Foraging of *Homo ergaster* and *Australopithecus boisei* in East African environments

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Abstract

In this paper we present the initial results of an agent-based model of foraging of hominids. The model represents foraging activities in a landscape that is based on detailed measurements of food availability in the modern East African environments. These current landscapes are used as a model for the environment of the hominids one million years ago. We explore the spatial and temporal consequences of foraging patterns in different types of semi-arid landscapes and different types of hominids (*Homo ergaster* and *Australopithecus boisei*) who are defined with different abilities and preferences.

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Introduction

This paper reports the initial results of an agent-based model of hominid foraging in a complex dynamic landscape. Optimal foraging theory argues that foraging behavior is a Darwinian adaptation to search for resources in a particular environment. Foraging agents make decisions as if they optimize a certain currency, say energy intake, given the environmental constraints (Pyke, 1984).

What the best foraging choices for a hominid would be depends on nutritional requirements, the cognitive and communication abilities of the agent, the abilities to make and use tools, the group size, the group dynamics, the complexity of the landscape, the existence of competitors and predators, etc. We have developed an agent-based model as a tool to explore the consequences and consistency of different assumptions. The two species we model are of particular interest to paleoanthropologists because they were sympatric in a number of different habitats in eastern Africa between 2.0 and 1.3 million years ago, and have distinctive morphological adaptations that have often been interpreted as evidence of dietary divergence (e.g. Potts, 1998; Wood & Strait, 2004). *Australopithecus boisei* has been described as a "megadont," with teeth, jaws and cranio-facial morphology showing evidence of a diet that included tough a range of tough plant foods that required crushing and grinding. Whether or not this species specialized in a diet of low quality plant foods, or was more typically omnivorous and only resorted to such foods in famine times is a matter of current debate. In contrast to their robust cousins, *Homo ergaster*, had a relatively small chewing capacity and lightly built face and jaw, suggesting that its diet would have consisted either of relatively soft, easy-to-chew foods, and/or foods that were processed with tools before being eaten. Because the larger brains of *H. ergaster* would have been costly, metabolically, many paleoanthropologists have suggested that *H. ergaster* evolved a dependence on eating significant amounts of meat, in addition to high quality (easily digestible) plant foods, both of which would have required the use of tools such as stone knives, carrying devices, and digging sticks. The East African archaeological record during this time span consists of simple stone tools associated with fossilized remains of animals that have been butchered, and it is generally assumed that *H. ergaster* was the stone tool maker who fed on the meat and marrow at these sites. But whether or not *A. boisei* also could have made tools and eaten meat is a matter of debate.

Some of the key paleoanthropological questions we address in our model include:

(1) to what extent would differences in chewing abilities and tool use limit access to various food types in the types of semi-arid landscapes in which these hominids lived?

(2) if these species preferred different types of foods, how would that have influenced differences in their ranging behavior and frequency of habitat use through time?

(3) as both these hominids existed in several types of semi-arid habitat during periods of climate change – how would their different morphological and technological traits have led them to respond to the selection pressures in these habitats in different ways?

Direct evidence of this early phase of human evolution comes from several sources: samples of fossilized remains of the hominids themselves; associated macrofossils of fauna and flora; archaeological evidence suggesting where stone tools were made and how they were used, and associated paleoenvironmental indicators such as soil chemistry and fossil microfauna, or pollen. Since we cannot make direct observations of the foraging behavior of these extinct species we base our inferences on these different sources of information interpreted within the comparative framework of evolutionary biology and comparative primate ecology, including observations of foraging of other primates (Ramos- Fernández, et al. 2004; Goldstone and Ashpole, 2004). Formal models help us to analyze in a consistent way the consequences of various assumptions.

Earlier work on hominid foraging and agent-based models focused on more cognitively rich agents on a relative simple landscape of resources (Lake, 2000; Reynolds, 2001, Costopoulos, 2001). Our agents are cognitively very simple, but they forage on a more complex and empirically-based landscape than related publications. We assume that selected samples of the current landscape in eastern Africa can be used as a model for the environments in which hominids were foraging 2.0 to 1.5 million years ago (Sept, 1994). This enables us to use detailed transect data sampled from modern semi-arid riparian landscapes to create a model landscape which includes the availability of various food types in space and time. The generated dynamic landscape is populated with agents with simple foraging related decision rules. We present in this paper some initial results of decision rules for two types of hominids: *H. ergaster* and *A. boisei* foraging in two different semi-arid riparian landscapes (dry and wet).

An agent-based model of foraging of hominids

The landscape the agents forage on is based on samples of Kenyan habitats analogous to sites where early hominids lived 2.0-1.5 million years ago (Sept 1984, 1994). We describe now in formal terms the landscape dynamics and the rules the agents use for foraging. Consider a population of N_A agents in a landscape of N_1 x N_2 regular cells. These cells represent areas of 100m by 100m. A cell ij represent one of different types of land cover L_{ij}, and contains different amount of units N^U_{ijf} for various types of food sources F.

Landscape dynamics

The landscape consists of three zones besides the river which cross the landscape (Figure 1): the channel and margins, the flood plain, and the unflooded zone. Detailed transect data from Sept (1984) are used to estimate density of vegetation per hectare (Eberhardt, 1978). Using the average density estimates of vegetation for the different land cover, we populated the landscapes with vegetation per ha by a stochastic process.

We distinguish two landscapes: Voi and Turkana. The Turkana area today is relatively drier than the Voi landscape, and the vegetation structure and composition in the two regions reflects this difference. We include about 30 different types of food items in the landscape, available in different periods of the year. The limited space available for this paper does not allow us to provide the detailed information, but this will be reported in a separate publication.

The landscape is updated every simulated day, and consists of four different seasons. The first season, from March to May has the main rains. The second season, from June to August, is mainly dry. The third season, from September to November, is dry with short periods of rain, and the forth season, from December to February, is mainly dry. For each season we have an estimate on the availability of every food item. To calculate the available food in a cell, we calculate the increase and decline of the availability of food. The potential amount of food is assumed to increase during the beginning of the season (growth), and declines in the second half (decay, consumed by other species). The actual available amount of food available is the difference between the potential and the amount that is consumed of that food item. The availability of vegetation is used to calculate the kcal available in the landscape by using estimates on the amount of food items (berries, seeds) per unit of bush, tree, etc, and the amount of kcal per food item.

In some simulations for *H. ergaster* we include meat on the menu (Wood & Strait, 2004). Since *A. boisei* is often assumed not to eat meat, we have assumed they are vegetarian for this initial version of the model. In the simulations where meat is included in the menu, carcasses of different sizes are placed randomly in the landscape. Our estimates of carcass density are based on modern data collected in the Serengeti and Ngorongo ecosystems of Tanzania and the Galana and Kulau ranches of the Tsavo East National Park in Kenya (Blumenshine 1986, Dominguez-Rodrigo 1996). The availability of a carcass declines rapidly over time, in order to simulate consumption by predators like lions and hyenas. Following Blumenschine and Dominguez-Rodrigo, we assume competition for carcasses is higher in the unflooded area (more open area) than in the more forested area around the river channel.

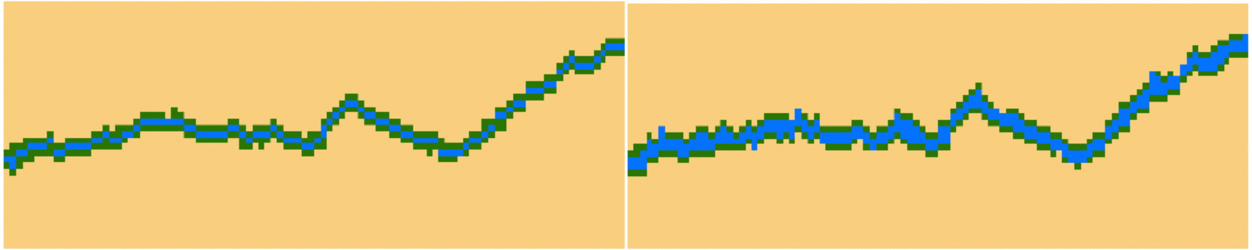

Figure 1: Stylized landcover of Voi (left) and Turkana (right): blue cells are channel and margin, green cells are floodplain, light brown is unflooded. Both areas are 4 by 10km.

Agents

An agent looks for food during a day until one of the following three conditions is met.

- The agent's stomach is full, (5kg gut capacity for all agents).
- The agent has consumed a minimum level of kcal (3000 kcal for *H. ergaster* and 2500 kcal for *A. boisei*).
- The agent has spent a maximum amount of hours that day on foraging. If food is scarce and agents move around to search for food, we assume they stop after 12 hours. Included in the model is time spent by agents on the various actions during foraging, i.e. harvesting food items, processing of the food, traveling, etc.

Each day agents are randomly selected to be updated. Each update consists of consuming food items or, in case of not finding food, one random movement to another cell. The searching process of an agent consists of defining the target, moving to the target, potentially encountering other food items, and handling the food item.

An agent has limited vision. It can see certain visible, "canopy" food resources in the cell in which it stands with probability v_{fC}. The agent can also see canopy food resources in other neighboring cells. We assume that the agent can see food items in the eight surrounding cells (the Moore neighborhood). The food items in the four neighboring cells that are adjacent to the cell are assumed to have a probability being seen of v_{fA}. Food items in the four neighboring cells at the corners of the cell are assumed to be identified with probability v_{fN}. The probabilities in adjacent cells and corner cells may be different since parts of the corner cells are further away from an agent in the center cell, compared to the adjacent cell, and therefore less visible.

An agent thus selected for action will first defines a target to approach. An agent looks for vegetation bearing food of interest in the Moore neighborhood. A bush/tree/plant is spot when a random number between 0 and 1 is larger than $(1–v)^M$, where v is the probability that vegetation can be seen from the current position of the agent, and M the number of plants/bushes/trees. The preference rating of spotted food items depend on the kcal per gram per minute handling rate.

The agent will then move toward its chosen target, but can encounter a more desirable food item which could not have been seen from the original position (such as low-lying squash plants or small berry bushes). The suite of food items available for a particular cell is checked for whether it is probabilistically encountered by the agent on its way to its target. If it encounters a food item, the agent stops and consumes the encountered food item. To calculate the probability of encountering we use the average number of vegetation per transect of 100 meter.

When we include meat we assume that carcasses can be spotted from a greater distance (500m) in the unflooded area (due to the presence of circling vultures). When a carcass is spotted, agents will always go to it. They move to it, not as an individual, but by a sample of the group (to compete with predators) and for simplicity's sake we assume that the available meat is shared among all agents in the group.

For this model we assume that agents sleep in a group, and return to a camp/nesting site by default until food availability around the sleeping site is depleted (the average consumed kcal is smaller then the minimum required amount of kcal), at which point the sleeping site is moved to a new nesting location, where agents of the group found the most food during that day. Such behavior is not a realistic reflection of primate nesting behavior today, but a useful starting point for our model. Primates such as baboons and other open-country monkeys will often forage and nest in groups for safety, while larger apes, such as chimpanzees, are often forced to forage and nest independently when food is scarce, though they will share feeding sites and seek to sleep in trees near each other when food availability makes that feasible.

Model experiments

We present some initial results of a group of 20 agents for simulations of a 100 year period. Basic experiments include four simulations, with one of each type of hominid on each type of landscape. Figure 2 shows that agents have difficulty meeting their basic energy requirements from the available plant foods alone. Especially in the harsh fourth season there is a problem for the agents to sustain themselves. The agents either reach their gut capacity with low-quality, fibrous plant foods, and/or run out of time searching for higher quality foods before they have enough food. It is not the availability of food itself, but the quality that leads to constraints.

Figure 3 shows the travel distance of *H. ergastus* in 2 different landscapes in the four different seasons. The power law distribution of travel distance is similar to empirical observation of spider monkeys (Ramos- Fernández, et al. 2004). Most of the days, the agents travel only a small distance, but in some days they travel a lot.

There are differences between the seasons which affect agent behavior. Season 4 is the harshest in the Voi landscape, leading to large distances of travel every day. The first 2 seasons are more resource-rich leading to less travel. The Turkana landscape has fewer differences between the seasons, in term of travel distances. Only in the second season there is more travel. Interestingly, travel is not more in season 3, when agents do not meet their required kcal.

When we include meat in the menu of *H. ergastus* the agents meet their required kcal (Figure 4). The agents also will travel more since they go after the carcasses and see opportunities on larger distances. Where do the hominids forage? Agents forage at higher density in the unflooded area of Voi and in the channel and margins of Turkana. There are small differences between the two types of hominids caused by the different preferences (Figure 5).

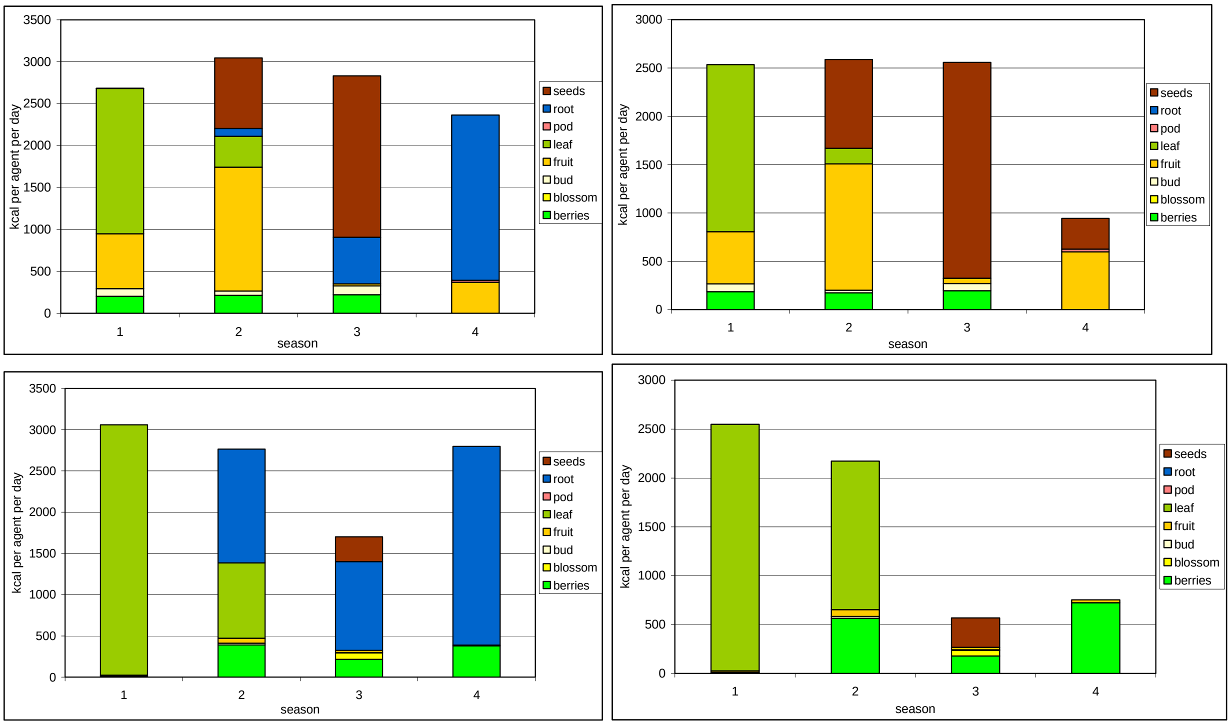

Figure 2: Menu of hominids aggregated into 8 types of food resources. The upper results are from Voi, the lower from Turkana. The left is from the *H. ergastus*, the right is from *A. boisei*.

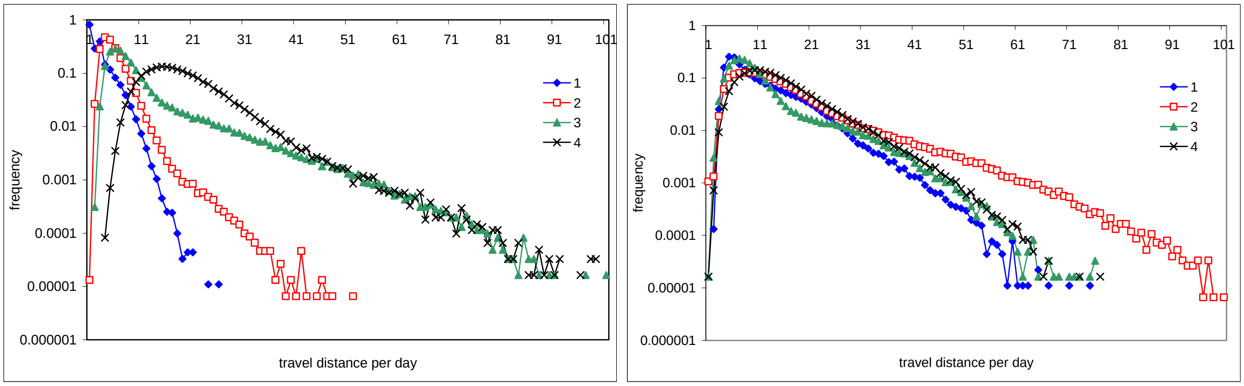

Figure 3: Distribution of travel distance (number of cells per day) per agent per day for the 100 year simulations of *H. ergastus*. Left is the Voi landscape. Right is the Turkana landscape.

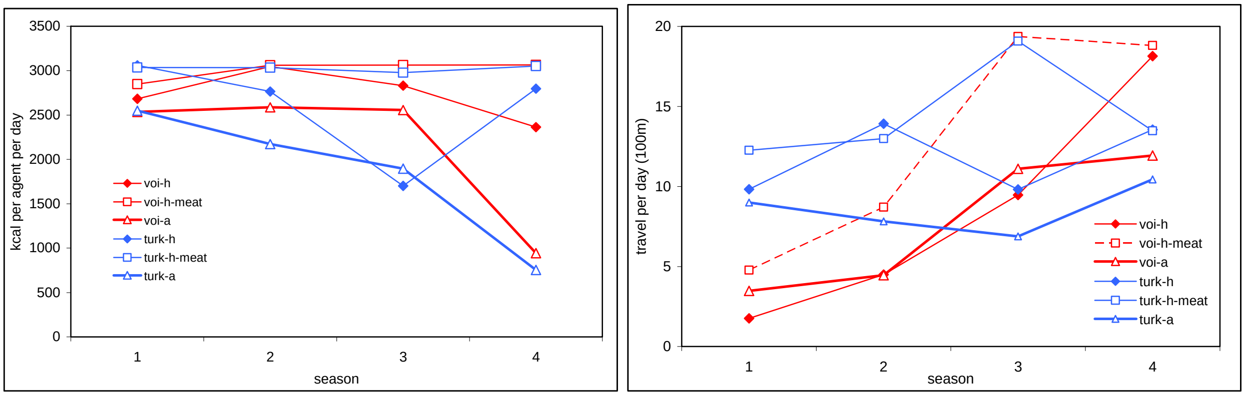

Figure 4: Left figure shows the average kcal per day for the different simulations. Right figure shows the average travel distance per day for the different simulations.

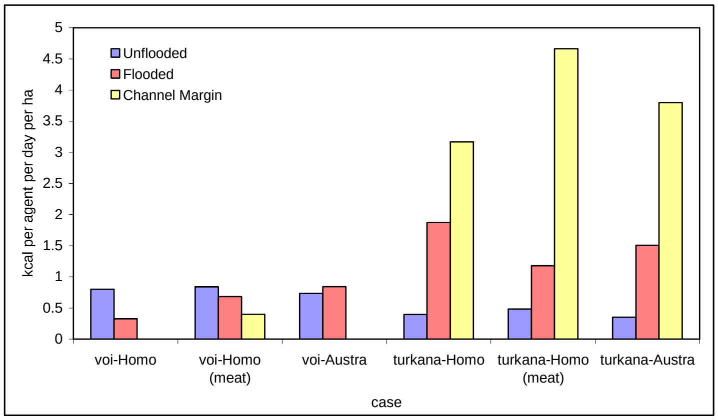

Figure 5: Average kcal per ha per agent per day for the different types of land cover in the 6 different simulations.

Discussion

We presented the initial results of the agent-based model of foraging of hominids in a complex dynamic landscape. Our main focus so far has been to create an empirically based landscape that covers the complex environment wherein the hominids where foraging. The agents for now are immortal clones with simple decision rules. Future work will explore more elaborate cognitive and social processes like decisions when to go after which type of food, the inclusion of spatial memory, and having the agents take on different roles in their group (age and gender differences, food sharing and provisioning), including the role of tools. We also want to use this framework in the longer term to under which circumstances what kind of agents emerge when we include evolutionary processes.

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