decreasing rapidly to reach 0 when $b = 0.4$. It should be noted that, when $b > 0.5$, two-steps cycles are not possible because the resource has been depleted to a value that prevents an immediate visit, until the relaxation has replenished it. We have not observed sub-cycles involving 3 sites in our simulations, but two-step cycles are clearly seen directly in the trajectories, as we show in Figure 4. In this graph we can also observe that, while the walker with $b = 0.1$ completes only one cycle during that range of time, the walker with $b = 0.4$ does four; the cycle of the first one is longer, but the effective sites visited are less.

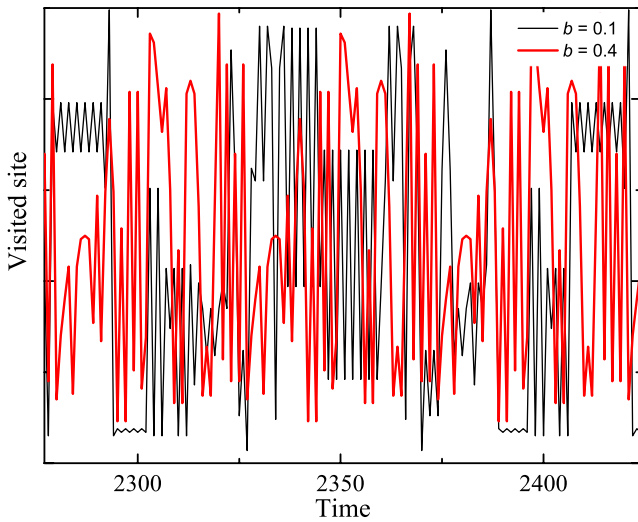


Fig. 4. Walks with (black, $b = 0.1$) and without (red, $b = 0.4$) two-steps sub-cycles. The vertical axis shows the site index (not correlated to its spatial position). Observe that the black line covers a long single cycle, while the red one, corresponding to a larger bite size, makes more than three in the same time. $N = 250$, and the walks are in the stationary state.

We also have explored a variation of the model in which the walker stays at a site with probability p . Then, if $p = 0$ we have the previous model while if $p = 1$ the walker stays at the same site as many time steps as it needs to deplete its resource, one bite of size b at a time, before moving on. In such a model the length of the sub-cycles shortens as the stay probability goes from 0 to 1. As already discussed, the necessary trade-off between harvesting and other activities (such as chewing, avoiding predation, moving away from competitors, etc.) produces a strong pressure favoring the “bite and move on” paradigm, which in the present model corresponds to $p = 0$ or very small. For this reason the results presented here correspond to it.

4 Efficiency

Among the multiple interests on foraging behavior it is particularly relevant the evaluation of its efficiency. The pioneering work of [41] set up the basis for the concept of optimal foraging [42,43], where the authors propose that one of the governing aspects of foraging behavior is the energy intake maximization.

Within the limitations of our model, the fact that the animals collect a harvest and follow a path within their home ranges allows several interesting observations in terms of the efficiency of the exploitation of the resource. Let us consider first a consequence of the results just discussed in the previous section.

We have seen that the walkers that take a larger bite follow *shorter* cycles (Fig. 1). We could say that larger bite sizes are more *efficient* for the exploitation of the resource, because of the increased cost of moving $\text{int}(f/b)$ times between sites to deplete them. If b is larger, there

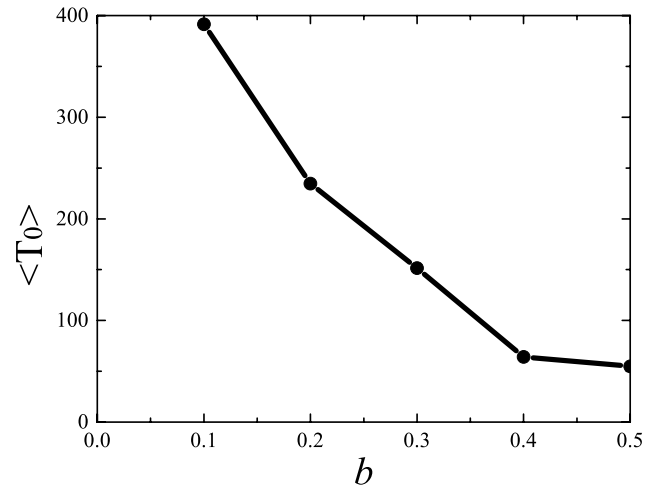


Fig. 5. Average length of the transient regime, $\langle T_0 \rangle$, vs. bite size b . $N = 250$, $\tau = 30$, 1000 realizations.

are less sub-cycles and each step is, in this sense, more efficient. Indeed, this concept of efficiency can be applied to the whole walk, even to the transient before the stationary cycle is reached. The walker with smaller bites would require more steps to “find” the cycle, because of the steps lost in sub-cycles, and the transient would be longer. Figure 5 shows that this is the case: the number of transient steps T_0 (averaged over 1000 realizations) as a function of b , shows a decay that stabilizes after $b = 0.4$, as expected. The walker with the smallest bite size ($b = 0.1$) needs on average 8 times more steps to establish a home range than the walker with 4 times the bite size, $b = 0.4$.

These arguments and results could indicate that, in real animals, there would be a strong evolutionary pressure towards larger bites or harvests, since they seem to ensure a more efficient use of the resource. For real animals, though, bite size is one of many interacting factors that play a part in foraging behavior [36]. As discussed by reference [31], herbivores’ decisions are based on a trade-off between food intake and other aspects of the resource and its use, such as chewing and swallowing, digestion, distance traveled, distance from refuge, patch residence time, etc. These tradeoffs may be very complicated and species specific; for example larger bites may mean an increased predation risk because of longer perching times to deplete a cluster of fruit, or *less* risk because of more spare time to scan for predators [44,45]. In summary, while larger bites enable the walker to increase nutrient intake (needed for survival, growth, reproduction), there might be penalizations that require a tradeoff with other factors shaping the movement.

A more precise way of quantifying the efficiency of the walkers consists in the consideration of an internal energy. Let us say that this energy increases with the ingestion of food at each step, and decreases with the distance traveled to obtain it. That is, if the walker is at site i at time $t - 1$ and visits site j at time t :

$$E(t) = E(t - 1) + g(b) - h(d_{ij}), \quad (1)$$

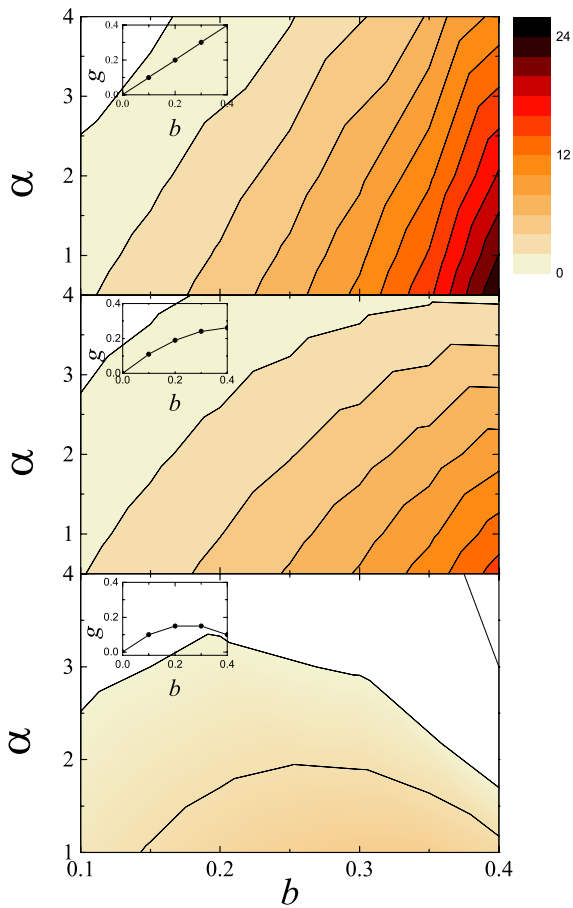


Fig. 6. Phase diagram of the energy per step, as a function of the bite size b and the energy loss rate α . Top: without penalization ($\beta(b) = 1$). Center and bottom: with penalization modelled as a linear $\beta(b) = \beta_0 - \beta_1 b$, with $\beta_0 = 1.25$ (both), $\beta_1 = 1.5$ (center) and $\beta_1 = 2.5$ (bottom). $N = 250$, 1000 realizations, $\tau = 50$. Darker colors indicate more energy harvested per visited plant on average.

where $g(b)$ and $h(d_{ij})$ are functions that characterize the changes in the internal energy of the walker. It is reasonable to expect h to be a monotonically increasing function of d_{ij} , but in principle we do not know the precise form of either g or h . Indeed, they may be different for different species or classes (for example mammals, birds and insects), and even for the same species in different stages of their natural history (breeding, preparing for hibernation, etc.).

Let us consider, for the sake of simplicity, that energy is lost in proportion to the distance traveled, as if the animal were moving at a constant speed: $h(d_{ij}) = \alpha d_{ij}$, with a rate α characterizing the energy loss, the “cost of movement” mentioned above. Similarly, one could consider a linear dependence of $g(b)$, assuming that each portion of food provides an amount of energy. In such a case a phase diagram for the total energy at the end of a prescribed time would look like the one shown in Figure 6 (top). A darker color indicates a higher energy, and it is seen that the most efficient walkers are the ones that gather

larger crops, while spending less during their movement, as expected.

However, the linear dependence of g on b is not the best to assume. Animals collecting small fruits from fruit clusters, for example, should spend time gathering each fruitlet. So, animals collecting larger crops need to spend more time at each site than those that take a single fruitlet or a small bite and move on. A real forager could tend to take a crop somewhere in the middle of the available resource at each site. This has been observed in the behavior of *Dromiciops gliroides* feeding on the fruits of *Tristerix corymbosus*, for example [46]. For these reasons it is more sound to consider a penalization for animals with larger bite size. The exact form is not important, for the reasons discussed above. So, let us consider the following: $g(b) = \beta(b) b$, where $\beta(b)$ penalizes the larger crops. Specifically, for the sake of simplicity, we choose $\beta(b) = \beta_0 - \beta_1 b$, so that the case shown in Figure 6 (top) corresponds to $\beta_1 = 0$. That is, we have:

$$E(t) = E(t - 1) + \beta(b) b - \alpha d_{ij}. \quad (2)$$

Typical phase diagrams corresponding to this model are shown in Figure 6 (center and bottom). Each plot corresponds to a different strength of the penalization of large bites, as shown in the insets by the function $g(b)$. The penalization of larger bite size is responsible for the reduced energy seen approaching the right side of the plot. For each set of parameters (α , τ , g , etc.), there is an optimum bite size and there would be an evolutionary pressure to adopt a strategy (a bite size b) to exploit it. Only if the penalization is strong enough, as in Figure 6 (bottom), corresponding to a non-monotonic $g(b)$, the maximum energy for a given energy loss rate α is achieved at an intermediate value of the crop size b . Otherwise, the maximum is found at the largest crop size which we keep below the mean value of the fruit load, $\langle f \rangle = 0.5$, due to limitations of the simulation in a finite system.

5 Discussion

We have analyzed a simple model of a forager with deterministic rules that moves modifying its substrate. The interplay between foraging and relaxation of the substrate produces several non-intuitive behaviors, akin to those observed in real systems.

First of all, the walker not only finds a home range (a cycle), but also sub-cycles inside that principal cycle. These regions of persistent interest are also a feature of real animals. The period and the space usage of the cycles, as well as the transient regime, are largely determined by the bite size, the portion that the walker gathers from each site, i.e. by its strategy in the use of the resource. When the resource is spatially distributed in a patchy environment there is a tradeoff between the energy saving due to a bounded mobility and the risk of locally depleting the resource. Thus, the benefits that a rich patch provides fades out with the exhaustion of the resource. The study of this phenomenon is addressed by the marginal value theorem [47]. In an ideal case, a forager should stay in a patch

until the harvesting has depleted the resource to a point at which the expected energy gained from staying is below the expected gain if traveling to a new unexploited patch. Energy balance and efficiency are then central aspects of the forager's behavior. Most models of optimal foraging theory consider that foragers possess cognitive and perceptual skills that allow them to collect information about patch locations. The time spent between patches is not associated to a search activity but to a directed travel. In this work we assumed that the foragers have limited perceptual or cognitive abilities [19,20] and that searching for the resource is part of the foraging behavior. We have shown that even considering these limitations, typical foraging patterns can emerge.

Our results show that the walker with a smaller bite size is less efficient in finding its home range. When found, the period of their cycles are longer, and their use of space is more limited (visiting fewer sites), than those corresponding to walkers with larger bites. The longer period of those inefficient walkers arises from the formation of sub-cycles: the walker visits two sites repeatedly in sequence until it depletes them and moves on. In this fashion they visit less sites and take more steps: this is the behavior that we have called *inefficient*. Our results show that the more voracious walker finds more easily its home range and exploits it more efficiently.

On the light of these results, it could be reasonable to expect an evolutionary pressure towards the choice of larger bites, other parameters being equal. Indeed, it is known that if large bites are available, animals can meet energy requirements more easily, allowing more time for other life requisites such as reproduction, competition avoidance, predator evasion and thermo-regulation [31,45,48,49]. There is however a caveat: bite size may interact with other factors of the foraging behavior and natural history, and a tradeoff may arise. We have analyzed a phenomenological model of such a tradeoff in the form of an internal energy that the walker stores by harvesting the resource, and dissipates by traveling. A monotonic dependence of the rate of energy intake on bite size does favor larger bites (Fig. 6 top and center). But even a small departure from monotonicity of $g(b)$ for larger bites (Fig. 6 bottom) shows that intermediate harvesting sizes may be more favorable. The action of such mechanisms might be behind the observed behavior of foragers that consume only part of the available crop at each plant, such as *D. gliroides* [46].

The manner in which an animal uses its habitat to collect resources certainly has an impact on the way it will interact with conspecifics or competitors sharing the space. With regard to this, the fraction of space usage is one of the relevant variables that would determine if home ranges overlap or not and, eventually, determine also the carrying capacity of the system. Let us briefly discuss a final characterization of the efficiency of different strategies of foraging, that is also relevant if more than one agent is present in the system, or if part of the habitat becomes destroyed or otherwise inaccessible. It is the number of attractors (distinct cycles) of the dynamics. Imagine placing

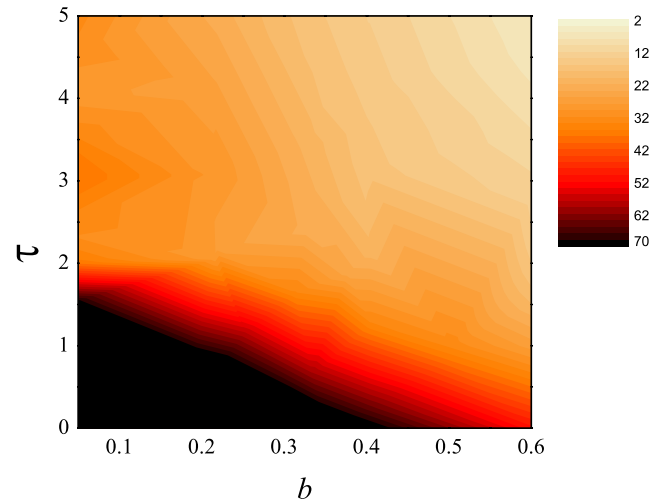


Fig. 7. Number of attractors for a single distribution of the resource, as a function of the bite size b and the relaxation time τ . $N = 400$, average of 10 realizations.

the walker at all the N possible initial positions of a given substrate. The question is: how many cycles the walker can find? And, moreover, how does this number depend on the parameters of the model?

Figure 7 shows the number of attractors given a distribution of the resource, as a function of the relaxation time τ and the bite size b , averaged over 10 realizations. We can see that the number of attractors depends on both parameters: the possible cycles are very few (lighter shade) if the bite size or the recovery time are large. On the other hand, if the bite size (or the relaxation time) is small, there are many possible ways of traversing the range and many possible home ranges. The presence of more animals competing for the same resource (even in the absence of any direct interaction) would affect the efficiency of its use. Even if larger bites would require less time to exploit the resource (the strategy that we have termed efficient), the overlap of the home ranges of several foragers might produce a pressure in the opposite direction. A strategy with a smaller bite, instead, which requires less space and allocates more attractors in the same substrate, may be favored. This aspect of the model is currently under study.

The emerging properties of our model improves over the baseline set by reference [14], providing a mechanistic explanation of many phenomena observed in the behavior of foraging animals. The study of the relevance of the present findings in systems such as the mutualistic interaction between *D. gliroides* and *T. corymbosus*, and their relevance as keystone species in the Andean temperate forest [50,51], will be further explored.

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