# Hominids foraging in a complex landscape: Could *Homo ergaster* and *Australopithecus boisei* meet their calories requirements?

Marco A. Janssen[1], Jeanne M. Sept[2], and Cameron S. Griffith[3]

[1]School of Human Evolution and Social Change & School of Computing and Informatics, Arizona State University, PO Box 872402, Tempe, AZ 85287-2402, Marco.Janssen@asu.edu
[2]Department of Anthropology, Indiana University, sept@indiana.edu
[3]Department of Anthropology, Indiana University, casgriff@indiana.edu

**Summary.** In this paper we present 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 use the model to explore possible rankings of food preferences for different types of hominids (*Homo ergaster* and *Australopithecus boisei*) in different types of semi-arid landscapes. We let the agents adjust their preferences to maximize their calories intake and show that *A. boisei* could not meet its calories requirements in different landscapes.

## Introduction

This paper reports 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 depend on nutritional requirements, the cognitive and communication abilities, the abilities to make and use tools, group size, 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 1.5 million years ago, and have distinctive morphological adaptations that have often been interpreted as evidence of dietary divergence (e.g. Potts 1998; Wood and Strait 2004). *Australopithecus boisei* has been described as a "megadont," with teeth, jaws and cranio-facial morphology showing evidence of a diet that included 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; Premo 2005). 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

### An agent-based model of foraging of hominids

The landscape on which the agents forage is based on samples of Kenyan habitats analogous to sites where early hominids lived 2.0-1.5 million years ago (Sept 1986, 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 represents 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. We use $N_1 = 100$ and $N_2 = 40$.

### Landscape dynamics

The landscape consists of three zones besides the river which crosses the landscape. 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.

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 October, is mainly dry. The third season, from November to December, is dry with short periods of rain, and the forth season, from January 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 maximum amount of food, $K_{max}$, in a cell is the number of plants times the number of food units per plant. During the year the amount of food units available increases during the season (growth), and then declines (decay, consumed by other species). On day 1 of a season the food availability is assumed to be 1% of $K_{max}$ in case this food type was not available in the previous season. The potentially availability of food $x_i$ grows according to a logistic growth function $x_i(t) = x_i(t-1)+g*x_i(t-1)*(1-x_i(t-1)/K_{max})$, where g is the growth rate per day. During the middle of the season the food availability reaches its maximum, after which the potential food availability decreases by a logistic function $x_i(t) = x_i(t-1)-d*x_i(t-1)*(1-x_i(t-1)/K_{max})$, with *d* the decay rate per day. The growth and decay rates are defined in such a way that the potential food availability grows to the maximum level, and decreases to zero again at the end of the season. In various cases a food type is available during multiple seasons. In those cases the growth and decay rates are adjusted, for example by assuming no decay when the food type will have the same potential availability in the next period.

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. The actual available food $x_{a,i}$ on a certain day t for a food type i on a cell is defined as $x_{a,i}(t) = x_i(t) – c_i(t-1)$, where $c_i(t-1)$ is the amount of food consumed till the previous time step. The accumulated consumed food $c_i$ holds only during the season when food is potentially is available. Thereafter $c_i$ is set to zero again.

In some simulations for *H. ergaster* we include meat as part of their menu (Wood and 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 on 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. The probabilities per cell per day are 0.00046 for channel margin, 0.0002 for floodplain, and 0.00027 for unflooded area.

Based on data from Blumenschine (1986) we estimated the decay of the weight the meat of the carcass (in kg) available as a function of the number of hours after it has died:

$$weight = \frac{e^{a}}{(hours + c)^{b}}$$

Where $c = \frac{e^{-a/b}}{weight_0^{1/b}}$, with weight$_0$ the initial weight of the carcass. The values of *a* and *b* are estimated for channel margin (*a*=1.55 and *b*=0.91), flood plain (*a*=2.24, *b*=0.91) and unflooded area (*a*=2.80, *b*=0.86). The initial weight is drawn from a normal distribution with mean 225 kg and a standard deviation of 50. One gram of meat is 1.76 kcal.

## Agents

The agents are modeled as simple reactive agents who individually forage for food. An agent looks for food during a day until one of the following three conditions is met.

- The agent's stomach is full, which means that the weight consumed is equal or more than 5000 grams for *H. ergastus* 1 and 4000 grams for *A. boisei*.
- The agent has consumed a minimum level of kcal. We assume that an agent stops eating when it consumed 3000 calories for *H. ergastus*, and 2500 calories 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 it stops after 12 hours. Time is spent on traveling, collective, and processing food, which vary for different food items.

Each day all agents forage for food, and during the day they are randomly drawn to be updated until they reach a stopping criterion. 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.

Due to the different amount of time spend searching and handling food items, agents are during a day not synchronized. After each activity the time budget spent on handling food and traveling are updated. In case we will implement activities of a whole group, we can synchronize the agents during the day, for example when they have discovered a carcass.

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 define a target to approach. An agent looks for vegetation bearing food of interest in the Moore neighborhood. A bush/tree/plant is spotted 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.

Based on the order in which an agent ranks different types of food items an agent makes a decision which food item to consume. Initially we used a ranking based on how many kcal of a food unit is collected per unit of time. The higher this score, the more preferred the food unit. However, with this ranking rule the agents were not able to derive sufficient calories to survive. We adjusted the model to the current version in which we explore what rankings of food items will lead to higher calories intake of the agents. We will describe later in the paper how we calculate this ranking.

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 which is more preferable than the target, the agent stops and consumes the encountered food item. If no food has been discovered, the agent makes a random move to one of the 24 neighboring cells, assuming a radius of 2 around the current cell. The agent is not allowed to go to cells it has already been to that day, and to cells that represent water.

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 by an agent who is in a cell with more then four agents, all agents in the cell will go to the carcass. They move to it, not as an individual, but as a group (to compete with predators) and the available meat is shared by all agents who went to the carcass. Note that we now assume that agents always go after the carcass independent of the distance it needs to travel, local availability of food, and whether they had meat lately. We may explore alternative behavioral rules in future versions of this research project.

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. We use a local search method to find food rankings that deliver sufficient calories for the agents. For each agent we give initially each food item a preference value randomly drawn from a uniform distribution between 0 and 1. After each year we evaluate the average calories these preference orders of all the agents have delivered. The higher the calories derived the higher the chance that this ranking is used the next year. With a small probability (1%) a preference of a food item gets a random value to introduce novel strategy. We simulate a 100 year period and the average calories per agents improve over time (see Figure 1). Results are presented for the last 50 years of the simulated 100 year period where the ranking orders have been stabilized.

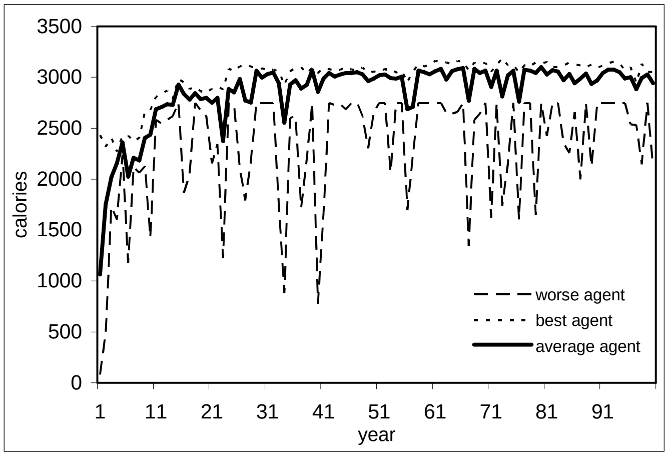

**Fig. 1.** Average calorie intake per day for *H. ergaster* in Turkana landscape for a simulated period of 100 years. The “worse agent” refers to the agent during that year which derived the lowest amount of calories. The same hold for the “best” and the “average” agent.

The resulting ranking orders maximize the calorie intake of the agents. Nevertheless, we find that agents do not derive sufficient calories during each season (Figure 2). Especially *A. boisei* is not able to derive sufficient calories during the dry fourth season in both landscape.

One of the reasons that *A. boisei* was not able to derive sufficient food items is due to the inability to handle tools to dig out roots. Another reason is that the agents run out of time since only food items are available which take a lot of processing and handling time to derive the required calories (Tables 1 and 2). Tables 1 and 2 also show the maximum distance an agent travels from the next per day on average, which varies from 800 to 1500 meters, the time spend on foraging, between 4 and 12 hours, and the average gram of food eaten.

**Table 1.** Average daily values during four seasons over a 50 year period for *Homo ergaster*.

| | Voi | | | | Turkana | | | |
|---|---|---|---|---|---|---|---|---|
| season | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Calories | 2553 | 3083 | 3013 | 2193 | 2815 | 2998 | 3102 | 3164 |
| Gram | 4862 | 2638 | 3006 | 4108 | 3536 | 3558 | 2529 | 2502 |
| Time (minutes) | 274 | 516 | 526 | 707 | 322 | 321 | 351 | 339 |
| Distance (100m) | 8.5 | 10.4 | 10.5 | 14 | 12.1 | 11.2 | 12.4 | 13.1 |

**Table 2.** Average daily values during four seasons over a 50 year period for *Australopithecus boisei*

| | Voi | | | | Turkana | | | |
|---|---|---|---|---|---|---|---|---|
| season | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Calories | 1992 | 2590 | 2372 | 926 | 2310 | 2049 | 2321 | 595 |
| Gram | 3789 | 2293 | 1816 | 2024 | 2901 | 2892 | 1321 | 1257 |
| Time (minutes) | 260 | 287 | 375 | 723 | 276 | 316 | 699 | 728 |
| Distance (100m) | 8.1 | 8.5 | 10.9 | 15 | 10.8 | 11.3 | 10.4 | 12.1 |

When we include meat in the menu of *H. ergastus* the agents meet their required kcal (Figure 3, Table 3). The agents also will travel more since they go after the carcasses and see opportunities on larger distances. About half of the calories are derived from meat in these simulations, but we acknowledge that this share is sensitive to assumptions on when and how often agents will go after carcasses. Such details are obviously unknown, and the center of the debate of hominid foraging.

**Table 3.** Average daily values during four seasons over a 50 year period for Homo ergaster, when eating meat

| | Voi | | | | Turkana | | | |
|---|---|---|---|---|---|---|---|---|
| season | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Calories | 2986 | 3106 | 2092 | 3015 | 2924 | 3152 | 3205 | 3179 |
| Gram | 4114 | 2635 | 2993 | 3841 | 3051 | 2918 | 2966 | 2993 |
| Time (minutes) | 413 | 404 | 442 | 557 | 535 | 393 | 430 | 455 |
| Distance (100m) | 21.1 | 15.4 | 17.9 | 26.1 | 28.2 | 25.1 | 22.9 | 22.1 |

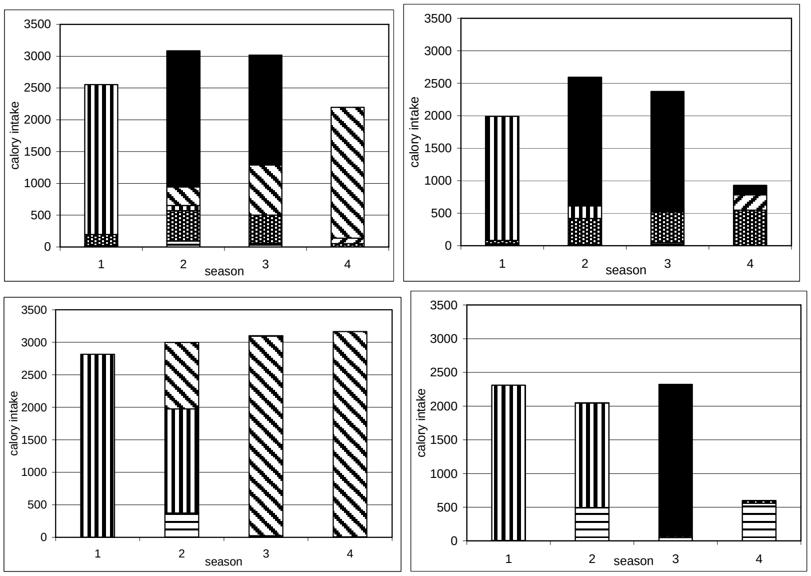

**Fig. 2.** Menu of hominids aggregated into 8 types of food resources (the 9th item meat is not included in these simulations). The upper results are from Voi, the lower from Turkana. The left is from the *H. ergastus*, the right is from *A. boisei.*

⊟ berries ▩ blossom ☐ bud ▓ fruit ▥ leafs

▨ pod ▧ root ■ seeds ⊡ meat

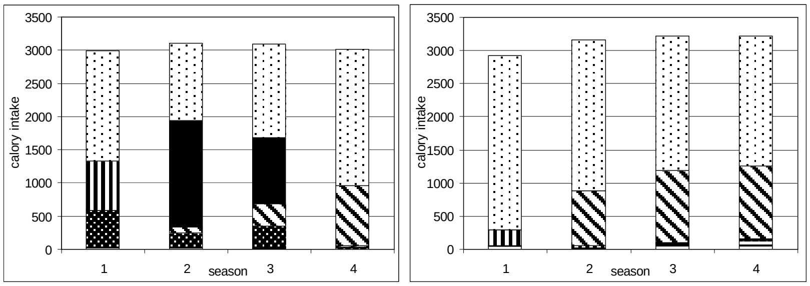

**Fig.3.** Menu of *Homo ergaster* aggregated into 9 types of food resources. The results on the left are from Voi, the results on the right are from Turkana.

Figure 4 shows where the calories are collected in the landscape by the *H.ergaster* (when we allow meat on the menu) and *A. boisei*. Having agents going for meat lead them to forage more disperse on the landscape. The *A. boisei* has more concentrated areas where calories are collected. Especially in the Turkana landscape, the calories are mainly derived from the food items growing in the floodplain.

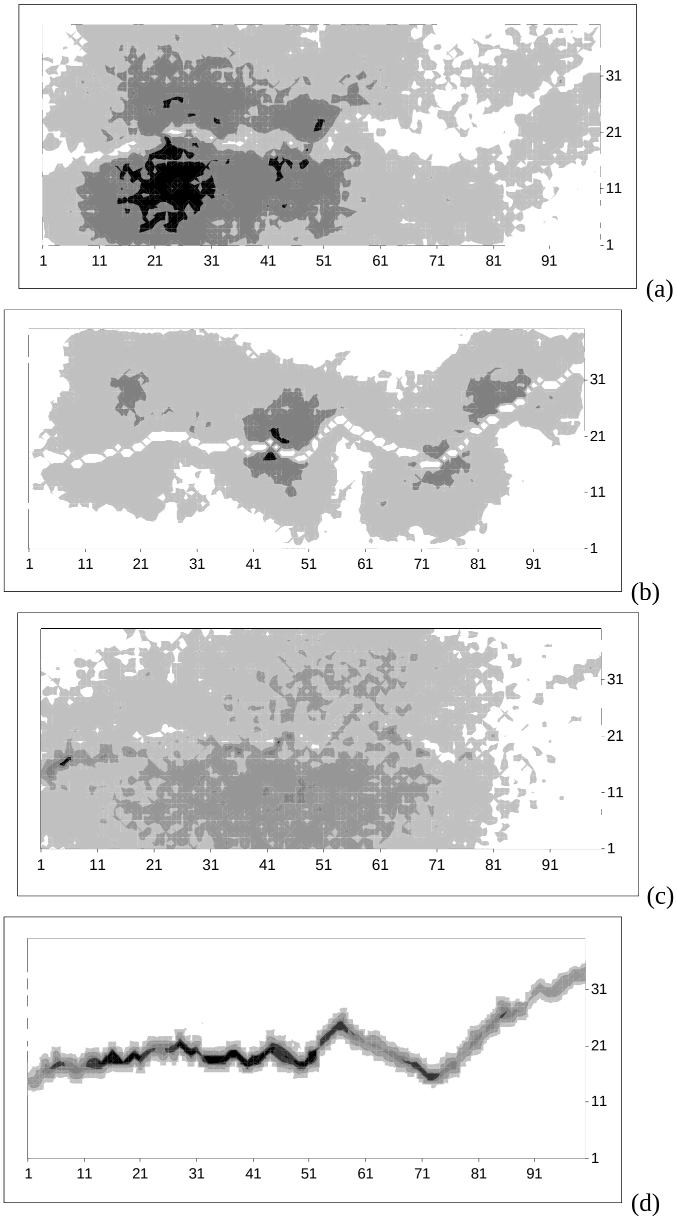

**Fig 4.** Density maps of calorie extraction by agents over a 50 year period. The darker the color the more calories extracted. The upper results (a and b) are from Voi, the lower (c and d) from Turkana. Figures a and c are from the *H. ergastus*, and b and d are from *A. boisei*.

## 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 forage. The agents for now are immortal clones with simple decision rules.

Using a fixed ranking order based on kcal collected per unit of time showed the difficulty of the agents to derived sufficient calories. But such an indicator does not include availability of food items during the seasons, or the total amount of calories that such a food item provides. The kcal derived during foraging are sensitive to the way agents rank different food items. We performed a number of hypothetical experiments to investigate whether different rankings of preferences leads to high amounts of calories consumed. Our artificial agents updated their ranking each year, so that agents will learn which ranking lead to maximum calorie intake. These experiments led to the conclusion that *H. ergastus* should have been able to feed itself in the empirical landscapes as we used, while *A. boisei* would this has difficulties to derive sufficient calories. Although this experiment lead to a potential higher fitness of *H. ergastus*, the experiments has their limitations. For example, we may not have included all the potential food items available during the actual existence of *A. boisei*. We also had to speculate on the cognitive abilities and physical constraints and demands of the hominids.

Future work will explore more elaborate cognitive and social processes like decisions on 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 explore under which circumstances what kind of agents emerge when we include evolutionary processes.

## References

Blumenschine RJ (1986) Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. Bar International Series 283, Oxford.

Costopoulos A (2001) Evaluating the impact of increasing memory on agent behaviour: Adaptive patterns in an agent based simulation of subsistence. Journal of Artificial Societies and Social Simulation 4(4) <http://www.soc.surrey.ac.uk/JASSS/4/4/7.html>

Dominguez-Rodrigo M (1996) A landscape study of bone conservation in the Galana and Kulalu (Kenya) ecosystem. Origini 20: 17-38.

Eberhardt LL (1978) Transect methods for population studies. Journal of Wildlife Management 42(1): 1-31.

Goldstone RL, Ashpole BC (2004) Human foraging behavior in a virtual environment. Psychonomic Bulletin & Review 11: 508-514.

Hemelrijk CK (2002) Understanding social behavior with the help of complexity science. Ethology 108(8): 655-671.

Lake MW (2000) MAGICAL computer simulation of Mesolithic foraging. In Kohler TA, Gumerman GJ (eds) Dynamics in Human and Primate Societies: Agent-Based Modelling of Social and Spatial Processes. Oxford University Press, New York, pp. 107-143.

Potts R (1998) Environmental hypotheses of hominid evolution. Yearbook of Physical Anthropology 41: 93-136.

Premo LS (2005) Patchiness and Prosociality: An Agent-Based Model of Plio/Pleistocene Hominid Food Sharing, In: Davidsson P, Logan B, Takadam K (eds): Multi-Agent and Multi-Agent-Based Simulation MABS 2004, Lecture Notes in Computer Science 3415, pp. 210 – 224.

Pyke GH (1984) Optimal foraging theory – a critical review. Annual Review of Ecology and Systematics 15: 523-575

Ramos-Fernández G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozc B (2004) Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behavioral Ecology and Sociobiology 55: 223–230

Reynolds R, Whallon R, Goodhall S (2001) Transmission of Cultural Traits By Emulation: An Agent-Based Model Of Group Foraging Behavior. Journal of Memetics, 4. http://jom-emit.cfpm.org/2001/vol4/reynolds_r&al.html

Sept JM (1984) Plants and early hominids in east Africa: a study of vegetation in situations comparable to early archaeological site locations. PhD dissertation. University of California, Berkeley,

Sept JM (1994) Beyond bones: archaeological sites, early hominid subsistence, and the costs and benefits of exploiting wild food in east African riverine landscape. Journal of Human Evolution 27: 295-320.

Wood B, Strait D (2004) Patterns of resource use in early Homo and Paranthropus. Journal of Human Evolution 46: 119-162.