

LET US PREY: SIMULATIONS OF GRAZING TRACES IN THE FOSSIL RECORD

Roy E. Plotnick and Karen Koy

Department of Earth and Environmental Sciences, University of Illinois at Chicago, 845 W.

Taylor St., Chicago, IL, 60607

Tel. +1 312-996-2111,

E-mail: plotnick@uic.edu, kkoy@uic.edu

Abstract

Trace fossils are the only direct record of the behavior of ancient organisms. They thus provide critical indications of the early evolution of sensory systems and of the behavioral response to environmental heterogeneity. An important category of traces preserve the foraging behavior of organisms on or just below the seafloor. Previous conceptual and numerical models of such traces have been based on either random walks or highly stereotypical movement patterns, with an implicit assumption of environmental homogeneity. Different trace morphologies have been interpreted as representing different behaviors. We have developed a individual based, spatially explicit movement model for trace formation that incorporates environmental heterogeneity, as well as contact and distance chemoreception. This model produces a wide range of trace morphologies from the same basic behavior. Changes in the occurrence of trace fossil types over time, in particular during the Precambrian-Cambrian transition, may thus be largely a consequence of the development of spatial heterogeneity on the ocean floor, rather than the development of new and more complex behaviors.

1. Introduction

1.1 What are trace fossils?

Trace fossils (ichnofossils) are the preserved remains of the activities of organisms. In a broad sense, trace fossils include any indication of the presence of ancient organisms other than the body of the organism itself. Ichnofossils thus include preserved features as diverse as burrows, tracks, trails, borings, excrement (coprolites), nests, and a variety of sedimentary structures built by organisms (Bromley, 1996; Ekdale et al., 1984). The study of these traces is ichnology.

Nearly all of the interest in trace fossils has come from paleontologists and geologists, rather than ecologists and others interested in animal behavior. Unlike shells, bones, and other body fossils, they are generally not subject to transport. As a result, they have been widely used as indicators of ancient environmental conditions. Ichnofossils have been used as indicators of depth of ancient sea-floors, as an approach to measuring rates of sedimentation and erosion, and as a proxy for oxygen levels in the water column (Savdra, 1992; Taylor et al., 2003)

Many of the conditions that lead to trace preservation are not conducive to the preservation of body fossils, and vice versa; it is thus rare to find traces and their generating organisms preserved together. In addition, many traces are produced by the actions of soft-bodied organisms, which rarely preserve. For these organisms, ichnofossils are the only record of their existence.

Identification is further complicated by the fact that many organisms can make similar traces when performing similar behaviors, whereas the same organism can make different traces when performing different behaviors (Ekdale et al., 1984). The preserved form of a trace, its morphology, is also affected by the nature of the surrounding sediment. As a result, the identity of many tracemakers is unknown or uncertain.

Because fossil traces result from a complex interaction between the biology of the organism generating the trace and the sedimentologic factors that lead to trace preservation, ichnologists use multiple schemes for classifying ichnofossils (Bromley, 1996). First of all, they can be classified principally on the basis of morphology, using the same binomial nomenclature applied to the organisms themselves; i.e., there are ichnogenera and ichnospecies. A second scheme involves the nature of preservation, such as being at the top, bottom, or interior of a bed and whether the trace is concave, convex, or three-dimensional. A third approach depends on being able to directly tie the trace to the tracemaker; for example, the footprint of a theropod dinosaur.

A fourth approach, originally proposed by Adolf Seilacher and since modified and expanded (Bromley, 1996), uses a series of “ethological categories” to classify traces by their interpreted behavior. Examples include: crawling traces (*repichnia*), which supposedly represent animals moving without necessarily feeding; grazing traces (*pascichnia*) which are generally meandering or spiral traces, presumably caused by an animal actively exploiting a food resource; and dwelling traces (*domichnia*), which are interpreted as at least semi-permanently occupied burrows.



Figure 1: (Left): traces from the Ordovician of Missouri. (Right): Spiral and meandering traces from the Cretaceous of Austria

Recent attention on trace fossils has focused on their origins and early evolution. The oldest definitive traces have been used as indicators of the origin of multicellular and bilaterally symmetrical organisms (Budd, 2000; Erwin, et al., 1997). The diversity of trace fossil types increases dramatically in the Cambrian, in parallel with the well-known diversification of animal taxa (Jensen et al., 2005).

In this paper we will focus on models for trace morphologies that have been interpreted as representing crawling and grazing behaviors. These traces form either at or just below the sediment-water interface. They exhibit a wide variety of geometries (Figure 1), ranging from more-or-less linear or curving structures to a variety of meandering, looping, or spiral forms.

The latter grade into the highly regular structures generally termed graphoglyptids. (Uchman, 2003), which have been interpreted as “farms” for microbes, rather than as feeding structures (Seilacher, 1986).

1.2. Previous Models of Trace Fossils

The modeling of trace fossils, in particular of grazing and crawling traces, was recently reviewed by Plotnick (2003) and Hayes (2003). Of these earlier models, probably the best known is the computer model of Raup and Seilacher (1969), which has been called one of the earliest examples of A-life (Prescott and Ibbotson, 1996). The underlying conceptual model presumes that an optimal foraging organism will cover an area “continuously and efficiently” (Seilacher 1986), in particular in areas with low food density (Kitchell, 1979; Kitchell et al., 1978). Efficiency (or optimization) is recognized by a lack of recrossings of a movement trail and by the close proximity of adjacent segments of a trail, thus maximizing area covered relative to trail length. The rules of the model are thus: 1) stay close to previous tracks (*thigmotaxis*); and 2) avoid crossing previous tracks (*phobotaxis*); i.e., self-avoidance (Hayes, 2003). Together, these rules produce a simple spiral trace. If an additional rule is added, 3) turn 180° after moving a particular distance (*strophotaxis*), then the simulated trail is a meander. Using these rules, Raup and Seilacher (1969) were able to reproduce the morphology of several well-known fossil traces. Seilacher (1986) has suggested that the history of traces shows increased optimization, although this has been questioned (Uchman, 2003).

The model of Raup and Seilacher (1969) formed the basis of the work of Papentin (Papentin, 1973; Papentin and Röder, 1975), who used a form of genetic algorithm to evolve simulated trace fossil movement patterns. The fitness criterion of the model was the extent to which path crossing occurred; solutions which produced the fewest path crossings survived and reproduced. Alternative initial parameter sets produced either straight or random paths. Both initial sets evolved into virtual organisms that showed either meandering or spiraling behavior, with little or no crossing.

Similarly, Prescott and Ibbotson (1996) developed a Lego-based robot model that attempted to recreate the behavior of trace-forming organisms. The robot used a light sensor to detect a trail of paper that it deposits as it moves. The robot control architecture was able to produce both spiraling and meandering traces.

An alternative approach has been to use random walk models (Hofmann, 1990; Kitchell, 1979). Kitchell and colleagues (Kitchell, et al. 1978; Kitchell 1979) examined the morphology of modern deep-sea traces and compared them to generated random movement pathways and to the expectations of the optimum feeding model. They found that although trace morphology tended to be non-random, they also did not match the predictions of the optimum feeding model. For example, in food scarce regions, recrossings of previous traces are quite common, whereas spirals and meanders were rare or absent (Kitchell et al., 1978). Hagadorn et al. (2000) also identified a lack of these optimum patterns in a Cambrian trace.

Many observed trails on the sea floor contain both spiral and meandering portions. Kitchell (1979) explained the structure of such traces as a consequence of “patch morphometry and initial relative position.” In particular, she envisioned resources on the deep sea as being patchily

distributed. In her conceptual model, an organism establishes itself near the center of the patch and spirals outward until it reaches the patch edge. It then converts to a meandering path, switching back and forth between the patch edges (see Kitchell, 1979, fig. 9). Kitchell (1979) is the only conceptual model for trace morphology that explicitly incorporates patchiness in resource distribution, although its importance was also recognized by Hagadorn et al. (2000).

We believe that realistic models of feeding traces must incorporate patchiness and other aspects of habitat heterogeneity. They must also incorporate realistic ideas about how organisms perceive their environment and possible alterations in behavior as environments change. Our research is generating models for the formation of grazing and movement traces that include such environmental heterogeneity and organism specific perception and response to this variability.

2. The Model

2.1 Conceptual Basis

The model developed under this study is a major modification and elaboration of the one described in (Plotnick, 2003) which, in turn, is based on the spatially explicit ecological model CAPS developed by Plotnick and Gardner (2002). It incorporates:

- \$ Spatial heterogeneity of the environment, such as resource distribution. The model thus allows representing different patterns of resource patchiness;
- \$ Preference by the moving organism for some aspect of the environment, such as a particular resource;
- \$ Detection of this resource by the organism;
- \$ Behavioral response to detection;
- \$ Alteration of the environment caused by the movement of the organism through it, such as ingestion of the resource.

Resources on the modern sea-floor are rarely, if ever, evenly distributed. Instead, their distribution is patchy on many scales (Levinton, 2001). Numerous studies have examined the impact of patchiness on foraging (Brown, 2000; Chase et al., 2001), but these focused on almost exclusively on terrestrial and freshwater environments.

Many benthic organisms, such as snails and lobsters, detect food chemically (Atema, 1996; Derby and Steullet, 2001; Zimmer-Faust et al., 1995). Chemoreception can either be *contact*, in which the food is in direct contact with the organism or *distant*, in which the detected molecules (odorants) are water born. Distant chemoreception should be especially important in patchy environments, where resources exist in spatially isolated units of variable density.

Under unidirectional flow, organisms would be expected to orient upstream toward a chemical signal (*rheotaxis*; Croll, 1983). In still-water conditions, animals have been observed to orient themselves using chemical gradients (*klinotaxis*; Croll, 1983; Estebenet, 1995) or random search patterns (Teyke et al., 1992).

For distant chemoreception, the strength of the chemical signal detected should depend on the initial concentration of the resource at a particular location and on the distance of the organism

from the resource; i.e., a close resource of low concentration may produce a stronger signal than a higher concentration resource at a greater distance. The ability of an organism to orient to a given resource signal should also be influenced by current directions and turbulence; e.g., mixing of chemical signals in turbulent environments should reduce an organism's ability to orient toward a particular source. Bilateral chemosensors have been observed to allow organisms to navigate within unidirectional turbulent plumes (Zimmer-Faust et al., 1995; Atema, 1996; Grasso, 2001)

2.2 Model structure

The model is written in Lahey-Fujitsu Fortran 95 with the Winteracter™ add-on for a Windows interface. Output is written to an ASCII text file for further analysis and plotting.

2.2.1 Spatial heterogeneity

Resources are distributed on 2-D or 3-D square lattices. Each cell in the lattices contains some level of resource, scaled from 0.0 to 1.0. Two-dimensional lattices represent distributions in a single layer, such as at the sediment-water interface. Three-dimensional lattices allow the modeling of changes in resource concentrations with depth. Numerous spatial patterns can be used.

For two-dimensional simulations, the distributions can be:

- \$ Even: resource distributions are the same at all locations;
- \$ Random continuous: the level of a resource in a particular cell is randomly selected from an even distribution, but all nodes have at least some resource. (Figure 2)
- \$ Random clumped: the level of resource in a cell is again selected from an even distribution, but values below a preset cutoff are set to zero. This produces a pattern of isolated resource patches of random size and shape; the greater the cutoff value, the greater the patchiness of the resource distribution (Figure 3)
- \$ Fractal: Fractal maps are produced using the midpoint displacement algorithm of Saupe (1988). Maps are characterized by a parameter H that ranges from zero to one (Plotnick and Gardner, 2002); low values of H (near zero) produce maps that are extremely fragmented, whereas H values near one produce highly aggregated maps. Fractal maps can be either continuous or clumped (Figure 4).
- \$ Imported: Map patterns can be generated in advance and imported into the program. For example, an isolated patch with a linear gradient of resource is shown in Figure 5. A similar patch, this time with a decreasing radial gradient, is illustrated in Figure 6. In both cases, resource values outside the patch are random and lower than inside the patch.

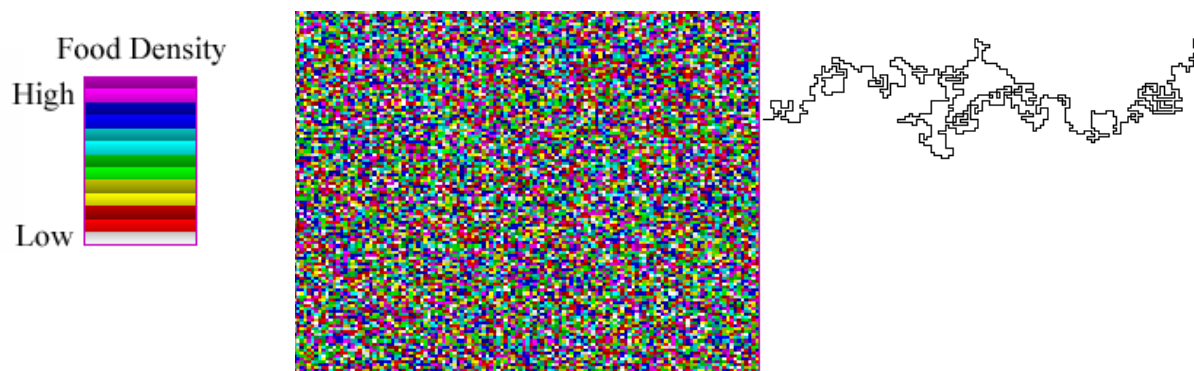


Figure 2: Random 2-D map and associated movement trail; key used in all figures.



Figure 3: Portion of random 2-D clumped map (cutoff = 0.7) and associated movement trail; key as in Figure 2. Dot is starting position.

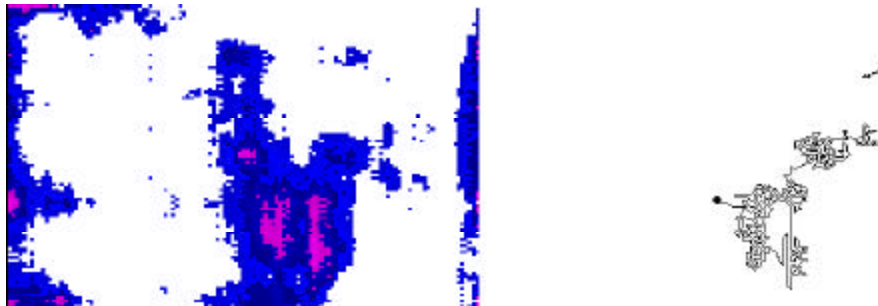


Figure 4: Clumped fractal 2-D map ($H = 0.7$; cutoff = 0.7) and associated movement trail; key as in Figure 2.

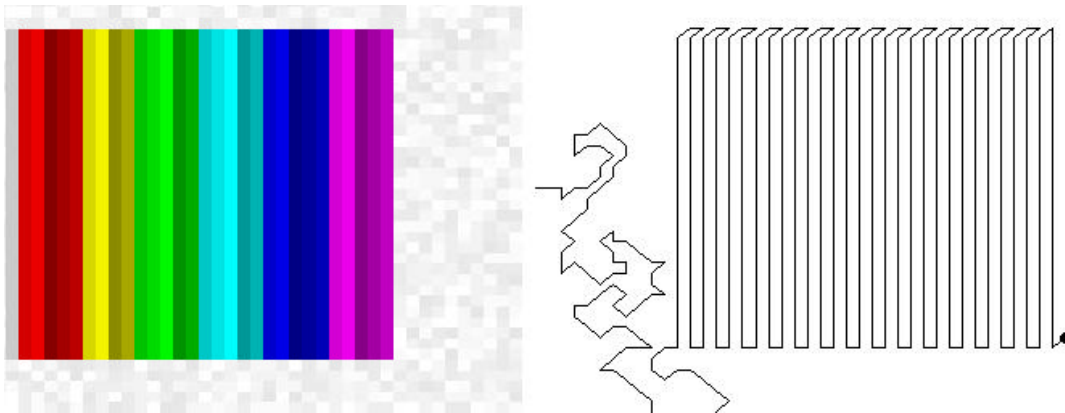


Figure 5: Isolated patch with internal linear gradient (highest to the right) and associated movement trail; key as in Figure 2.

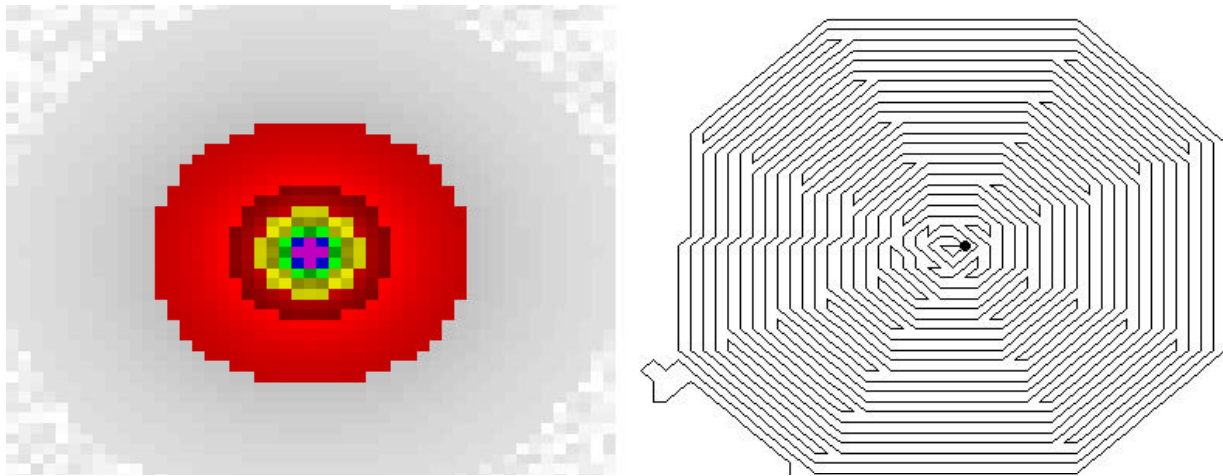


Figure 6: Isolated patch with internal circular gradient (highest in middle) and associated spiral movement trail; key as in Figure 2. Reversals of direction probably result from use of a square lattice.

There are currently four options for three-dimensional lattices.

- \$ Random continuous - same as for the 2-D case
- \$ Random clumped - same as for the 2-D case;
- \$ Random with gradient: a gradient is imposed on the random distribution, so that the resource availability increases towards the surface (Figure 7);
- \$ Random, gradient, clumped - produces random clumps, with the size and richness of the clumps increasing upwards.

Movements in three-dimensional lattices represent burrows. In the remainder of this discussion we will focus solely of two-dimensional movements.

The size of the lattices can be arbitrarily large, although very large lattices slow computation time, especially in the case of fractal maps. Lattices can be saved and reused.

Organisms can be placed on the lattice at the location of the minimum or maximum resource values, at the middle, or at a specific location of the user's choice.

2.2.2 Chemical signals, detection, and response

Each cell on the lattice releases a chemical signal s , with the strength of the signal released directly proportional to the amount of resource present in that cell. The signal can either be detected by direct contact chemoreception ("taste") or by distant chemoreception ("smell"). It is assumed that contact chemoreception has precedence over distant chemoreception.

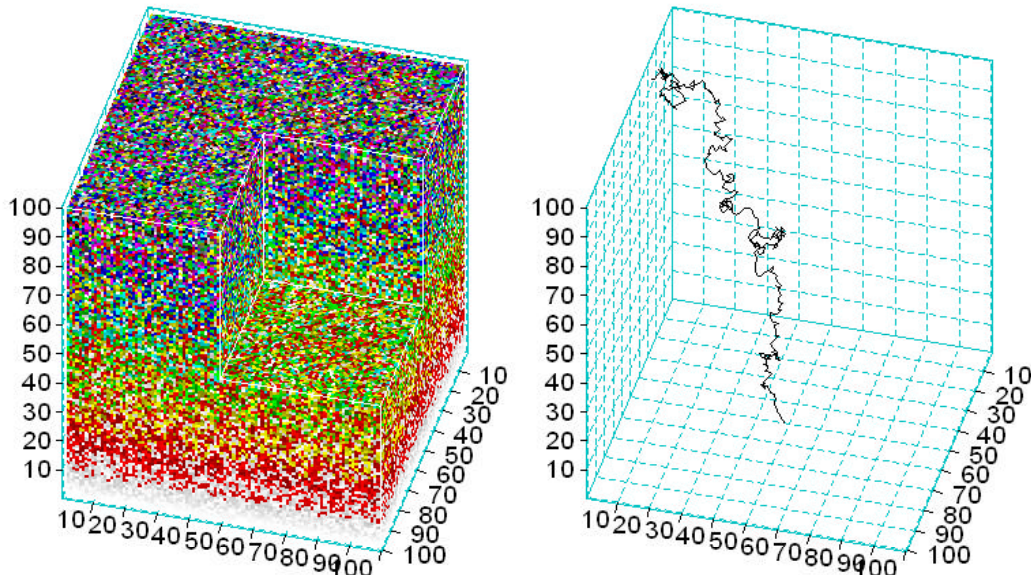


Figure 7: 3-D resource distribution, increasing to the top and associated movement trail; key as in Figure 2.

For contact chemoreception in two dimensions, the eight adjacent cells (next nearest neighbor) are examined and the "organism" simply moves to the cell with the highest concentration of resource, i.e., to the cell with the maximum value of s . When an organism moves into a cell, the level of resource in it drops to a low "background" level or zero, representing ingestion.

If all of the adjacent cells are empty, then the model organism detects the chemical signal from more distant cells. This represents distant chemoreception. It does so by assuming that each of the eight empty adjacent cells receives a summed chemical signal from other, more distant cells within a given radius R of each. Only cells within this radius contribute to the summed signal in the neighboring cells. The higher the value of R , the more likely it is to detect distant resources. However, because, the number of cells N included increases proportional to R^2 , this number is usually set fairly low. For example, when $R = 1$ the signal comes from the four nearest neighbor nodes and $N = 4$. When $R = 12$, the signal comes from a neighborhood of 440 sites.

The summed signal S in each of the eight adjacent cells C is thus:

$$S(C) = \sum_N s_i a(d_i) \quad (1)$$

where s_i is the signal from cell i within the radius R and $a(d_i)$ is the attenuation of the signal as a function of its distance d from C . Again, the organism moves to the cell with the maximum value of S . If no chemical signal is detected in any of the adjacent cells, then the movement is random.

A variety of functions are available to represent signal attenuation; they are designed to include a wide range of realistic representations of chemical dispersal. Signal attenuation functions include (Figure 8):

- < Uniform: no attenuation of distance;
- < Inverse square root of distance;
- < Exponential decline with distance
- < Normal distribution.

Details of the functions are in Plotnick and Gardner (2002).

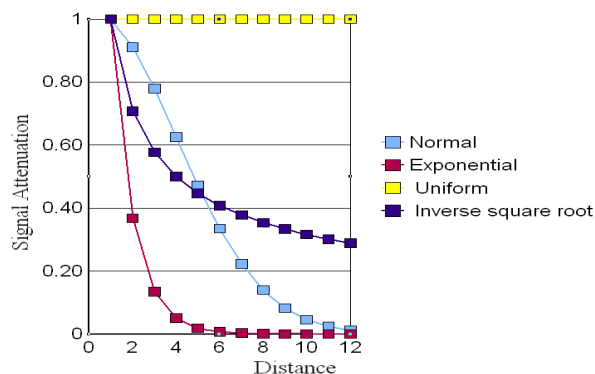


Figure 8. Signal attenuation functions. Maximum distance $R = 12$. From: Plotnick and Gardner, 2002

At this time, it is assumed that signal dispersal is equal in all directions. We are currently adding an option to allow biased dispersal in order to mimic directional currents.

For most runs, it is assumed that there is no directionality to signal detection; i.e., that chemoreception is equally sensitive in all directions. One option, however, allows either or both contact and distant chemoreception to have biased; e.g., the organism is “bilateral,” with the most sensitive detection in front and the least sensitive to the rear.

In sum, the behavior described by this model is very simple: detect a chemical signal and move in the direction of its highest value, then ingest what is present. Any variations in movement pattern, therefore, result only from differences in the spatial structure of the environment, rather than from behavioral differences. We suggest, therefore, that this simulation can function as a “null model” for the study of the evolution of behavior.

3. Results and Discussion

Representative spatial patterns and corresponding movement pathways for two dimensional paths are shown in Figures 2 to 5. For all of these simulations:

- \$ there is no bilateral bias in signal detection maximum
- \$ signal detection range for distance chemoreception is set to 2
- \$ signal attenuation is set to the square root of the distance.
- \$ all maps are 128 x 128 pixels (illustrated maps have been cropped).

It can be clearly seen that the geometry of the movement trail is strongly controlled by the spatial distribution and density of the resources. "Loose" or open meandering trails, in which successive loops are not in close contact, have been interpreted as being less advanced, in terms of behavioral optimality, than "tight" trails in which the loops are in close contact (Seilacher, 1986). Similarly, Seilacher (1986, p. 69) described a trail with conspicuous kinks as representing a trace maker with "problem in the execution of the meander program." As can be seen by comparing Figures 2-4, this variability in features can be produced by biologically realistic variation in spatial heterogeneity, rather than requiring different behavioral patterns

Especially important are the implications of these results for the formation of meandering and spiral trails; in particular the necessity for an organism to follow the rules underlying the model of Raup and Seilacher (1969) in order to produce these trails. Again, the only two behaviors explicit in the model are to move to the site of the greatest resource and ingest what is at that site, reducing that to low level. Phobotaxis, the avoidance of crossing a previous trail, thus results from the detection of low levels of resource in a previously exploited locality. Similarly, thigmotaxis, staying close to older parts of the trail, occurs if resources exhibit local concentrations larger than the ability of the organism to ingest in a single pass (See Figures 5 and 6). Neither behavior needs to be "hardwired" into the organism for the resulting paths to forms.

Hayes (2003, p.394) expressed puzzlement over the third rule, that of strophotaxis, in which the organism periodically makes 90° turns, "something one would like to see emerge from simpler rules rather than being a built-in axiom." As can be seen from Figure 5, the inferred behavior simply results from the encounter of an organism with a boundary; this in agreement with the suggestion originally made by Kitchell (1979).

4. Summary and Conclusions

We have developed a individual based movement model on square lattices in order to examine the influence of spatial heterogeneity on organism movement and thus on the morphology of movement traces preserved in the fossil record. Experiments to date with this model show that it is possible to simulate many possible trace fossil morphologies, including random movements, zigzags, and spirals, with a single simple behavior. Variability in patterns observed in the fossil thus may represent spatial differences in the distribution of food resources, rather than changes in behavior.

This suggests that at least some of the observed evolutionary patterns in grazing trace morphology, such as during the Precambrian-Cambrian transition (Crimes 1992, Seilacher 1974), may be related to changes in the spatial packaging of resources rather than the evolution of new "more efficient" behaviors. This heterogeneity may result from the onset of burrowing, which greatly increases the spatial heterogeneity of the environment (McIlroy and Logan, 1999; Jensen et al., 2005). This in turn, may be related to the advent of oxygenation in the ocean sufficient to make energetically expensive burrowing possible (McIlroy and Logan 1999).

5. Acknowledgements

Supported by NSF Grant EAR-0207194 to RP. Chris Ebey Honeycutt is thanked for useful discussions and for photographing Figure 1 (right).

6. References

- Atema, J., 1998,. Eddy chemotaxis and odor landscapes, exploration of nature with animal sensors. *Biological Bulletin*, **191**, 129-138.
- Bromley, R.G., 1996, *Trace Fossils, Biology, Taphonomy and Applications*. (London: Unwin Hyman.).
- Brown, J.S., 2000, Foraging ecology of animals in response to heterogeneous environments. In, M.J. Hutchings, L.A. John and A.J.A. Stewart (Editors), *Ecological Consequences of Environmental Heterogeneity*. (Malden, MA Blackwell Science) , pp. 181-214.
- Budd, G.E. and Jensen, S., 2000, A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Reviews*, **75**, 253-295.
- Chase, J.M., Wilson, W.G. and Richards, S.A., 2001, Foraging trade-offs and resource patchiness, theory and experiments with a freshwater snail community, *Ecology Letters*, **4**, 304-312.
- Croll, R.P., 1983, Gastropod chemoreception. *Biological Review*, **58**, 293-319.
- Derby, C.D. and Steullet, P., 2001, Why do animals have so many receptors? The role of multiple chemosensors in animal perception. *Biological Bulletin*, **200**, 211-215.
- Ekdale, A.A., Bromley, R.G. and Pemberton, S.G., 1984, *Ichnology, Trace Fossils in Sedimentology and Stratigraphy. SEPM Short Course, 15*. (Tulsa, Oklahoma: Society of Economic Paleontologists and Mineralogists).
- Erwin, D., Valentine, J. and Jablonski, D., 1997, The origin of animal body plans. *American Scientist*, **85**, 126-137.
- Estebenet, A.L., 1995, Food and feeding in *Pomacea canaliculata* (Gastropoda, Ampullariidae). *The Veliger*, **38**, 277-283.
- Grasso, F.W., 2001, Invertebrate-inspired sensory-motor systems and autonomous, olfactory-guided exploration. *Biological Bulletin*, **200**, 160-168.
- Hagadorn, J.W., Schellenberg, S.A. and Bottjer, D.J., 2000. Paleoecology of a large Early Cambrian bioturbator. *Lethaia*, **33**, 142-156.
- Hayes, B., 2003, In search of the optimal scumsucking bottomfeeder. *American Scientist*, **91**, 392-397.
- Hofmann, H.J., 1990. Computer simulation of trace fossils with random patterns, and the use of goniograms. *Ichnos*, **1**, 15-22.

- Jensen, S., Droser, M.L. and Gehling, J.G., 2005. Trace fossil preservation and the early evolution of animals. *Palaeogeography Palaeoclimatology Palaeoecology*, **220**, 19-29.
- Kitchell, J.A., 1979. Deep-sea foraging pathways, an analysis of randomness and resource exploitation. *Paleobiology*, **5**, 107-125.
- Kitchell, J.A., Kitchell, J.F., Johnson, G.L. and Hunkins, K.L., 1978, Abyssal traces and megafauna, comparison of productivity, diversity, and density in the Arctic and Antarctic. *Paleobiology*, **4**, 171-180.
- Levinton, J.S., 2001, *Marine Biology , Function, Biodiversity, Ecology*.(New York: Oxford University Press)
- McIlroy, D. and Logan, G.A., 1999, The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. *PALAIOS*, **14**, 58-72.
- Papentin, F., 1973, A Darwinian evolutionary system III, experiments on the evolution of feeding patterns. *Journal of Theoretical Biology*, **39**, 431-445.
- Papentin, F. and Röder, H., 1975, Feeding patterns, the evolution of a problem and a problem of evolution. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1975**, 184-191.
- Plotnick, R., 2003, Ecological and L-system based simulations of trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **192**, 45-58.
- Plotnick, R. and Gardner, R. 2000., A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. *Ecological Modeling*, **147**, 171-197.
- Prescott, T.J. and Ibbotson, C., 1996. A robot trace-maker, modeling the fossil evidence of early invertebrate behavior. *Artificial Life*, **3**, 289-306.
- Raup, D.M. and Seilacher, A., 1969, Fossil foraging behavior, computer simulation. *Science*, **166**, 994-995.
- Saupe, D., 1988, Algorithms for random fractals. In, H.-O. Petigen and D. Saupe (Editors), *The Science of Fractal Images*. (New York: Springer-Verlag.), pp. 71-136.
- Savdra, C.E., 1992, Trace fossils and benthic oxygenation. In, C.G. Maples and R.R. West (Editors), *Trace Fossils. Short Courses in Paleontology*. (Paleontological Society), pp. 172-196.
- Seilacher, A., 1986, Evolution of behavior as expressed in marine trace fossils. In, M.H. Nitecki and J.A. Kitchell (Editors), *Evolution of Animal Behavior*. (New York Oxford University Press), pp. 62-87.
- Taylor, A., Goldring, R. and Gowland, S., 2003, Analysis and application of ichnofabrics. *Earth-Science Reviews*, **60**, 227-259.
- Teyke, T., Weiss, K.R. and Kupfermann, I., 1992, Orientation of *Aplysia californica* to distant food sources. *Journal of Comparative Physiology A-Sensory Neural and Behavioral Physiology*, **170**, 281-289.
- Uchman, A., 2003, Trends in diversity, frequency and complexity of graphoglyptid trace fossils, evolutionary and palaeoenvironmental aspects. *Palaeogeography Palaeoclimatology Palaeoecology*, **192**, 123-142.

Zimmer-Faust, R.K., Finelli, C.M., Pentcheff, N.D. and Wethey, D.S., 1995, Odor plumes and animal navigation in turbulent water flow, a field study. *Biological Bulletin*, **188**, 111-116.