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Early hominins: Successful hunters, catchers, or scavengers? An agent-based model about hunting strategies in tropical grasslands

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ABSTRACT

We can see an increasing consumption of meat together with the corresponding behavioral adaptations in early hominins, such as *Homo erectus*. This new development was driven by one or more behavioral adaptations, such as a shift to a higher-quality diet, increased social interactions and/or changes in the life history strategies. The methods by which these hominins obtained meat—through scavenging the carcasses of large herbivores or hunting themselves—remain a topic of debate. They seem to have thrived in expanding grasslands, which offered few resources except for herds of large, gregarious mammals. In our study, we developed an agent-based model that simulates the behavior of a group of hunter-gatherers foraging in a reconstructed tropical grassland environment. The environmental parameters, including plant availability and prey population densities, are derived from the Serengeti National Park. In this model, agents gather or hunt various species either alone or as a group, using strategies early hominins may already have access to. The basic behavior and the implemented hunting strategies are based on data from recent hunter-gatherer societies living in tropical grasslands. Our model demonstrates how foragers may have thrived in tropical grasslands by either adopting fast hunting strategies, which often require access to sophisticated hunting tools, or by cooperating extensively, which would rely on an enhanced social structure to promote cooperative behavior. Our model can be used to study other scenarios by offering the option to change the environmental conditions and aspects of the agent behavior.

1. Introduction

Homo erectus emerged in eastern Africa during a period of increasingly arid conditions. Once semi-evergreen forest transitioned into deciduous woodland, which later changed into tropical grassland around 1.8 million years ago (Tallis and Hamilton, 1983; Agustí and Lordkipanidze, 2019). *Homo erectus* stands out from its predecessors due to several notable characteristics: larger body size, altered body proportions, increased brain size relative to body size, reduced masticatory apparatus, and changes in the speed of growth and maturation (Aiello and Key, 2002; Swedell and Plummer, 2019). These evolutionary developments may have been driven by one or more behavioral adaptations, such as a shift to a higher-quality diet that was easier to chew (Leonard and Robertson, 1992), modifications in life history strategies (Dean, 2010), or an enhancement of social interactions (Kaplan et al., 2000).

These changes are believed to have developed as *Homo erectus* adapted to the new drier and more open environmental conditions.

Locating and gathering plant resources in these habitats would have been more challenging for hominins than in the previously denser wooded environments which offered a variety of plant and animal species (Foley, 1982; Marean, 1997). In contrast, more open vegetation is characterized by an abundance of herbs and shrubs, with fewer but larger animal species (De Vos, 1969; Mishra and Young, 2020). The Serengeti in Tanzania today may best represent these conditions, still home to a diverse array of large ungulates. These large herbivores might have been exploited by early hominins, and evidence suggests that *Homo erectus* increasingly relied on hunting animals compared to their hominin predecessors (Foley, 1982). Therefore, we can conclude that they somehow developed the ability to effectively exploit the large gregarious mammals they encountered in these open habitats.

This prompts the question how early hominins managed to secure adequate resources with the tools and strategies at their disposal. Being a successful hunter requires the foragers to prepare tools, have knowledge about the location of potential prey, and the ability to select

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the fitting strategy. Mastering these tasks and being capable of hunting effectively are thought to correlate with enhanced cognitive capabilities, the emergence of complex social structures, and technological progress (Bunn and Ezzo, 1993; Domínguez-Rodrigo, 2002; Stuart-Fox, 2014). At what point early hominins gained the ability to actively hunt is still under debate (Pobiner, 2020). It has also been proposed that early hominins while lacking the ability to hunt themselves, they first started scavenging carcasses left by larger predators (Domínguez-Rodrigo, 2002). While several hypotheses have been proposed regarding how these early humans might have hunted various animal species, assessing the efficiency of their tools remains a significant challenge (Oliver et al., 2019).

The limited archaeological and paleoanthropological evidence makes is difficult to reconstruct the potential subsistence strategies of early hominins in tropical grasslands and their methods for acquiring resources. Reconstructing their behavior from the fossil record has its challenges, as many behavioral indicators do not fossilize. Nonetheless, the significance of grasslands in the evolutionary narrative of early hominins has led to numerous foraging models that explore the unique challenges and opportunities presented by these environments (Kurland and Beckerman, 1985; Wheeler, 1992; Domínguez-Rodrigo, 2001; Hernandez-Aguilar et al., 2007; Thompson et al., 2019). However, our understanding of how modern or early hominin hunter-gatherers foraged within tropical grasslands remains largely speculative as most recent hunter-gatherer societies that have been studied inhabit either dense forests or extremely arid grasslands—habitats that were often penetrated by pastoralist communities before thorough research has been conducted (Marean, 1997). These habitats differ significantly in terms of plant and animal life from the moist savannas with patchy forests that characterized many tropical grasslands where early hominins might have roamed.

In our study, we utilize simulations—a widely recognized approach for examining and determining the underlying parameters of phenomena that are not directly observable or replicable (Breitenecker et al., 2014). More precisely, our study employs agent-based modeling (ABM) because foraging behavior is governed by individual choices and interactions (Nonaka and Holme, 2007; Sellers et al., 2007). Throughout the development phases of a model we selected variables to be tested that are likely to influence the process. This approach yields a model that offers a streamlined representation of the process in question (Vallacher et al., 2017). Within our model, each agent symbolizes either an individual or a group navigating a virtual landscape, with the capability to engage with their surroundings and other agents. ABMs are frequently applied in exploring early hominin behavior, focusing on various aspects and scales such as the impact of social and geographical factors on foraging returns (Wren et al., 2019), the emergence of central place foraging strategies (Sikk and Caruso, 2020), competitive dynamics in scavenging scenarios (Rodríguez et al., 2023), or the significance of small-game hunting practices (Seuru et al., 2023).

Our study aims to explore and evaluate the potential subsistence strategies of hominin foragers in tropical grasslands. Given the hypothesized significance of an increased meat consumption which may have started in *Homo erectus*, our primary focus is on their methods of meat acquisition. We first want to assess all the potential hunting strategies available to hominin foragers and how they differ in factors like the duration of each hunting attempt and the potential for collaboration among hunters. Simultaneously, we evaluate how the used strategies may differ in their efficiency depending on the characteristics of the targeted prey like body size.

We want to gain insights into the main factors which determine if a meat procurement strategy is viable in our model and identify the key factors that would allow a group of hunter-gatherers to thrive in tropical grasslands.

In this paper, we start with an introduction to our model—an advanced version of the ForeGatherer v1.0 ABM developed by Reschke et al. (2023). Our primary focus will be on the aspects which

differentiate our model from its predecessor. We will explain how we adapted the model to represent the important environmental features of tropical grasslands and how the foraging agents use the newly implemented hunting strategies to acquire meat. In our experiments a group of hunter-gatherers will use one strategy to hunt prey of two different size categories. We will measure how efficient they are in acquiring meat by calculating the average returns from each hunting trip and if the subsistence scenarios result in changes in the movement pattern of the group. Finally, we will discuss which factors determine if a subsistence strategy is viable when foraging in a tropical grassland environment and which strategies might have been used first by early hominins to thrive. As the model depends heavily on data from recent hunter-gatherers the resulting behavior is more a representation of recent hunter-gatherer behavior under varying scenarios than a fitting representation of early hominin behavior

2. Material & Methods

The ForeGatherer v2.0 ABM permits analyzing of various hunting strategies and environmental conditions on a group of hominin foragers (Reschke et al., 2024). This model is an enhanced version of the ForeGatherer v1.0 ABM (Reschke et al., 2023), which provides a basic structure for adding and testing a range of subsistence strategies and environmental conditions, particularly in relation to their impact on return rates and mobility. The simulated hominin group in our model comprises several individuals who are collectively searching for resources within a simulated environment, moving as a unit once local resources have been exhausted. To evaluate the effect of different scenarios, the model calculates the average yield per hour spent hunting, as individual foraging success directs the movement of the group. Additionally, it tracks the group's resource consumption by determining the diet composition and calculates the number of residential moves per year.

Foragers' daily routines are determined by the need to acquire a specific amount of energy each day, regardless of the activities they engage in. They gain energy by consuming resources they acquired using different foraging strategies. Which strategy the group may be able to use can be selected during the setup of each run. They may gain the ability to collect plants as gatherers or acquire meat by catching small animals or hunting one of several mobile entities that symbolize herds of larger animals. Foraging agents are either gatherer or hunter and perform the linked foraging strategy throughout the complete run. The gathering process is straightforward; the gathering agents search for plants by leaving their base camp and moving in a random direction (Reschke et al., 2023). When the gathering agents find a cell with plants, they can gather all the resources they can carry, up to 5 kg within one hour. The process of acquiring meat is newly implemented into the model and permits the hunting agents to detect animals within the area they can travel to and back within one day and move directly towards them while foraging (20 kilometers). The hunting agents decide which cell to exploit bevor leaving the camp by choosing the cell with the highest amount of energy available from the prey species in relation to the distance from the camp. As they need to be back at the base each evening, therefore they also consider the expected duration of each potential hunting trip and only chose between those options they can finish in time.

Upon reaching the animal's location, they can initiate a hunting or catching attempt. The outcome of each encounter is determined by an ability check; the hunting agent creates a random number between 0 and 100 and if it is below a difficulty threshold set by both the employed strategy and the size of the prey the hunt is successful, and a single individual of the herd is killed. The chance of a successful hunting attempt depends on the used strategy and the size of the targeted prey. If they catch smaller animals, they can carry up to 5 kg of meat back to the camp, while if they hunt larger animals, they can carry large pieces of meat back weighting up to 45 kg as they either carry

complete smaller animals back alone or together with other hunters (Lupo, 2006) or prepare large pieces of meat for transport (O'Connell et al., 1988). While recent hunter-gatherers carry these large amounts of meat, for smaller early hominins like *H. erectus* this would be a heavy burden (Kramer, 2004), therefore our results are more closely to recent hunter-gatherer behavior. After acquiring resources, the foraging agents return to the camp to convert them into food. They consume as much food as necessary to meet their daily energy requirements and store any surplus amount at the camp. The stored food is available to other foraging agents, at least for the rest of the day, but potentially for longer if the group has means to preserve it. If a foraging agent cannot find sufficient resources during the day and there is no stored food available, it alerts the group to begin searching for a new camp location. The group will search for a location which is twice the distance of longest distance of a logistical trip away from the old location to ensure the new surroundings does not overlap with the old, exploited area (Binford, 1980). If possible, they move close to a source of meat they can exploit.

2.1. Environment

The environment consists of a grid of 100 ×100 cells. Each cell symbolizes 1 square kilometer of a simulated environment, offering various resources for the foraging agents to utilize. The environment features three types of habitats: open grassland, wooded grassland and a procedurally generated river system. This river system starts at a randomly chosen location at the top middle of the map and the process was coded to create different river courses each run with several river branches while preventing the emergence of large accumulations of water. During the model's setup, each cell is assigned a specific amount of easily harvested plant biomass. In the wooded habitat the available plant mass fluctuates monthly as it is based on precipitation data, representing new growth of seasonally available resources. Open grassland provides edible plant mass for gatherers throughout the year, depending on the scenario's annual average precipitation. The model introduces minor variations between the cells from this average value for the plant mass by adjusting the plant biomass quantity up to +/-10 % at the beginning of the model run at cells. A cell never changes its assigned habitat even though environments clearly change over time, for example river courses may change throughout a year. These three distinct habitats are favored by specific herbivore species based on their dietary preferences. Each herbivore herd will only roam within their preferred habitat. The model operates with one tick representing an hour of activity. After 12 ticks corresponding to 12 hours, a day ends and after 30 days, a new month begins. Following 12 months, either a new year starts, or the model stops.

2.2. Prey

Prey species range from populations of small animals such as birds or small mammals, to herds of large herbivores with up to two hundred members. Characteristics of each prey species are stored as a cell variable, facilitating easy interaction for hunting agents. The species occurring in our experiments are shown in Table 1. Each herbivore herd consists of several members which are targeted individually during hunting attempts. While being a cell variable these species still move around the landscape as dynamic patch properties. The diet of each species dictates their preferred habitat: grazers favor open grasslands, while browsers inhabit wooded areas. Mixed feeders have the freedom to move between both habitats, and certain species, requiring water proximity, only move within the river system. At the start of a run, the herbivore herds are randomly distributed across the landscape within their preferred habitats. All herbivore herds move once every week between one and four kilometers in any direction towards a cell with their preferred habitat. The remaining time, populations remain stationary at one location. This movement behavior is kept simple on purpose as the main purpose of the model is to study the effect of hunting strategies, therefore the most important aspect of the prey is their size and how it affects the hunting success rate.

The interaction between hunting agents and various species depends on their body mass. Small animals exist as stationary populations that can be captured by hunting agents using a process with a 95 % success rate that yields up to 5 kg of meat as the hunter can only carry one or several small animals back to the camp (Hilton and Greaves, 2004). Larger prey species are represented as herbivore herds within the model, falling into the medium (20 to < 200 kg), large (200 to < 1000 kg), or megafauna (> 1000 kg) size categories. Hunting larger herbivores presents more challenges, and the meat procurement strategy employed determines the duration of the hunting encounter and whether other hunting agents can participate. A hunted herbivore provides a certain amount of meat which is based on the average weight of the species from which 45 % are edible (O'Connell et al., 1988). After a successful hunt all participating hunting agents gain equal access to the meat and carry it back to the camp. When targeting small species, each hunting agent can capture several individuals within an hour. Larger herbivores provide an abundance of meat that multiple hunting agents can each carry up to 45 kg to the camp. Herbivore herds maintain a count of their members. Once the last member has been successfully hunted, the herd vanishes until the onset of a new annual interval. If the model spans multiple years, all herbivore herds are replenished and redistributed across the map at the start of each year.

Table 1
Species list: Overview of larger herbivores occurring near Lake Eyasi and the Serengeti.

Species	Weight (kg)	Herd size	Ind/km²		Habitat
			Lake Eyasi	Serengeti	
Eudorcas thomsonii	20	200	1.17	12.60	open
Aepyceros melampus	42	50	0.74	2.62	open & wooded
Nanger granti	50	20	0	0.92	open & wooded
Redunca redunca	50	10	0.10	1.05	open
Ammelaphus imberbis	80	10	0.07	0	wooded
Struthio camelus	110	20	0.10	0.20	open
Damaliscus lunatus	130	10	0	1.55	open
Alcelaphus buselaphus	150	30	0.16	0.41	open
Connochaetes taurinus	210	200	0.45	33.97	open
Equus quagga	280	15	1.05	0	open
Syncerus caffer	625	30	0.23	0.79	riparian
Taurotragus oryx	750	25	0.15	0.43	wooded
Giraffa camelopardalis	1000	10	0.25	0.32	wooded
Hippopotamus amphibius	1400	30	0.03	1.35	riparian
Loxodonta africana	4500	10	0.16	0.10	open & wooded

2.3. Creating a tropical grassland environment

Tropical grasslands are characterized by high net primary productivity and support a large variety of animals (Mishra and Young, 2020). They also provide an abundance of underground storage organs (USOs) throughout the year and several species of edible fruits during the wet season for hominins to gather (Marean, 1997; Murray et al., 2001; Marlowe and Berbesque, 2009). To represent the high density of USOs 75 % of all cells belong to the open grassland habitat which provides a consistent amount of edible plants all year round. 25 % of the cells belong to the wooded grassland habitat and offer fruits based on seasonal precipitation data, resulting in an abundance of fruits during the wet season and less during the dry season. The river system covers 5 % of the environment and is generated after the two main terrestrial biomes have been distributed. Therefore, each run a different amount of the wooded or open habitat is covered by the river system which results in small variations in the exact composition of the habitats.

To simulate the conditions of a moist tropical grassland, we decided to represent the conditions of the Serengeti ecosystem in Tanzania, as it is a well-preserved and extensively studied region dominated by tropical grasslands (Marean, 1997). For calibration purposes, we also replicated the conditions experienced by the Hadza in Tanzania. In our model, we base the seasonality of these two regions on precipitation data from 1970 to 2000 obtained from WorldClim (Fick and Hijmans, 2017). The average precipitation in the Lake Eyasi region is around 550 mm per year compared to 1000 mm per year in the Serengeti. This average value directly influences the quantity of aseasonal plants (Fig. 1). The most significant difference between these two regions is the extensive dry period experienced by the Hadza, which does not occur in the Serengeti.

We gathered data from literature on all social species weighing over 20 kg, including their weight, average herd size, and population density in both regions (Table 1 based on Nowak, 1999; Kanga et al., 2011; Strauss et al., 2015; Santini et al., 2018). From their overall population density only 10 % are accessible by the hunters at any given point, the remaining animals cannot be hunted due to environmental factors like dense inaccessible environment or very open conditions which offer no hunting opportunities. The accessibility does not change the number of members within the herd herbivores but results in a reduced number of overall herds to keep the number of herds as low as possible to reduce computational load while still maintaining the same overall species composition. Both regions are home to a diverse spectrum of species weighing less than 20 kg which occur in high densities (Timbuka and Kabigumila, 2009; Santini et al., 2018; Mwakalebe, 2019). Consequently, there are 250 small animal populations randomly distributed throughout the environments which each provide up to 3000 kg of meat.

2.4. Foraging Agents

The foraging group in the model consists of two main types of agents. The first, known as the camp agent, symbolizes the existing base structure of the group and their designated night-time location. It also acts as the group's collective will, determining the group's next destination during a residential move. Each run has only one group, which consists of one group agent and several foraging agents, moving in the environment. This second type of agent represents individual adult foragers. They acquire resources from the area surrounding the camp to meet their daily energy needs by travelling up to 4 cells per hour, equivalent to 4 kilometers fitting the average movement speed of a foraging Hadza women (Peter, 2008). All acquired resources are first transported back to the camp, then processed into food and afterwards consumed. There are two distinct categories of foraging agents, each interacting differently with their environment. Gathering agents exploit plant resources using the 'opportunistic foraging' strategy as outlined in the Foregatherer Model (Reschke et al., 2023), which means that they depart in an arbitrary direction and start gathering until they have reached maximum carrying capacity. In contrast, hunting agents use a newly implemented 'targeted foraging' strategy to target the various animals within the environment. During the setup of a run the proportion of these two strategies can be changed to create different scenarios that vary in the significance of hunting within the subsistence strategy.

The hunting agents use a strategy involving extensive cooperation between all hunters by sharing information about the presence of potential prey after returning to the base camp with all present hunters. When a new camp is established, the hunting agents evaluate the area they can travel to and back within one day (20 km) by assigning a foraging value to each cell containing animals. This value is calculated by dividing the body mass of the present species by the distance to the base. However, a variable error rate during this initial assessment can result in some cells being inaccurately rated. The ability to know the location of all the herbivore herds surrounding the camp can be attributed to accumulated knowledge of the hunters about the movement of the different herds over long periods of time and passive perception of potential prey by all members of the group during daily activities outside of the camp (Lovis and Whallon, 2016). Before leaving the camp to start a hunting trip, hunting agents select a cell based on their knowledge of the environment. Upon returning to the camp after having potentially killed a member of the herd, they inform all other hunting agents about the new state of the cell. This allows the hunting agents to stepwise correct their knowledge about the surrounding and monitor both animal movements and ongoing exploitation. A hunting encounter starts when the hunting agents reaches the cell with their chosen prey. The outcome of each encounter is determined by an ability check; the hunting agent creates a random number between 0 and 100 and if it is below a difficulty threshold set by both the meat procurement strategies employed and the size of the prey the hunt is successful. If a hunting attempt fails, the hunting agent must return to camp empty-handed but can still assist other hunters if an opportunity arises while moving back to camp.

Certain hunting strategies permit nearby hunting agents to participate in a hunting encounter initiated by another hunting agent as a collaborator which enhances the likelihood of success and in the case of
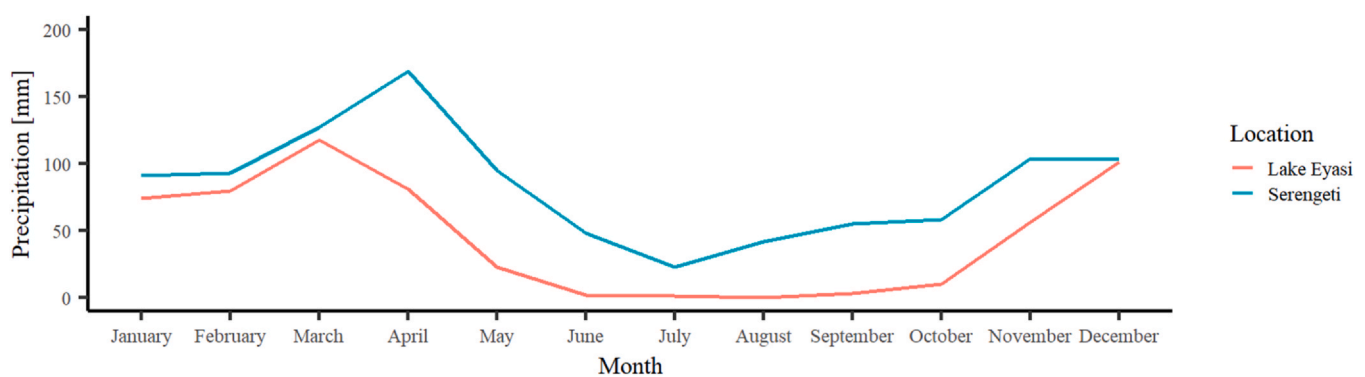

Fig. 1. Precipitation Comparison: Monthly precipitation of the Serengeti and Lake Eyasi from 1970 to 2000 taken from WorldClim (Fick and Hijmans, 2017).

the tactical hunting strategy the time to prepare the trap. Only three strategies facilitate the inclusion of other hunting agents, as they are based on tactics commonly employed in groups by recent hunter-gatherer, while the remaining strategies are specifically designed to be performed by a single individual. Other hunting agents can join a hunting attempt if they are within a 4-kilometer radius, enabling them to reach the hunting site within a maximum walking time of one hour as they could have interacted with one another during the current hour/tick. If two or more hunting agents participate in the hunt, the group receives two additional opportunities to pass the ability check required for a successful hunt. With six or more members, the group overall has four chances to succeed. The tactical hunting strategy requires the hunters to first prepare a trap. Based on data from recent hunter-gatherer, four hunter need 8 hours for the preparation, if more hunters participate in the preparation, they only need 4 hours (Lupo and Schmitt, 2023). A once established trap is usable by other hunters for one week which reduces the duration of a hunting attempt to two hours. Following a successful hunt, all participants gain access to the carcass and can collect meat to bring back to camp. The butchering process is currently considered part of the overall hunting duration rather than being treated as a separate process, which overlooks the time required to butcher larger animals (Lupo and Schmitt, 2016). Afterwards, the carcass becomes inaccessible as hunters can only interact with the carcass during the first hour after the kill.

2.5. Hunting Strategies

How the hunting agents acquire meat depends on their known strategies. We have compiled a variety of strategies which may have been employed by hominin foragers in terms of access to tools and their abilities but there is a lack of archaeological evidence for the usage of any of those strategies apart from scavenging by early hominins before the middle Paleolithic (Table 2). The strategies currently included were selected specifically because they do not depend on any form of assistance or tool which early hominins would certainly not have had access to. These five distinct strategies vary in terms of the hunter's level of engagement with their prey, the necessity for certain tools, the duration of the hunt (tracking and pursuing the prey), and whether other hunters can participate to aid.

The first meat procurement strategy is catching, which is implemented as a very broad process which allows hunters to target the populations of smaller animals (> 20 kg) distributed across the environment. Compared to larger animals, these smaller animals are often defenseless and rather immobile (Janssen and Hill, 2014). Recent Hunter-gatherer mostly catch prey with a weight below 5 kg with an average catching attempt having a pursuit time of just several minutes (Lupo and Schmitt, 2016). In our model a hunting agent therefore spends one hour performing several catching attempts which are summarized in one attempt with a 95 % success rate.

The scavenging strategy has the hunting agents either searching for recently deceased animals or waiting near herds for a predator species

to kill an herbivore (Domínguez-Rodrigo, 2002). This strategy relies on encountering a fresh carcass; therefore, the hunters spend 4 hours searching or waiting at the prey's location. Compared with the other strategies it has a lower success rate as the hunters do not actively pursue their prey themselves. The characteristics of persistent hunting have been taken from "Persistence Hunting by Modern Hunter-Gatherers" by Liebenberg, 2006, who described this hunting strategies based on observations from recent hunter-gatherers. Most of his observations come from hunters of the Kalahari San in the Kalahari Desert (Liebenberg, 2006). The persistent hunting strategy requires the hunter to chase an individual until it is exhausted and can be killed. This activity takes 4 hours to complete due to the required chase.

Intercept hunting is based on observations from recent hunter-gatherers where they wait for prey behind blinds and shoot poisoned arrows (Hawkes et al., 1991). As our hominin foragers certainly had no access to ranged weapons like bows, this strategy instead has a single hunter hiding and waiting to kill passing prey with a thrusting spear, a strategy which may have allowed a single early hominin to kill larger herbivores (Agam and Barkai, 2018). When using this strategy, a hunting agent waits two hours for prey to come close enough to be killed. The encounter hunting strategy can be observed in several hunter-gatherer societies and is the most used hunting strategy of recent hunter-gatherers and has one or several hunters actively pursue their prey (Hawkes et al., 1991, Janssen and Hill, 2014). At last, our tactical hunting strategy is based on observations of several hunter-gatherer societies in grasslands (Marean, 1997) and has hunters use the environment to set up traps that either kill their prey or make it easier for them to kill it (Agam and Barkai, 2018, Lupo and Schmitt, 2023).

The hunting strategies differ in their efficiency depending on the targeted prey sizes as some strategies like persistent hunting, may be relatively effective when targeting medium-sized prey, but should have a lower success rate when targeting larger animals like elephants. Therefore, the model offers the option to give each combination of meat procurement strategy and targeted prey size an individual success rate. The values that determine the success rate is in some cases based on recent hunter-gatherer data. The persistence hunting of medium sized prey and using the encounter strategy to hunt different sized prey has been observed (Liebenberg, 2006; Lupo and Schmitt, 2016). The values for the other strategies or certain prey sizes are approximations but due to a lack of data we decided to have the success rate of different hunting strategies only vary based on prey size, decreasing when hunting larger herbivores as observed in recent hunter-gatherers (Lupo and Schmitt, 2016).

2.6. Observed responses

The model calculates several output values to evaluate the impact of different input settings on the hunter-gatherer group on both an individual and group level. The resulting mobility pattern is describes using responses which have previously been used in the ForeGatherer Model (Reschke et al., 2023) and are based on studies of recent hunter-

Table 2
Overview Hunting Strategies: Summary of the implemented hunting strategies and their model related properties.

Strategy	Description	Preferred Target	Duration [hour]	Cooperation?	Source
Scavenging	search for recently deceased animals and fight of other scavengers	medium, large	4	Yes	Domínguez-Rodrigo, (2002)
Persistent	chasing an animal until it is totally exhausted and easy to kill	medium	4	No	Liebenberg, (2006)
Intercept	prepared ambush by hiding in the vegetation and waiting for prey	large, megaherbivore	2	No	Hawkes et al., (1991); Agam and Barkai, (2018)
Encounter	active pursuit of prey with open confrontation	medium, large	1	Yes	Hawkes et al., (1991); Janssen and Hill, (2014),
Tactical	prepared trap by augmenting the environment or using existing natural traps	large, megaherbivore	8	Yes	Agam and Barkai, (2018); Lupo and Schmitt, (2023)

gatherer societies. At an individual level, the model calculates the average yield per hour spent foraging by all hunting agents. The observed length of a hunting trip includes the time spent moving to the potential prey, tracking the prey, the hunting attempt, and the process of carrying the meat back to camp. The foraging success of each individual influences the group's movement; a lower foraging success necessitates more frequent movement. Subsequently, we can use the number of residential moves to estimate the group's efficiency in exploiting the given environment. A low residential mobility is desired by hunter-gatherer as it requires time and energy to move to a new location which cannot be used to perform any other tasks, therefore in a given environment a hunter-gatherer group will try to minimize the number of residential moves they have to perform (Hamilton et al., 2016).

When the model has hunting agents, the model also calculates the diet composition of the overall group differentiating between the size categories.

2.7. Calibration

Most parameters in the model utilize values from existing literature, except for the available plant mass. This value is based on precipitation data and a 'precipitation-converter'. We used the environmental conditions of Lake Eyasi and the subsistence behavior of the Hadza living in this region to establish a suitable correlation between precipitation and available plant mass. In our recent hunter-gatherer scenario, which is based on the Hadza, the hunting agents primarily target medium- and large-sized animals through encounter hunting (Hawkes et al., 1991). Their diet consists to 35 % of meat while 65 % of the consumed resources are plants (Kelly, 1983). After conducting a series of tests, we determined that with a precipitation-converter value of 0.2, our modeled foraging group moves an average of 5.7 times per year over a distance of 19 kilometers. This compares to the Hadza's average of 6.5 residential moves and an average distance of 12 km (Kelly, 2013), indicating that our model group moves similarly in frequency but covers greater distances.

In the current version of the model, the group's movement is equally driven by the hunting agents who prompt the group to move to areas with available prey and the gathering agents after they exploited all edible plants in the surrounding. We chose to use the same value for experiments conducted in the Serengeti as a lower 'precipitation-

converter' would result in more frequent group movements due to gathering agents not finding enough plants during dry seasons. In contrast to the Lake Eyasi region the Serengeti has an overall higher precipitation i.e. more available plant mass and lacks a distinct dry period (Fig. 1), as a result in all following experiments all residential moves are caused by the hunting agents, while the gathering agents never completely exhaust the surrounding before the hunters cannot find any more prey to target.

2.8. Initialization and experiments

For each experiment, we performed 100 runs with the same input settings to account for variations in the environmental setup over a period of 4320 ticks (12 ticks per day for 360 days). We determined the necessary number of runs for a statistically robust result by comparing the variance from an increasing number of individual runs until it did not deviate from the average by more than 5 % (Hoad et al., 2010; Lorig, 2018).

Each experiment represents a certain subsistence scenario which has been proposed to be used by hunter-gatherers in tropical grassland. Except for the first scenario, in which the hunting agents only target small animals, the group always uses one specific strategy to target two different size categories of prey. The name in the experiment always indicates the largest targeted prey size of the scenario (Table 4).

3. Results

3.1. Yield per hour of hunting

Fig. 2 shows the average yield in kilocalories per hour spent hunting across our six subsistence scenarios. In the 'catching-small' scenario in which foragers do not hunt any larger herbivores the hunting agents forage with an average return of approximately 1000 kcal/hour (Fig. 2). If the group hunts medium and large sized herbivores, the yield per hour increases. In the 'scavenging-large' and 'persistent-large' scenarios they have an average yield of 2300 kcal (Fig. 2). The 'encounter-large' scenario has the highest overall yield at 4300 kcal/hour (Fig. 2). In the two scenarios where megaherbivores are targeted, the 'intercept-mega' scenario results in an average yield of 3100 kcal per hour, while the 'tactical-mega' scenario has an average yield of 2800 kcal/hour (Fig. 2).
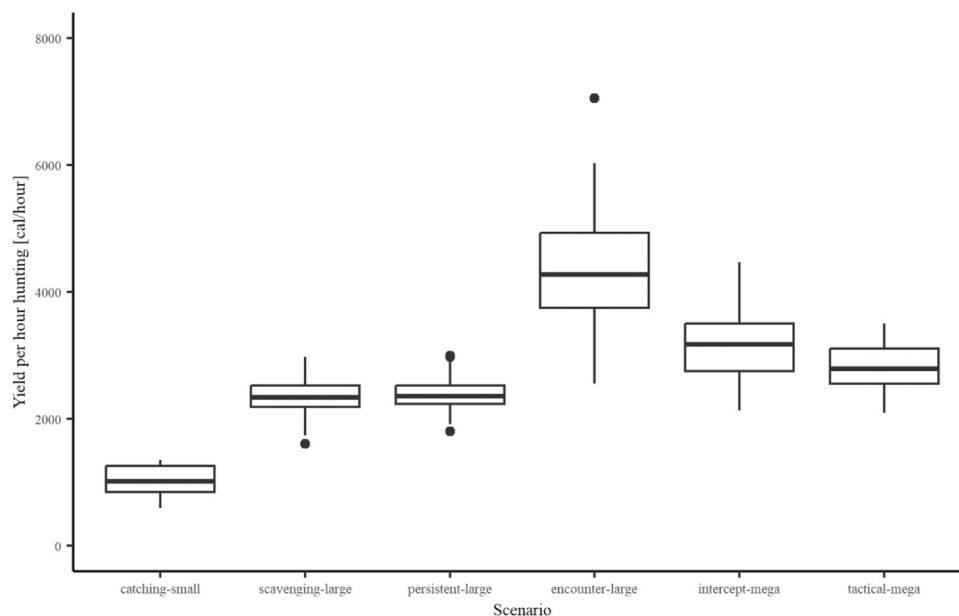

Fig. 2. Average Yield: Effect of the subsistence scenarios on the average yield in cal/hour of the hunters.
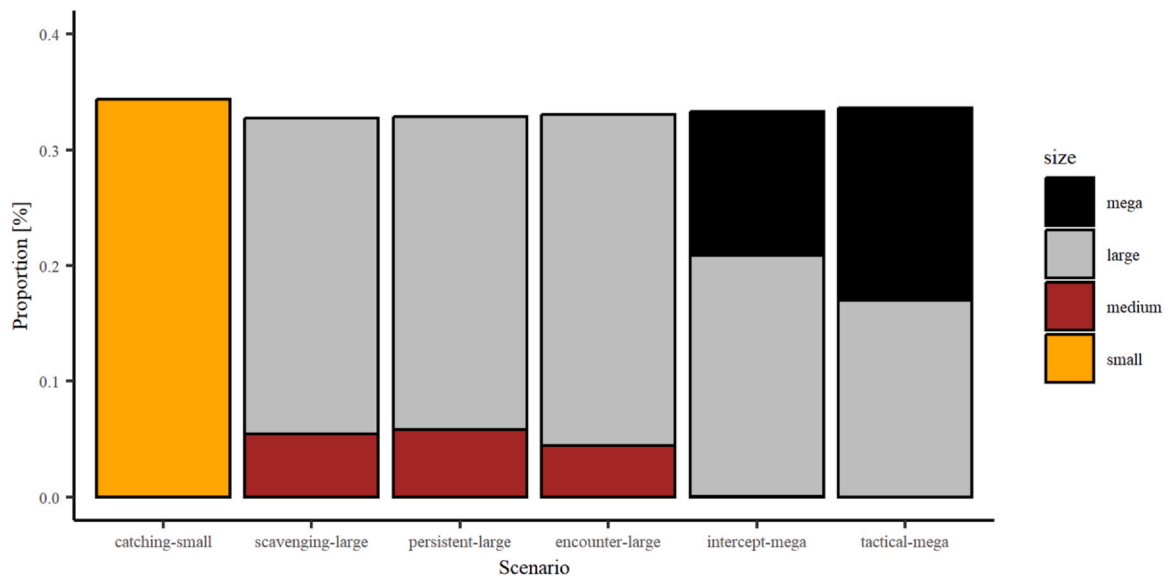
Fig. 3. Diet: Effect of the subsistence scenarios on the proportion of different prey size categories in the diet.

3.2. Diet composition

Fig. 3 illustrates the percentage of meat consumption from each size category. In the 'catching-small' scenario, hunters exclusively target and consume small animals. However, in all other scenarios the majority of their diet consists of large herbivore meat. If they can target medium sized prey the consumption fluctuates between 3 % and 5 %, with the lowest percentage found in the 'encounter-large' scenario (Fig. 3). In all scenarios the group diet consists bewtween 32 % and 34 % of meat (Fig. 3). When megaherbivores are accessible, hunters regularly target them. Consequently, in the 'intercept-mega' and the 'tactical-mega' scenario, their diet is largely composed of both megaherbivores and large animals (Fig. 3). In all scenarios where hunters have the option to target animals larger than small ones, they consume only minimal amounts of small animals (Fig. 3).

3.3. Residential moves per year

The hunting strategies employed in tested subsistence scenarios have an impact on the group's mobility pattern. The number of residential moves was used to calibrate the amount of available plants (2.7 Calibration), these results should therefore used with caution. Fig. 4 illustrates the correlation between our six subsistence scenarios and the yearly number of residential moves. The group moves least frequently in the 'catching-small' scenario (Fig. 4). In contrast, the 'scavenging-large', 'persistent-large', and 'encounter-large' scenarios have an overall higher number of residential moves but we see a decrease in the number of residential moves when comparing the three scenarios (Fig. 4). The group moves approximately ten times in the 'persistent-large' scenario, while in the 'encounter-large' scenario, they move on average five times per year (Fig. 4). The 'scavenging-large'
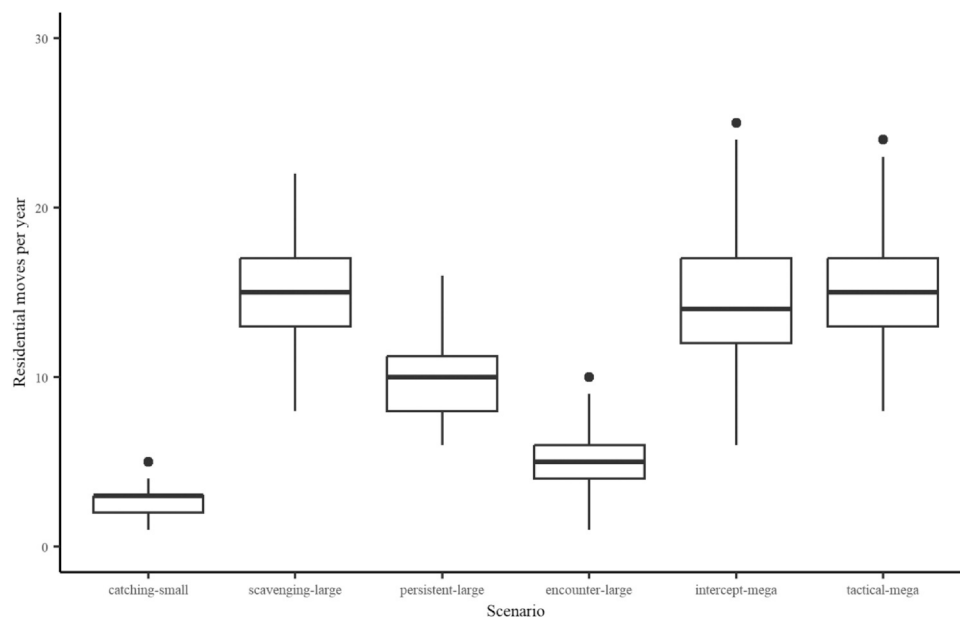

Fig. 4. Residential moves: Effect of the subsistence scenarios on the number of residential moves per year.

together with the two scenarios which has the group target mega-herbivores exhibit the highest mobility, with over fifteen moves per year (Fig. 4).

3.4. Distance covered per residential move

The subsistence scenarios have a small effect on the average distance moved during a residential move. In all scenarios they move on average around ten kilometers per residential move (Fig. 5). In the 'encounter-large' scenario the group move slightly longer distances (Fig. 6).

4. Discussion

4.1. Foraging success and subsistence strategies

In our experiments we tested five different subsistence strategies which have been developed based on proposed subsistence strategies of hominin foragers (Table 2). The subsistence scenarios differ in the targeted prey size and the used hunting strategies. The results of the different scenarios should be mostly compared with one another as they are based on a wide array of different parameters with varying levels of confidence in the chosen values.

If we assume that early hominins already consumed small animals as part of their diet before targeting larger animals, our catching scenario ('catching-small') can be considered the oldest subsistence scenario performed by early hominins (Thompson et al., 2019). According to our findings, a group can meet the targeted 35 % of their daily energy demand by catching small animals while moving less than three times per year in the modelled environment. In our model a group which solely relies on catching small animals exhibits an even lower residential mobility then the encounter scenario which is the scenario most closely to the behavior of recent hunter-gatherer societies living in similar environments and which has been used to calibrate the model. For instance, groups like the Hadza (6–7 residential moves), the !Kung (6 residential moves), or the Wikmunkan (14 residential moves) move a comparable number of times per year (Kelly, 1983; Binford, 2001; Kelly, 2013) to the encounter scenario (5 residential moves). Therefore, not targeting larger animals and focusing on small animals can be considered a viable strategy for the group in our model (Fig. 4).

In scenarios in which the hunting agents target medium- and large-sized herbivores, their behavior changes with them increasing their average yield (Fig. 2) as they can bring back much larger portions of meat to the camp. However, both scavenging and persistent hunting strategies result in relatively low average yields compared to other strategies (Fig. 2). The low yield from scavenging in our model is due to the long duration (4 hours) and the comparable low success rate. Research on hunter-gatherers has shown that although scavenging opportunities can be easily detected by watching out for avian predators, these opportunities occur infrequently (Hawkes et al., 2018). As a result, the group fails to achieve the desired 35 % diet proportion (Fig. 3) and must move the camp around fifteen times per year (Fig. 4). The persistent hunting scenario appears more viable than scavenging, although the average yields are quite similar (Fig. 2), as the higher success rate enables the hunters to acquire meat more reliable, as indicated by the lower residential mobility (Fig. 4). However, unlike scavenging, persistent hunting does not permit cooperation among our hunting agents. If the hunting agents have access to the encounter hunting strategy, which combines a high success rate, short duration, and the possibility of others participating, the average yield further increases while reducing the number of residential moves (Fig. 4).

For a group to meet their dietary goals and maintain a low residential mobility while targeting medium- and large-sized animals, they must have access to hunting strategies with a short duration, have a high success rate, or enable other hunting agents to participate. When hominins began to target larger animals, it has been proposed that they started scavenging and/or hunting. The very first hunting strategy may have been persistent hunting (Liebenberg, 2006), but alternatives like intercept hunting have also been proposed (Agam and Barkai, 2018). The two hunting strategies and scavenging are complex to execute, require knowledge, planning, and communication. The proportion in which they have been used likely varied based on environmental factors (Swedell and Plummer, 2019). However, compared to other hunting methods, they can be successfully executed without the need for sophisticated tools or weapons (Pobiner, 2020). Our model suggests that targeting larger herbivores can be viable even when only hunting strategies which take long to perform (duration) are available, provided the success rate is high enough or the strategy permits cooperation among several hunters (Janssen and Hill, 2014).

Recent hunter-gatherers in tropical grasslands primarily engage in encounter hunting (O'Connell et al., 1988), a strategy that fulfills all three requirements previously outlined (Table 2). These hunter-gatherers often employ specialized tools for this method of hunting. For
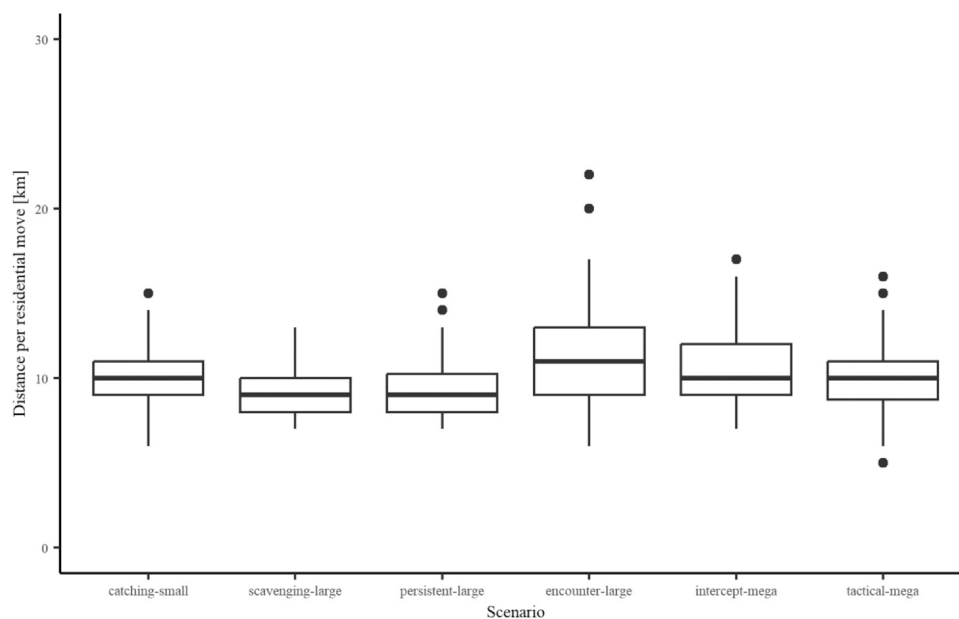

Fig. 5. Residential distance: Effect of the subsistence scenarios on the average distance the group travels per residential move.

instance, the Hadza use bows and frequently poisoned arrows during their encounter hunts (O'Connell *et al.,* 1988). Early hominins for a long time did not have access to any form of tool which allowed long-range hunting (Churchill and Rhodes, 2009). They might have used heavy wooden spears as thrusting weapons which compared to throwing spears are easier to produce (Haidle, 2009) and this usage of thrusting spears has been observed in chimpanzees (Pruetz and Bertolani, 2007). If it is possible to perform encounter hunting with a weapon which cannot be used from a distance, is challenging to assess since its use in encounter hunts has never been documented among recent hunter-gatherers (Milks, 2020). Still, our model demonstrates how a group can thrive in a tropical grassland environment without access to long-range weapons by using persistent hunting. The potential subsequent development of tools enabling them to execute the encounter strategy would expedite meat acquisition, aiding in obtaining the desired quantity of meat (Fig. 2). In conclusion, transitioning away from consuming only smaller animals can be feasible, but it necessitates groups moving more frequently to get closer to the various mobile herds they aim to exploit.

In our two final scenarios the hunting agents target megaherbivores using two different strategies: Intercept hunting, which in the model takes two hours to perform and does not allow cooperative behavior, and tactical hunting which requires the hunters to prepare a trap but also allows other hunting agents to participate in both the preparation and the hunting attempt (Table 2). A comparison of these strategies reveals that tactical hunting ('tactical-mega' scenario) results in a slightly lower average yields compared to when the hunters use intercept hunting (Fig. 3). In term of average yield per hour the two scenarios fall in between the scenarios with the highest average yield ('encounter-large' scenario) and the two other scenarios which have the hunters target large herbivores (Fig. 3). In both scenarios, the group primarily consumes large herbivores and fewer megaherbivores (12 % 'intercept-mega' and 16 % 'tactical-mega' (Fig. 4). Both strategies have the group move relatively often with also a high variance in the number of residential moves per year (Fig. 4).

Our results suggest that the option to cooperate increases the likelihood of a meat procurement strategy being viable as it results in an increased success rate and subsequently a higher average yield (Fig. 3). But cooperative behavior alone does not guarantee success and has its limitations which becomes evident when comparing the results of our two subsistence scenarios in which the hunter target megaherbivores. The option to cooperate when using the tactical hunting strategy results in a very similar average yield (Fig. 3) and mobility (Fig. 4) when compared to the 'intercept-mega' scenario. Our results show how targeting megaherbivores does result in a higher average yield compared to most other hunting strategies but overall seems not to be a viable strategy in our model as it still results in a high number of residential moves. While tactical hunting is one the proposed strategy early hominins had the ability to use relatively early (Plummer, 2004) as compared to other strategies it is believed to require less sophisticated tools and benefits from several members cooperating (Milks, 2020). Our findings suggest that in regions with large herbivore populations, hunter-gatherers may not need to resort to strategies which take longer to perform (duration) like tactical hunting if there is an abundance of edible plants and resident animals (Marean, 1997). There are some instances of recent hunter-gatherers hunting megaherbivores in tropical grassland environments. However, these activities typically required numerous participants or the construction of highly labour-intensive traps (Lupo and Schmitt, 2016, Lupo and Schmitt, 2023). Hunter-gatherers primarily use tactical hunting in regions where large numbers of animals gather for migration during specific seasons, which allows them to kill multiple individuals at once (Marean, 1997).

4.2. Prey selection

While the characteristics of the available meat procurement strategy has a big impact on the success of the hunters, the chosen species

targeted during each hunting attempt also plays an important role. Recent hunter-gatherers consider a wide range of changing factors before each hunting attempt, on the most basic level they try to avoid species which become too dangerous when provoked, are overall difficult to kill, or simply too hard to locate and track within their preferred habitats (Lupo and Schmitt, 2016). While it is more dangerous and riskier to hunt large animals, they also provide high return rates after a successful hunt. Therefore, they are often seen as the preferred prey for recent hunter-gatherers and subsequently early hominins (Broughton et al., 2011). One theory proposes that big game hunting was a key driver in the rise of social complexity and central place foraging as it would have promoted the increased sharing of resource and the emergence of joint provisioning of offspring (Isaac, 1978; Hawkes et al., 2018).

The advantage of selecting prey based on body size is debatable, as hunting larger and more mobile prey often involves higher opportunity costs due to extended pursuits and a high likelihood of failure (Lupo and Schmitt, 2016). Recent hunters appear not to target megaherbivores solely for their own meat consumption or to acquire food for other members of the group. Instead, several factors seem to influence their choice of prey, they use hunting as a show-off strategy to attract mates and as a form of participating in the social network of sharing and trading (Plummer, 2004; Swedell and Plummer, 2019). It is difficult to estimate the impact of social factors on the prey selection of hominin foragers and how they may have differed from recent hunter-gatherer societies. The abundance of megaherbivore remains in the archaeological record shows that like giraffids and hippopotamids were already exploited 1.8 million years ago (Ungar, 2006; Sahnouni et al., 2013; Domínguez-Rodrigo et al., 2014) and it has been proposed that at least during periods like the Late Pleistocene, these species were hunted more frequently than recent hunter-gatherer societies target megaherbivores (Haynes and Klimowicz, 2015). However, whether early hominins developed a widespread "big game specialization" requires further investigation (Lupo and Schmitt, 2016).

Given the prevalence of large-game hunting in existing literature, our hunting agents primarily want to target the largest prey in their vicinity (Lupo and Schmitt, 2016). They consider both the distance to the prey and the overall available energy of the herd. The available energy is highest in herds of larger animals even though herds of smaller animals may have much more members. This allows them to find the herds with both large animals but also high numbers. If a herd of larger herbivores has already lost several members, other herds with smaller animals may become more viable to target. While they occasionally target smaller species if they are close by, their primary focus is consistently on the largest accessible prey (Fig. 3). When discussing the development of a more elaborated process of prey selection in our model several options are viable. One parameter which certainly should be implemented in a future version of the model is the anticipated success rate. The hunting agents would evaluate the foraging value of a cell with prey by using the distance, the body mass of the prey species and the success rate. This would decrease the foraging value of large species as they have lower success rate while increasing the likelihood that hunters chose to hunt one of the smaller species due to the higher chance of success.

4.3. Review hunting strategies

At what point in time early hominins started to increasingly consume meat and which method they used remain topics of debate. As chimpanzees and other apes hunt smaller animals like arboreal monkeys, it can be assumed that already our last common ancestors may have begun to add meat into their diet (Pobiner, 2020). The earliest evidence for the potential butchering of medium and large sized animal dates to 2.6 million years (Domínguez-Rodrigo et al., 2005) or possibly even 3.4 million years ago (McPherron et al., 2010). From around 1.8 million years ago, we also find evidence of early hominins interacting

Table 3

Hunting Success rates: Hunting strategies and their success rate depending on the targeted prey size.

Strategy	Medium	Large	Megaherbivore
Active Scavenging	40 %	25 %	10 %
Persistent	80 %	50 %	20 %
	Liebenberg, (2006)		
Intercept	80 %	50 %	20 %
Encounter	80 %	50 %	20 %
	Lupo and Schmitt, (2016)	Lupo and Schmitt, (2016)	Lupo and Schmitt, (2016)
Tactical	80 %	50 %	20 %
			Lupo and Schmitt, (2023)

with the carcasses of megaherbivores like giraffids or hippopotamids (Ungar, 2006). But in all these cases the method on how these hominins gained access is unclear, they may have killed them themselves or scavenged the remains left by other predatory species. Consequently, we examined various strategies that hominin foragers might have employed to access herbivores of all sizes, either through hunting or scavenging.

All implemented hunting strategies are based upon recent hunter-gatherer societies which previously have been used as reference models for early hominin behavior in earlier studies (Grove, 2009; Samson et al., 2017; Hawkes et al., 2018). They are used to create behavioral reconstructions as it is assumed that these societies still use techniques and strategies which are not unlike the methods early hominins used (Porter and Marlowe, 2007). However, it is crucial to note that the use of recent hunter-gatherer societies as reference models has been a subject of debate for years (Gould and Watson,1982; Wylie, 1985; Stahl, 1993; Currie, 2016). It is difficult to assess how accurately behaviors observed in these societies can represent those of the different early hominin species (French, 2018) and the authenticity of their behavior itself is questionable since all studied groups consumed at least some domesticated food by the 1990s, which indicates changes in their behavior (Crittenden and Schnorr, 2017). While this uncertainty must be acknowledged, we can still use recent hunter-gatherers as references in models to test the effects of different behavioral patterns as the results can help to identify the common features or differences in behavior within the tested environmental conditions.

Several factors determine if a hunting attempt is successful, this includes the used strategy, the target species, the number of participants, and the environmental context. However, there is no comprehensive data on the success rates for all hunting strategies (Table 3). As such, we have chosen to differentiate our implemented strategies primarily based on how long they take to be performed (duration) time and whether they permit other hunters to participate to increase the success chance. We have implemented the basic trend that an increase in prey size generally results in a lower success rate for the hunting attempt (Lupo and Schmitt, 2016). While some strategies permit for other hunting agents to participate and thus increase the success rates, quantifying the precise impact of cooperation is challenging due to insufficient data in existing literature. The environmental conditions also affect the behavior of hunters, a process which currently is not implemented into the model. For instance, carnivorous species tend to find ambush hunting easier in wooded areas (Bunn and Pickering, 2010), while those hunting in open habitats rely on speed and stamina

to capture their prey (Oliver et al., 2019). In a future version of the model, the environment might impact the success rate and the choice of the strategy. This would enable the model to study how changes in the environmental conditions may influence the behavior of the hunting agents as they would choose their prey depending on the available strategy and how suitable this strategy is to hunt in the habitat the potential prey is located in.

4.4. Using the Serengeti as our reference grassland

We have chosen to use the Serengeti National Park as our primary reference point, given its status as one of the largest and most extensively studied wild areas featuring tropical grassland. The park is expected to provide suitable conditions for larger herbivores and serve as a representation of an undisturbed tropical grassland. However, several factors potentially diminish its value as a reference. Like most parks and reserves in Africa, the Serengeti National Park is too small to fully accommodate the needs of an ecosystem (Myers, 1972). To determine how the Serengeti compares to other tropical grasslands, we assessed the animal density of other national parks dominated by savannah Table 4.

Both the Murchison Falls National Park in Uganda and the Amboseli National Park in Kenya have a lower species density compared to the Serengeti (Table 5). The Serengeti and the Amboseli National Park are similar in that they are both inhabited by large herds of wildebeest (*Connochaetes taurinus*) which make up a large amount of the herbivore biomass. While the overall biomass in the Amboseli National Park is 70 % lower, the proportions of three different size categorizes are similar (Table 1). The situation differs in Murchison Falls where wildebeest are not recorded in the Tetradensity database (Santini et al., 2018) which results in a much lower biomass which is dominated by megaherbivores.

The data shows how the Serengeti is located at the upper end in terms of species density in tropical grasslands and may be the closest representation of an intact tropical grassland available in the present. How close the Serengeti is to Pleistocene tropical grasslands is difficult to assess, Pleistocene tropical grasslands as the Serengeti today have been dominated by Grazers between 100 and 1000 kg but they also sustained a more diverse herbivore composition and more megaherbivores (Owen-Smith, 2013). The higher biodiversity could have increased the stability of the ecosystems which in turn reduces subsistence risk (Tallavaara et al., 2017). When focusing on the aspects related to hunting the Serengeti may be the most intact tropical

Table 4

Overview Experiments: Tested Scenarios based on subsistence strategies potentially performed by early hominins.

Exp. No	Name	Description
1	catching - small	Hunting agents only catch smaller creatures like recent apes
2	scavenging - large	Hunting agents are not being able to hunt themselves instead only relying on scavenging medium and large sized herbivores
3	persistent - large	Hunting agents target medium and large sized herbivores using persistent hunting.
4	encounter - large	Hunting agents target medium and large sized herbivores using encounter hunting based on recent hunter-gatherer data.
5	intercept - mega	Hunting agents target large & megaherbivores by performing ambush hunting.
6	tactical – mega	Hunting agents target large & megaherbivores by preparing traps before the hunt.

Table 5

Comparison Population Density: The biomass per km² was calculated using the individuals per km² from Santin *et al.,* 2018 and the average body mass taken from Nowak, 1999. For the Serengeti several megaherbivores like *Giraffa camelopardalis* and *Hippopotamus amphibius* are missing in the original database.

National park	Area size	Biomass/km²	%Medium	%Large	%Megaherbivore
Serengeti (Tanzania)	15,000 km²	11350 kg	7 %	70 %	23 %
Amboseli (Kenya)	400 km²	3500 kg	3 %	75 %	22 %
Murchinson Falls (Uganda)	4000 km²	1000 kg	16 %	22 %	62 %

grassland of the present but could still be in the lower spectrum in term of species density and diversity when compared to tropical grasslands in the Pleistocene.

4.5. Outlook

Our goal when developing the model was to include all relevant environmental factors of tropical grasslands which influence the behavior of a hunter-gatherer group on a large scale. Essential resources for the survival of a hominin group, such as water and access to lithic raw material sources, are often scarce in grasslands (Marean, 1997). In our model, foraging agents may obtain these resources while searching for food or in the second half of the day after meeting their energy needs. However, incorporating these activities directly into the model would significantly increase its complexity. The procurement of water and raw materials would necessitate the inclusion of lithic sources and additional water sources like waterholes in the model. These locations would be randomly distributed in the environment, influencing the group's behavior as studies show that hunter-gatherer's factor in the location of water when deciding where to set up their next camp (Rashford, 2023). Given that our model is already has many randomly distributed resources like moving animal herds, we decided against adding the acquisition of both water and lithics in this version of the model.

The model's most fundamental environmental aspect is the presence of edible plants, which are represented in a highly simplified manner. Gathering plants is as consistent and reliable strategy to acquire food in contrast to the riskier and more complex hunting but the return is lower compared to the potential yield after a successful hunt. After exploiting all the plants surrounding the camp moving longer distances during gathering trips quickly becomes unviable. Gathering resources is always successful, so acquiring enough per day is solely dependent on the available amount which can be quickly depleted which then requires the group to move to a new location. Determining the available edible plant mass in a specific area is challenging. Metrics such as precipitation data or net primary productivity are used to estimate the total available plant mass, but these values cannot be directly incorporated into the model. The proportion of the total plant mass that a hominin gatherer can access at any given time depends on various factors (Kelly, 1983). We utilize precipitation data to track monthly fluctuations in available plant mass and apply a straightforward conversion factor (termed 'precipitation-converter') to calculate the accessible edible plant mass in kilograms per cell. However, these resulting values are approximations, the process certainly needs further refinement to better reflect fitting environmental conditions. The model includes different habitats representing for example open areas populated with plants that develop underground storage organs, which hunter-gatherers collect during periods of low or no rainfall (Murray et al., 2001). The prevalence of these non-seasonal resources within the model can be adjusted to account for other environmental variables such as temperature.

The second basic and easy to acquire resource are populations of small animals. Catching these small animals has a high chance of being successful but returns smaller amount of meat compared to the yield of a successful hunt of a larger herbivore. Our results show that in our model focusing solely on catching is a viable strategy and has the group staying for long periods at each location (Fig. 4). However, it is important to use this result cautiously as the availability of small animals

in our model is less realistic due to limited data compared to larger animals. In the current version we merge different species of small mammals, birds, reptiles, amphibians, and insects in one generalized category. The model would certainly benefit from a more detailed catching process with the populations differing in size and how the foraging agents interact with them.

Our primary objective when implementing larger herbivores into our model was to use representative data on population density and have a fitting representation concerning their suitability as prey. The movement of these herbivore herds is simplified, with random short-distance movements between cells on a weekly basis. The model is not focused on the aspect of hunters struggling to find fast moving prey but on the efficiency of varying hunting strategies. Still the model could benefit from a more elaborated process which determines how frequent the herbivores move. In tropical grassland herbivores move several kilometers per day depending on species and season (Owen-Smith and Goodall, 2014). Moreover, the large herbivore herds in the model lack a key characteristic: the performance of mass migrations that occur seasonally in grasslands. For instance, wildebeest, zebras, and gazelles in the Serengeti migrate from open grassland to more wooded areas at the onset of the dry season (Fryxell and Sinclair, 1988). These extensive migrations influence various aspects of the ecosystem, including the composition and biodiversity of grasses, trees, animals and impact the local communities (Hopcraft et al., 2014). Such large-scale migrations are well-documented in the Serengeti but also occur in other tropical grasslands like the Boma-Jonglei ecosystem in South Sudan (Fryxell and Sinclair, 1988). Today, the Hadza continue to benefit from these animal migrations that pass through their region but increasing deforestation and livestock grazing have affected their size and routes (Marlowe, 2002). However, our model is designed to represent a downsized yet comprehensive version of a tropical grassland. As such, it seems inconsistent for herbivorous herds to completely leave the model and move out of the grassland.

If we were to establish a different type of grassland, the most critical factor would be the precipitation data potentially obtained from a present-day reference location. This data, in combination with the 'precipitation-converter', would determine the base amount of available plant resources. However, resource availability is not solely determined by precipitation; temperature also plays a significant role (Kelly, 1983). If the region has a lower average temperature compared to the currently modeled tropical grassland, the resource composition would need to change. A lower average temperature results in fewer aseasonal resources (Marean, 1997), which increases the seasonality in the availability of edible plant. This change can be reproduced in the model by reducing the ratio of aseasonal plants. For a group of hunter-gatherers, a more temperate grassland would overall offer fewer edible plants which are also more seasonal in their availability (Marean, 1997).

The population density of herbivores is influenced by several distinct factors. In Africa, for instance, a higher precipitation correlates with a larger population of large mammals (Coe et al., 1976). If we want to study a grassland under drier climatic conditions, we will need to reduce the number of exploitable large mammals in the model. Recreating the presence of animals in more temperate grasslands would likely necessitate new population density estimates which are difficult to acquire. In the present many regions or biomes lack suitable reference areas, like the Serengeti, to determine appropriate herbivore

population densities. Not only do temperate grasslands in general have less wildlife but a higher number of species are very mobile (Fryxell and Sinclair, 1988). Modelling these conditions may not only require a system for large-scale migration but also a more realistic representation of daily movement as already discussed.

The agent behavior still has several aspects which can be further developed in future versions of the model. Currently, foraging agents are driven by a fixed energy demand that they must meet daily, regardless of their activity. In future iterations, different activities such as movement, gathering, or hunting may have varying energy costs. This would result in a change in required energy at the end of the day based on the activity performed. Strategies like intercept hunting would likely benefit from this change, as they involve longer waiting periods. Conversely, other hunting strategies that are faster may require more energy due to increased movement during the hunt.

One of the parameters that differentiates the implemented hunting strategies is duration, which is the time it takes to acquire the resource after encountering it. This parameter, as shown in our experiments, is important because faster hunting strategies have a higher yield per hour (Fig. 2). If we want to use yield per hour to evaluate the viability of a foraging strategy, certain aspects of the model may need to be improved regarding their duration, processing time, and how they change depending on certain conditions. One key aspect missing in the current iteration is the butchering process. Currently, hunters can process their prey within the final hour of the hunting attempt regardless of prey size, despite the fact that processing time is directly related to prey size (Lupo and Schmitt, 2016). Introducing the butchering process would result in a decrease in average yield when targeting larger or megaherbivores, making them less viable as targets compared to smaller prey. Furthermore, transporting large amounts of meat does not affect foraging agents, although carrying resources can be challenging as it slows them down and increases energy consumption, making some resources less viable to target (Kramer, 2004). In the future, resources could differ in how easily they can be carried back to camp and how this may affect energy expenditure and walking speed of foraging agents.

In the current version of the model, the group mostly moves to follow larger herbivores. Our used 'precipitation-converter' and the long dry period in the Lake Eyasi environment results in the group having to move to find plants, while using the same value for our 'precipitation-converter' in the Serengeti they always find enough plants even during the drier months. This is caused by the overall higher precipitation in the Serengeti throughout the year (Fig. 1). In hunter-gatherer groups, the main reason for residential moves is the depletion of nearby plants (Kelly, 1983; Venkataraman et al., 2017). This suggests that hunters are either able to secure enough meat to prevent the group from the necessity to move earlier, or they can use plants gathered by other group members if their own hunting efforts are unsuccessful. The Hadza diet consists of meat by approximately 30–40 % (Kelly, 1983), but these values do not account for seasonal fluctuations throughout the year. The resources consumed vary depending on both season and location; during certain months, meat makes up only 10 % of the Hadza diet (Marlowe and Berbesque, 2009). In the future this flexibility should be implemented into the model. The dry season with its lower availably of plants should force the group to either move more often or increase the amount of consumed meat and vice versa. During the calibration process test with different 'precipitation-converter' values showed that a lower value would result in residential moves caused by missing plants in the serengeti but the same value would result in a much higher residential mobility in the Lake Eyasi setting as acquiring sufficient plants in this environmental setting is already a challenge for the group during the dry season.

While the model currently only records the final dietary proportions, our guidelines for group movement necessitate that the hunting agents secure enough meat on a daily basis. In a future version of the model, we should permit the group to achieve their targeted meat proportion by the end of the month or the year, allowing for fluctuating resource consumption throughout the year. This would require a resource exchange system between hunting and gathering agents, as well as a communication system to coordinate resource acquisition and prevent overexploitation. A more flexible diet setting would permit the group to react to environmental changes like recent hunter-gatherers do. During seasons with an abundance of plants, they would offset any potential meat shortages, while conversely consuming more meat during seasons with fewer available plants. As a reaction to the changes, we have a higher number of members of the group hunting, thereby increasing their chance of achieving the desired dietary composition. The remaining gathering agents would then need to collect enough plants to support any potentially unsuccessful hunting agents.

The increased resource exchange that would accompany the development of the more flexible diet previously described would likely require a revision of the current storage system. The model currently enables the group to store both plant and meat resources for longer periods as early hominins like *H. erectus* may already had access to methods of meat preservation without the need for fire, such as drying, submersing them in water, or burying them in soil (Soffer, 1989; Agam and Barkai, 2018). In our experiments, the group only stores meat for longer periods, while plant resources are lost at the end of each day. A more sophisticated storage system might provide the option to set a maximum number of days each resource can be stored. This would permit the group to store large quantities of meat, for instance after killing a megaherbivore, for several days - a trait which has been identified as necessary for efficiently exploiting very large herbivores (Hawkes et al., 1991).

5. Conclusions

The results of this study indicate that hominin foragers had different options to thrive in tropical grasslands by hunting the large herbivores and using one of the strategies with a short durationor allow cooperation between hunters. Although such hunting strategies might have required sophisticated tools, we also identified strategies hominin foragers may have used while only having access to rudimentary tools. This suggests that from the start on early hominins might have also hunted rather than only scavenging carcasses. In our model more advanced hunting strategies also offer higher returns which would have motivated early hominins to continuously improve their hunting skills and gain access to these strategies. While the hunting strategies we tested are based on paleoanthropological evidence, our model relies on estimated values due to limited data and the model would benefit from further research into how these strategies vary in terms of preparation, execution, and success rates. In future studies the model can be used as a tool to study foraging behavior as it offers options to be adapted to different environmental and behavioral scenarios which may even be outside of the field of paleoanthropology.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to improve the readability and spelling. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

Jan-Olaf Reschke: Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Susanne Krüger:** Writing – original draft, Visualization, Validation, Conceptualization. **Christine Hertler:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Conceptualization.

Declaration of Competing Interest

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