

Why do many animals move with a predominance of roughly forward directions?

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Animal movements can influence their ecology and demographics. Animal movements are often characterized by path structures with directional persistence. The extent to which directional persistence improves forage success is investigated in this paper using theoretical simulations. It is shown that a movement strategy with directional persistence enables simulated animals to find more forage as compared to a random movement strategy. Situations where resources are chosen with certainty (optimally) are even more successful. Choosing resource with certainty cannot result in directional persistence. However, in cases where animals choose with certainty adjacent cells with resource but continue in their existing direction if none of these have resources then results include directional persistence. It is posited here that this combined strategy is the most effective because if optimal foraging works it is optimally efficient but where foraging is sub-optimal, for a variety of reasons, directional persistence will benefit foraging.

Historically population ecology focused on temporal fluctuations but recently a growing body of research is addressing the spatial aspects of population dynamics, for both terrestrial¹ and marine² environments, of which animal movement is an important component. Random walk type models have been used successfully to

characterize movement for various organisms as long as path lengths are at scales that capture the true path structure³. Many animals have a tendency to move in preferred directions, a situation better modelled by a correlated random walk where turning angles are taken from biased distributions, see Bartumeus et al.⁴ for example.

Much of the literature that considers the turn angle and individual segment length distributions of moving organisms show that there are often angles and distances that predominate⁵⁻¹⁰. In fact, in all of these particular studies, the turn angles that predominate move the organism in a roughly forward direction (approximated best by a correlated walk). These examples are from a variety of organisms, which include species of mammal, bird, amphibian, fish and bacterium, and measured in a variety of environments, heterogeneous and homogeneous. For other organisms, roughly backwards directions predominate^{6,8} or both forwards and backwards directions predominate^{11,3}. Here backwards directions refer to situations where the animal reverses its existing direction.

Animal movements are often characterized by long-tailed power-law distributions of movement lengths called Lévy distributions¹². Reynolds and Rhodes¹³ discuss in some detail the possibilities for the Lévy walk animal movement paradigm and this is not considered further in this paper.

Correlated walks appear to predominate as an animal movement strategy (Schultz and Crone¹⁰ give one of the few examples of completely random walk strategy). Situations where directional preferences include reversals in direction can be seen as an endeavour to remain in larger habitat patches^{6,8} or an evolved response to random environments as hypothesized for the case of bacteria¹¹. Of

interest here is the predominance of organisms with turn angle distributions that move them generally in forward directions. Possible reasons relate to foraging itself as a correlated random walk will cover more area over time than a random walk³. Here I hypothesize that a correlated walk will also increase forage success. To test this hypothesis a simple spatially explicit consumer resource cellular-automaton model is used.

Figure 1 shows fluctuations in the numbers of animals and resourced cells over time for a simulation of consumers living and dying according to their ability to locate and consume resource. This ability is based only on a predetermined movement strategy. For the first 1000 simulation steps in Figure 1 the animals use a random walk strategy (RW). After 1000 steps they use a correlated random walk strategy with tight directional persistence (CRWT). For a CRWT as compared to a RW, animal numbers increase on average by 0.75 and resource decreases on average by 0.45 (Figure 1). The trend is not sensitive to parameter variation. Thus, the consumer is able to locate and utilise resource more efficiently using the CRWT. For a situation using a broader directional persistence (CRWB) this change is less evident with animal numbers increasing on average by 0.45 and resource decreasing by 0.27 as compared to the RW (not shown).

This model is very simplistic but captures the essential population dynamics between a consumer and its food resource allowing one to test the effectiveness of the different movement strategies. As predicted consumers that move in roughly forward directions can be more efficient foragers (as defined by increasing their numbers and finding more forage). While not completely intuitive this might be easily explained in that by continuing in a general direction there is a greater

probability of encountering a resource cell that has not yet been consumed at least by that individual. It has been demonstrated that static objects found and destroyed using CRWs are more efficient than using RWs⁴. The difference here is that population dynamics are included and the resource cells regenerate over time. Thus, the density and layout of resource are determined by the dynamic and not by fixed design.

Bartumeus et al⁴ suggested that “correlated random-walk properties (i.e., scale-finite correlations) may be interpreted as the by-product of locally scanning mechanisms”. The present study suggests that that animal use of a CRW strategy could be partially innate. The simulations here are dynamic with birth and death processes but the simulated animals do not perceive their environment, they merely use a movement strategy. Moreover, running simulations with optimal foraging, where animals select any resourced adjacent cell, placed randomly, produces completely random distributions of turn angles. Thus, for resources that are positioned randomly, even if animals choose with absolutely certainty of getting resource does not create a CRW with animals heading roughly forwards.

One might argue that resources in real environments can be positioned spatially with correlated bias, which they can be. For example river courses can have resources along their lengths. Also, the need to drink water can create straight movement toward water bodies. However, in most environments optimal resources will almost inevitably have a random component to their spatial positions. Thus, I am suggesting that regardless of the complex nature of an actual resource structure resource uncertainty should result in some foraging advantage for moving roughly forward.

As shown in Figure 2 the optimal foraging strategy described above does improve the absolute efficiency of foraging (there are on average more animals and less forage than in Figure 1 with all other parameters the same). As already mentioned this strategy cannot create a CRW with animals heading roughly forwards. However, for simulations run with the additional procedure that when no adjacent cells have resource an animal continues in its existing direction results in a distribution of turn angles that does include significant numbers of forward movements, creating a bias of going forward. The effect on efficiency is minimal. Thus, the following simple explanation becomes possible. Animals where possible use an optimal foraging strategy but where this is not possible they move roughly in their existing forage direction. This combined strategy is more optimal in the sense that when the optimal foraging strategy fails in the short term (their immediate choices are sub-optimal) then a moving forward strategy will be more efficient than an unbiased strategy. Sub-optimal foraging could be the result of a number of factors such as a lack of suitable forage locally or other needs such as water. Also, predation pressure or dominant individuals can prevent optimally foraging. For the same reasons, the CRW should benefit foragers who have less than perfect knowledge of the positions of optimally resourced patches (which is likely¹⁴). Thus, the use of a CRW strategy, which in effect takes into account the improved probability of finding future forage in cells further away, should benefit foraging when optimal foraging fails locally or foragers do not have perfect knowledge of resource positions.

Bacteria have been shown to use CRW strategies in isotropic media^{5,11} and thus this behaviour appears innate. These bacteria have flagella that propel them and this could well be conducive to moving in straight directions. However,

similar results are found for mites on a coverslip washed in distilled water¹⁵ and as arthropods mites have a physical structure quite different to bacteria. As these bacteria and mites had no forage in those experiments^{5,11,15} this fits the explanation that movement forward is an innate method to locate forage when not immediately apparent.

Bartumeus¹⁶ argues for the existence of intermittent biological mechanisms to explain the statistical patterns found in movement data. What simpler mechanism than for animals to forage roughly in forward moving directions when unable to forage optimally? This research indicates that a strategy of moving generally in a forward direction provides some foraging advantage and is thus probably an innate behaviour likely to be found in many animals.

METHODS

A consumer resource model is developed using the Netlogo programming platform¹⁷. The consumer animals move on a square lattice with 2500 grid cells and periodic boundary conditions. Periodic boundary conditions are used to remove edge effects (the right edge of the lattice is connected to the left edge and the top edge to the bottom edge). The size of lattice is sufficient in that a lattice with double these cells produced comparative results. Grid cells either have a unit of food resource or are empty with an initial probability of 0.5 of cells resourced. Thus, approximately half of the cells have food and half are empty, distributed randomly throughout the grid. Twenty animal model agents (referred to throughout as animals) are initially placed in random positions on the simulation grid and given a random amount of energy up to 6 units (units are arbitrary). New positions for the animals are found using one of the methods for

changing direction (given below) and moving one cell in that direction, while incrementing the time by one and decreasing the animal's energy by one. If an animal moves to a resourced cell it consumes that cell's resource and increments its own energy by 3 units. This amount of energy is required for consumer population survival. Resource returns to a cell (re-growth) after a number of time steps (arbitrarily set equal to 45 time steps). If an animal's energy goes below zero it dies. Animals reproduce at 0.04 of the population.

Three movement strategies are considered:

1. A random walk (RW) where changes in direction are randomly taken from an even distribution of angles -180° to 180° .
2. A correlated random walk with broad directional persistence (CRWB) where angles are taken from a normal distribution of turn angles with a mean of 0° and standard deviation of 90° . At each step in the simulation the 0° corresponds to the animal's existing direction.
3. A correlated random walk with tight directional persistence (CRWT) where angles are taken from a normal distribution of turn angles with a mean 0° and standard deviation 20° .

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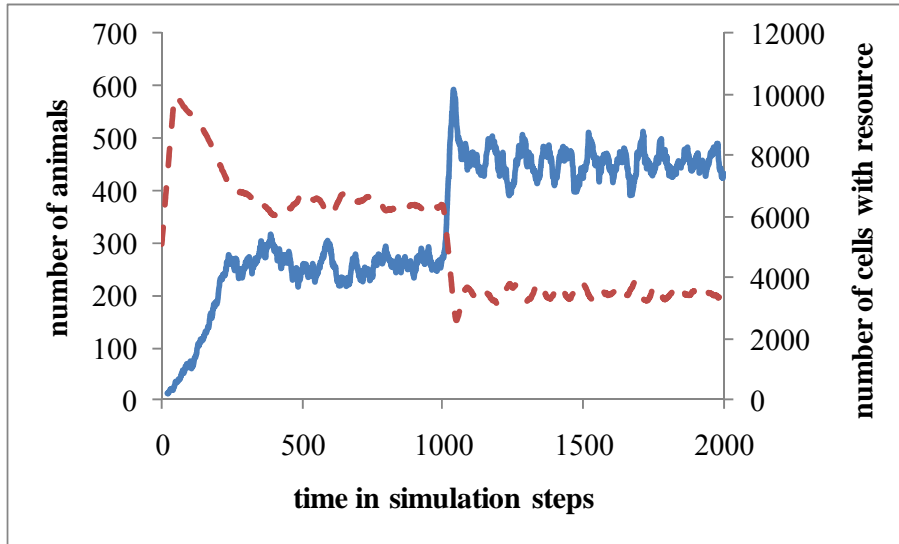


Figure 1 Resulting numbers of animals (solid line) and cells with resource (dashed line) for a simulation of foraging animals. After 1000 time steps the strategy is changed from a RW to a CRWT. Other parameters values are given in the methods.

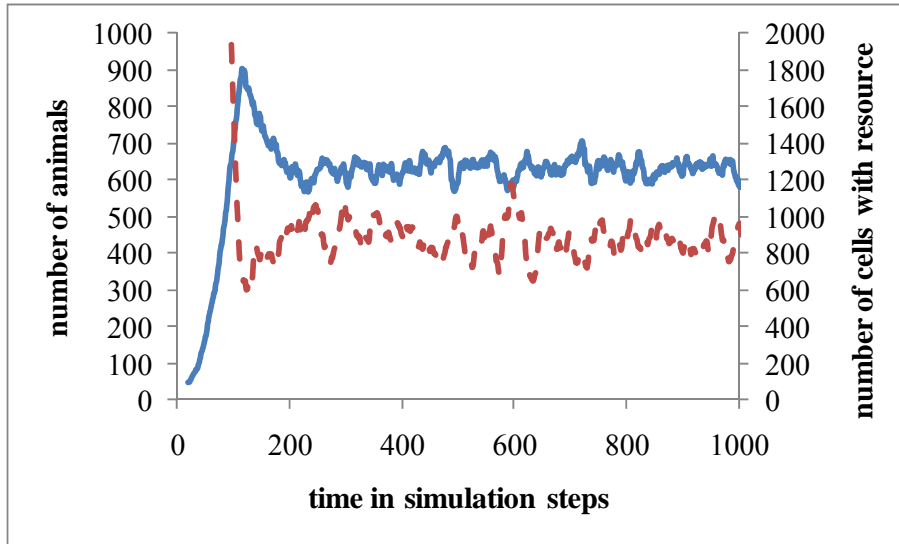


Figure 2 Resulting numbers of animals (solid line) and cells with resource (dashed line) for a simulation of foraging animals where animals choose adjacent cells with forage. Where there are a number of choices they choose one randomly. When confronted by no adjacent cell with resource they choose a new direction randomly. Parameter values are the same as in Figure 1.