**N O T E S**

# Human brain evolution in a Malthusian economy

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**Abstract**

Why did the human brain evolve? This study develops a Malthusian growth model with heterogeneous agents and natural selection to explore the evolution of human brain size. We find that if the cognitive advantage of a larger brain dominates its higher metabolic costs, then the average brain size increases over time, which is consistent with the rising trend in human brain size that started over 2 million years ago. Furthermore, an improvement in hunting-gathering productivity (e.g., the discovery of using stone tools and fire in hunting animals and cooking food) helps to trigger this human brain size evolution. As the average brain size increases, the average level of hunting-gathering productivity also rises over time. Quantitatively, our model is able to replicate the trend in hominin brain evolution over the last 10 million years.

## 1. Introduction

[A]rchaic and early modern humans slowly but steadily acquired new skills, mastered the use of fire, developed increasingly sophisticated blades, handaxes, and flint and limestone tools, and created artworks. A key driver of these cultural and technological advancements, which came to define humankind and set us apart from other species, was the evolution of the human brain. Galor (2022, p. 13-14)

As humans evolved, the volume of the human brain has increased. Over 2 million years ago, a dramatic increase in the growth rate of human brain size occurred, which coincided with the emergence of the earliest members of the human genus *Homo*.[1] *Homo habilis* is one of the earliest known humans and lived in Africa from up to 2.8 million to 1.7 million years ago according to existing fossil evidence, and they had a brain size of about 550 cm$^3$ to 690 cm$^3$. *Homo ergaster* also lived in Africa from roughly 2.0 million to 1.4 million years ago and had a brain size of about 700 cm$^3$ to 900 cm$^3$. The well-known *Homo erectus* lived from roughly 1.9 million to 110,000 years ago in different parts of the world (including Africa, Asia and Europe) and had a brain size of about 600 cm$^3$ to 1250 cm$^3$. *Homo heidelbergensis* lived in Africa and Europe from about 600,000 to 200,000 years ago and had a brain size of about 1100 cm$^3$ to 1400 cm$^3$. *Homo neanderthalensis*, who is commonly known as the Neanderthals, lived in mainly Europe from possibly 430,000 to 40,000 years ago and had a brain size of about 1200 cm$^3$ to 1750 cm$^3$. Finally, *Homo sapiens* emerged in Africa about 300,000 years ago and has an average brain size of about 1400 cm$^3$. Therefore, except for the Neanderthals who had an even larger brain size than modern

humans,[2] human brain size has been increasing from early members of genus *Homo* to modern humans.[3]

In this study, we develop a hunting-gathering Malthusian growth model with heterogeneous agents to explore the evolution of human brain size driven by natural selection. Our results can be summarized as follows. If the cognitive advantage of a larger brain dominates its higher metabolic costs,[4] then the average brain size of human population increases over time. This implication is consistent with the rising trend in brain size of archaic human species. We also find that an improvement in hunting-gathering productivity (e.g., the discovery of using stone tools and fire in hunting animals and cooking food) helps to trigger this human brain size evolution. For example, Fonseca-Azevedo and Herculano-Houzel (2012) argue that the shift to a cooked diet may be an important reason for the rapid rising trend in human brain size. Ofek (2001, p. 73) also wrote that "the hunting-gathering feeding ecology [that led to an improvement in the quality and quantity of diet] facilitated a growing brain." Furthermore, we find that as the average brain size increases, the average level of hunting-gathering productivity also rises over time. This implication is consistent with Galor's (2022, p. 16–17) observation that "[t]he evolution of the human brain was the main impetus for the unique advancement of humanity, [. . .which] in turn, shaped future evolutionary processes, enabling human beings to adapt more successfully to their shifting environments and to further advance and utilise new technologies." Finally, we use our Malthusian growth model to perform a quantitative analysis to replicate the trend in hominin brain evolution over the last 10 million years.

This study relates to the literature on evolutionary growth theory based on natural selection in the Malthusian growth model.[5] A seminal study in this literature by Galor and Moav (2002) explores how natural selection and the quality–quantity trade-off of children affect the transition of an economy from pre-industrial stagnation to modern economic growth;[6] see also the interesting studies by Lagerlof (2007) and Dalgaard and Strulik (2015) on the selection of human body mass, Galor and Michalopoulos (2012) on the selection of entrepreneurial spirit, Galor and Ozak (2016) on the selection of future-oriented mindset, and Galor and Klemp (2019) on the selection of child quality.[7] A recent study by Chu (2023) explores natural selection and the extinction of archaic human species in a hunting-gathering Malthusian economy. Another related study by Chu and Xu (2024) explores the subsequent transitions of human society from hunting-gathering to agriculture and then from agriculture to industrial production also in a Malthusian economy.[8] This study contributes to this literature by exploring natural selection of human brain size and its evolution in a Malthusian growth model.

This study also relates more broadly to the scientific literature on human brain size evolution; see Heldstab et al. (2022) for a survey. A recent study by Gonzalez-Forero and Gardner (2018) provides a quantitative analysis on the evolution of human brain and finds that ecological challenges for "finding, caching or processing food" are the main reason for human brain evolution. Robson and Kaplan (2003) provide an economic analysis on the development of human brain as health capital that is accumulated by bodily investment to reduce mortality. We contribute to this literature by also providing an economic analysis based on a microfounded Malthusian growth model, in which fertility decisions of heterogeneous agents give rise to natural selection and the underlying natural selection mechanism for human brain evolution is also ecological in nature that is driven by the advantage of a larger brain in hunting-gathering and food production.

The rest of this study is organized as follows. Section 2 sets up the Malthusian model. Section 3 presents our results on human brain evolution. Section 4 explores some extensions to the baseline model. The final section concludes.

## 2. A Malthusian model with human brain evolution

The Malthusian growth model is based on the seminal work of Malthus (1798), who observed that population growth is limited by the availability of natural resources. In this section, we consider a

canonical Malthusian growth model; see for example, Ashraf and Galor (2011). There is a group of humans, who may be *Homo sapiens* or any other archaic humans, such as *Homo erectus* or Neanderthals. The group engages in hunting-gathering within a fixed area of land $Z$. The novel element is heterogeneity in brain size, which in turn affects consumption and hunting-gathering productivity.

### 2.1 Endogenous fertility and population dynamics

Within the human population, there is a large number of families indexed by $i \in \{1, \ldots, m\}$. Each family $i$ has an adult population $N_{i,t}$ at time $t$. Therefore, the total adult population size at time $t$ is

$$N_t = \sum_{i=1}^{m} N_{i,t}. \tag{1}$$

Each family $i$ is endowed with an exogenous brain size denoted as $b_i \in [b^{\min}, b^{\max}]$, where $b_i$ is heterogeneous across families and follows a general distribution within the lower bound $b^{\min}$ and upper bound $b^{\max}$ on brain size.

Given the metabolic costs of the brain, a family with a larger brain size faces a higher subsistence requirement on per capita consumption denoted as $\kappa_i = \kappa(b_i)$, which is assumed to be an increasing function in brain size $b_i$. We consider overlapping generations of agents, and each agent lives for two periods. Each adult agent of family $i$ has the following utility function $u_{i,t}$ at time $t$:

$$u_{i,t} = (1 - \gamma) \ln (c_{i,t} - \kappa_i) + \gamma \ln n_{i,t+1}, \tag{2}$$

where $\gamma \in (0, 1)$ is the degree of preference on fertility relative to consumption $c_{i,t}$. $n_{i,t+1}$ is the agent's number of children, who then become adults at time $t + 1$. Raising children is costly, and the level of consumption net of the fertility cost is

$$c_{i,t} = y_{i,t} - \rho n_{i,t+1}, \tag{3}$$

where the parameter $\rho > 0$ determines the cost of fertility and $y_{i,t}$ is the per capita output of food production in family $i$.

The utility-maximizing level of consumption is

$$c_{i,t} = (1 - \gamma)y_{i,t} + \gamma \kappa_i, \tag{4}$$

and the utility-maximizing level of fertility is

$$n_{i,t+1} = \frac{\gamma}{\rho}(y_{i,t} - \kappa_i), \tag{5}$$

where fertility cost $\rho$ is identical across families for simplicity. Equations ([4]) and ([5]) show that a family with a larger brain size $b_i$ allocates a larger amount of food output to consumption (due to the higher subsistence requirement $\kappa(b_i)$) at the expense of fertility. Therefore, if a larger brain size does not carry a cognitive advantage, then families with larger brains would have an evolutionary disadvantage.

Each adult agent in family $i$ has $n_{i,t+1}$ children, and the number of adult agents in family $i$ at time $t$ is $N_{i,t}$. Therefore, the law of motion for the adult population size in family $i$ is

$$N_{i,t+1} = n_{i,t+1}N_{i,t} = \frac{\gamma}{\rho}(y_{i,t} - \kappa_i)N_{i,t}, \tag{6}$$

which is decreasing in the subsistence requirement $\kappa_i$. The growth rate of $N_{i,t}$ at time $t$ is

$$\frac{\Delta N_{i,t}}{N_{i,t}} \equiv \frac{N_{i,t+1} - N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho}(y_{i,t} - \kappa_i) - 1, \tag{7}$$

and the growth rate of total adult population $N_t$ at time $t$ is

$$\frac{\Delta N_t}{N_t} = \sum_{i=1}^{m} s_{i,t} \frac{\Delta N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho} \sum_{i=1}^{m} s_{i,t}(y_{i,t} - \kappa_i) - 1, \tag{8}$$

where $s_{i,t} \equiv N_{i,t}/N_t$ and $\Delta N_t/N_t$ will be simply referred to as the population growth rate.

### 2.2 Hunting-gathering

To capture the cognitive advantage of a larger human brain, we assume that the level of hunting-gathering productivity denoted as $\theta_i = \theta(b_i)$ in each family $i$ is also increasing in its brain size $b_i$. The food production function of family $i$ is

$$Y_{i,t} = \theta_i (l N_{i,t})^\alpha (Z_{i,t})^{1-\alpha}, \tag{9}$$

where $l N_{i,t}$ and $Z_{i,t}$ are, respectively, the amount of labor and land devoted to hunting-gathering by family $i$. Individual labor supply $l > 0$ is exogenous, and the parameter $\alpha \in (0, 1)$ measures labor intensity of the hunting-gathering process.

For simplicity, the amount of land occupied by family $i$ for hunting-gathering is assumed to be proportional to its population share $s_{i,t}$:[9]

$$Z_{i,t} = s_{i,t} Z = \frac{N_{i,t}}{N_t} Z. \tag{10}$$

Substituting ([10]) into ([9]) yields the level of food output per capita in family $i$ as

$$y_{i,t} \equiv \frac{Y_{i,t}}{N_{i,t}} = \frac{\theta_i (l N_{i,t})^\alpha (Z_{i,t})^{1-\alpha}}{N_{i,t}} = \theta_i l^\alpha \left(\frac{Z}{N_t}\right)^{1-\alpha}, \tag{11}$$

which is increasing in the family's brain size $b_i$ via its hunting-gathering productivity $\theta(b_i)$.

## 3. Natural selection and brain size evolution

Substituting ([11]) into ([7]) yields the population growth rate of family $i$ as[10]

$$g_{i,t} \equiv \frac{\Delta N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho} \left[ \theta_i l^\alpha \left(\frac{Z}{N_t}\right)^{1-\alpha} - \kappa_i \right] - 1, \tag{12}$$

which is increasing in hunting-gathering productivity $\theta_i$ but decreasing in the subsistence requirement $\kappa_i$. Recall that both $\theta_i = \theta(b_i)$ and $\kappa_i = \kappa(b_i)$ are increasing functions of brain size $b_i$. Therefore, a larger brain size $b_i$ has a positive effect on fertility via a higher level of hunting-gathering productivity $\theta_i$ and also a negative effect on fertility via a higher subsistence requirement $\kappa_i$. If we were to assume $\kappa_i = \kappa$ to be homogeneous across families, then families with the largest brain size $b^{\max}$ would dominate the population by having the highest hunting-gathering productivity $\theta(b^{\max})$ and the highest population growth rate. Conversely, if we were to assume $\theta_i = \theta$ to be homogeneous across families, then families with the smallest brain size $b^{\min}$ would dominate the population by having the lowest subsistence requirement $\kappa(b^{\min})$ and the highest population growth rate. In general, families that have the highest population growth rate would dominate the population in the long run. For the rest of this analysis, we assume that the productivity benefit $\theta(b_i)$ is weakly concave in $b_i$ whereas the metabolic cost $\kappa(b_i)$ is weakly convex in $b_i$. We first examine the condition under which the average human brain size evolves toward $b^{\max}$.

### 3.1 Expanding brain size in human evolution

If the positive effect of brain size $b_i$ on fertility always dominates its negative effect (i.e.,

$$\frac{\partial g_{i,t}}{\partial b_i} > 0 \Leftrightarrow l^\alpha \left( \frac{Z}{N_t} \right)^{1-\alpha} \frac{\partial \theta_i}{\partial b_i} > \frac{\partial \kappa_i}{\partial b_i} \tag{13}$$

for all $b_i \in [b^{\min}, b^{\max}]$ and $N_t \in [N_0, N^*]$ where $N^*$ is the steady-state level of total population),[11] then the population growth rate of family $i$ is increasing in its brain size $b_i$. In this case, the growth rate of the population share of family $i$ is also rising in its brain size:[12]

$$\Delta s_{i,t} \approx \frac{\Delta N_{i,t}}{N_t} = s_{i,t} g_{i,t} \Rightarrow \frac{\partial \Delta s_{i,t}/s_{i,t}}{\partial b_i} \approx \frac{\partial g_{i,t}}{\partial b_i}.$$

As a result, families with the largest brain size would have an evolutionary advantage and eventually dominate the population. In the long run, $s_{i,t}(b_i = b^{\max}) \to 1$ because given ([13]), its population growth rate $g_{i,t}(b_i = b^{\max})$ in ([12]) is the highest among all families such that $s_{j,t}(b_j < b^{\max}) \to 0$. In this case, total population $N_t$ converges to the steady-state population level of the families with the largest brain size $b^{\max}$:

$$\lim_{t \to \infty} N_t \to N^* = \left[ \frac{\gamma \theta(b^{\max}) l^\alpha}{\rho + \gamma \kappa(b^{\max})} \right]^{1/(1-\alpha)} Z, \tag{14}$$

which is derived from ([12]) by setting $b_i = b^{\max}$.

As their population share $s_{i,t}(b_i = b^{\max})$ rises over time due to their higher population growth rate, the average brain size $b_t \equiv \sum_{i=1}^m s_{i,t} b_i$ of human population also increases over time, which is consistent with the rising trend in human brain size that started over 2 million years ago. Eventually, the average brain size converges to the upper bound (i.e., $b_t \to b^{\max}$ as $s_{i,t}(b_i = b^{\max}) \to 1$). As the average brain size increases over time, the average level of hunting-gathering productivity $\theta_t \equiv \sum_{i=1}^m s_{i,t} \theta_i$ also rises over time and converges to $\theta(b^{\max})$.[13]

When does this expanding brain size in human evolution occur? To explore this question, we substitute $N^*$ from ([4]) into $N_t$ in ([13]) to derive

$$\frac{\rho + \gamma \kappa(b^{\max})}{\gamma \theta(b^{\max})} \theta'(b^{\max}) > \kappa'(b^{\max}). \tag{15}$$

Recall from ([13]) that the positive effect of $b_i$ is decreasing in $N_t$. So, if the inequality in ([13]) holds for $N^*$, it would also hold for $N_t \in [N_0, N^*]$. In the following section, we consider a parametric example to demonstrate when ([15]) holds.

### 3.1.1 A parametric example

Suppose $\theta(b_i)$ and $\kappa(b_i)$ take the following functional form: $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i$, where $\overline{\theta} > 0$ and $\overline{\kappa} > 0$ are productivity and cost parameters, respectively. To be more precise, as the productivity parameter $\overline{\theta}$ increases, hunting-gathering productivity $\theta(b_i)$ rises, and this positive marginal effect of $\overline{\theta}$ on hunting-gathering productivity $\theta(b_i)$ is increasing in brain size $b_i$.[14] Similarly, as brain size $b_i$ increases, hunting-gathering productivity $\theta(b_i)$ also rises, and this positive marginal effect of $b_i$ on hunting-gathering productivity $\theta(b_i)$ is also increasing in the parameter $\overline{\theta}$, which therefore captures the marginal effect of brain size on hunting-gathering productivity. In other words, an increase in the parameter $\overline{\theta}$ represents an improvement in hunting-gathering productivity that is complementary to brain size (i.e., a family $i$ with a larger brain size $b_i$ is better able to benefit from the increase in $\overline{\theta}$). For example, the discovery of stone tools (an exogenous increase in $\overline{\theta}$ in our model) is only useful for a hominin species that is intelligent enough to make use of the tools.

Given $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i$, ([15]) simplifies to

$$\overline{\theta} > \frac{\gamma}{\rho} \overline{\kappa}. \tag{16}$$

In this case, in order for human population to evolve toward a larger average brain size, the productivity parameter $\overline{\theta}$ needs to be sufficiently large relative to the product of the cost parameter $\overline{\kappa}$ and the ratio $\gamma/\rho$.[15] The comparison between hunting-gathering productivity and metabolic cost is intuitive, whereas the ratio $\gamma/\rho$ also plays a role because fertility and population size are increasing in fertility preference $\gamma$ and decreasing in fertility cost $\rho$. As ([13]) shows, a larger population reduces the marginal benefit of brain size on hunting-gathering productivity due to the decreasing returns to scale in food production. An implication of ([16]) is that a high level of hunting-gathering productivity $\overline{\theta}$ that is complementary to brain size (e.g., the discovery of using fire in hunting animals and cooking food or the development of "increasingly sophisticated blades, handaxes, and flint and limestone tools") helps to trigger the emergence of an expanding brain size in human evolution;[16] see for example, Gowlett (2016) who provides evidence that the discovery of fire "has fuelled the increase in brain size through the Pleistocene."

### 3.1.2 Summary of results

Proposition 1 summarizes all our results in this section.

**Proposition 1.** *The population growth rate of family $i$ is increasing in its hunting-gathering productivity $\theta_i$ but decreasing in its subsistence requirement $\kappa_i$. If the positive effect of a larger brain size $b_i$ on hunting-gathering productivity $\theta_i$ always dominates its negative effect (via a higher subsistence requirement $\kappa_i$) on fertility, then families with the largest brain size $b^{\max}$ have an evolutionary advantage, and the average brain size in human population increases over time. As the average brain size $b_t$ increases, the average level of hunting-gathering productivity $\theta_t$ also rises over time. Suppose $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i$. Then, an improvement in hunting-gathering productivity $\overline{\theta}$ that is complementary to brain size helps to trigger the emergence of an expanding brain size in human evolution.*

### 3.2 Optimal brain size in human evolution

We now explore the more interesting case in which the average brain size $b_t$ evolves toward an interior steady state $b^* \in (b^{\min}, b^{\max})$. If there exists a certain level of population threshold $\widetilde{N}$ under which

$$l^\alpha \left( \frac{Z}{\widetilde{N}} \right)^{1-\alpha} \frac{\partial \theta(b^*)}{\partial b_i} = \frac{\partial \kappa(b^*)}{\partial b_i}, \tag{17}$$

then there exists an interior optimal brain size $b^* \in (b^{\min}, b^{\max})$ from an evolutionary viewpoint. To determine this optimal brain size, we also need the steady-state population level:

$$N_i^*(b_i = b^*) = \left[ \frac{\gamma \theta(b^*) l^\alpha}{\rho + \gamma \kappa(b^*)} \right]^{1/(1-\alpha)} Z = \widetilde{N}, \tag{18}$$

where $\widetilde{N}$ and $b^*$ are determined jointly by ([17]) and ([18]). In other words, families with the optimal brain size $b^*$ have the highest steady-state population growth rate and dominate the population in the long run (i.e., $s_{i,t}(b_i = b^*) \to 1$ because its steady-state population growth rate $g_i^*(b_i = b^*) = 0$ is the highest among all families such that $g_j^*(b_j \neq b^*) < 0$).[17]

Combining ([17]) and ([18]) yields the following condition that determines $b^*$:

$$\frac{\theta'(b^*)}{\kappa'(b^*)} = \frac{\gamma \theta(b^*)}{\rho + \gamma \kappa(b^*)}. \tag{19}$$

**Table 1.** Human brain size

| *Homo* species | brain size (*cm³*) | normalized |
|---|---|---|
| *habilis* | 620 | 1.00 |
| *ergaster* | 800 | 1.29 |
| *erectus* | 925 | 1.49 |
| *heidelbergensis* | 1250 | 2.02 |
| *neanderthalensis* | 1475 | 2.38 |
| *sapiens* | 1400 | 2.26 |

The left-hand side of ([19]) is weakly decreasing in $b^*$ because $\theta'' \leq 0$ and $\kappa'' \geq 0$. As for the right-hand side of ([19]) defined as $\Phi(b^*) \equiv \gamma\theta(b^*)/[\rho + \gamma\kappa(b^*)]$, it can be shown that ([19]) implies $\Phi'(b^*) = 0$. Therefore, we need to assume that at least one of $\theta'' \leq 0$ and $\kappa'' \geq 0$ is a strict inequality to ensure the existence of a solution $b^*$. If $b^*$ falls within the range of brain size $b_i \in [b^{\min}, b^{\max}]$, then families with the optimal brain size $b^*$ will dominate the population in the long run and have a steady-state level of population that is equal to the threshold $N$ in ([18]). In this case, given an initial value $b_0$, the average brain size $b_t \equiv \sum_{i=1}^{m} s_{i,t} b_i$ rises toward $b^*$ as $s_{i,t}(b_i = b^*) \to 1$.[18]

### 3.2.1 Another parametric example

Suppose $\theta(b_i)$ and $\kappa(b_i)$ now take the following functional form: $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i^2$, where $\overline{\theta} > 0$ and $\overline{\kappa} > 0$ are parameters. In this case, the optimal brain size $b^*$ from ([19]) is determined by the following quadratic equation:

$$(b^*)^2 + \frac{2b^*}{\overline{\theta}} = \frac{\rho}{\gamma\overline{\kappa}}, \tag{20}$$

in which the solution $b^* > 0$ is increasing in hunting-gathering productivity $\overline{\theta}$ that is complementary to brain size. If $\overline{\theta}$ becomes sufficiently large, it is possible for $b^*$ to even exceed the upper bound $b^{\max}$, in which case the average brain size $b_t$ converges to $b^{\max}$ as in Section 3.1. Solving ([20]) yields

$$b^* = -\frac{1}{\overline{\theta}} + \sqrt{\frac{1}{\overline{\theta}^2} + \frac{\rho}{\gamma\overline{\kappa}}} \in (b^{\min}, b^{\max}), \tag{21}$$

which depends positively on the parameter $\overline{\theta}$ and the composite parameter $\rho/(\gamma\overline{\kappa})$. Proposition 2 summarizes our result in this section.

**Proposition 2.** *Suppose $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i^2$. Then, $b^*$ in ([21]) is the evolutionarily optimal human brain size, which is increasing in hunting-gathering productivity $\overline{\theta}$ that is complementary to brain size.*

### 3.2.2 Quantitative analysis

In this section, we compute the value of the optimal brain size $b^*$ in ([21]) and explore its quantitative implications. The introduction features a discussion on the range of brain size of different human species. Table 1 presents a summary based on the midpoint of the range of brain size of each of these species. It also uses the brain size of the first human species, *Homo habilis*, as the benchmark and presents the relative brain size of the subsequent human species.

    Suppose the brain size of each human species was optimal (given the level of hunting-gathering productivity $\overline{\theta}$) at its time. Then, we compute the change in $\overline{\theta}$ required for the optimal brain size to increase from $b^* = 1$ for *Homo habilis* to $b^* = 2.26$ for *Homo sapiens*. In addition, this

**Table 2.** Changes in productivity $\overline{\theta}$

| $\rho/(\gamma\overline{\kappa})$ | $\overline{\theta}$ for $b^* = 1$ | $\overline{\theta}$ for $b^* = 2.26$ | percent increase in $\overline{\theta}$ |
|---|---|---|---|
| 6 | 0.40 | 5.01 | 1153% |
| 10 | 0.22 | 0.92 | 315% |
| 14 | 0.15 | 0.51 | 230% |
| 18 | 0.12 | 0.35 | 198% |
| 22 | 0.10 | 0.27 | 181% |
| 26 | 0.08 | 0.22 | 170% |
| 30 | 0.07 | 0.18 | 163% |
| 34 | 0.06 | 0.16 | 158% |
| 38 | 0.05 | 0.14 | 154% |
| 42 | 0.05 | 0.12 | 151% |
| 46 | 0.04 | 0.11 | 148% |
| 50 | 0.04 | 0.10 | 146% |

simulation also involves the fertility cost parameter $\rho$, the fertility preference parameter $\gamma$ and the subsistence consumption parameter $\overline{\kappa}$. Specifically, the simulation requires an assigned value of the composite parameter $\rho/(\gamma\overline{\kappa})$. Given that we do not know its value, we consider a range to examine how the value of this composite parameter affects our calculation. Table 2 presents the results. As $\rho/(\gamma\overline{\kappa}) \to 5$, the percent increase in $\overline{\theta}$ (required for $b^*$ to increase from 1 to 2.26) approaches infinity. Therefore, we start with a value of 6 for $\rho/(\gamma\overline{\kappa})$ as a lower bound. Then, we examine how large the percent increase in $\overline{\theta}$ would be under a range of values of $\rho/(\gamma\overline{\kappa})$ for illustration. It turns out that as $\rho/(\gamma\overline{\kappa})$ increases, the percent increase in $\overline{\theta}$ remains over 100%. Thus, we conclude that the dramatic increase in human brain size over the last 2.5 million years was driven by a rapid improvement in hunting-gathering productivity $\overline{\theta}$ that is complementary to brain size.

We now consider hominin brain evolution over the last 10 million years. According to DeSilva et al. (2021), the cranial capacity in fossil apes (Miocene hominids) from 10 million years ago is about 250 $cm^3$, which is about 40% of the brain size of *Homo habilis*. If we consider a value of 10 for $\rho/(\gamma\overline{\kappa})$ as a benchmark, then the implied value of $\overline{\theta}$ for $b^* = 0.40$ is 0.08. Suppose $\overline{\theta}$ increases linearly from 0.08 to 0.22 between 10 million years ago and 2.5 million years ago and from 0.22 to 0.92 between 2.5 millions years ago and the dawn of the Agricultural Revolution about 10,000 years ago. Then, we simulate the path of the optimal brain size $b^*$ in ([21]) as $\overline{\theta}$ gradually increases from 10 million years ago to recent times in Figure 1, which closely replicates the trend of hominin brain size in DeSilva et al. (2021).[19] Specifically, the growth trend of hominin brain size was steadily slow from 10 million years ago to 2.5 million years ago and then accelerated about 2.5 million years ago before decelerating until recent times. This pattern is robust to other values of $\rho/(\gamma\overline{\kappa})$ with the recent deceleration becoming less rapid at larger values of $\rho/(\gamma\overline{\kappa})$.[20]

## 4. Extensions

In this section, we consider a number of extensions to our baseline model.[21] Section 4.1 considers the presence of a scale effect in hunting-gathering productivity. Section 4.2 considers the evolution of human body mass.

### 4.1 Scale effect

In this section, we introduce a scale effect on hunting-gathering productivity to our baseline model.[22] For simplicity, we assume that subsistence requirement $\kappa_i = \kappa$ is homogeneous across families. In this case, our baseline model predicts that families with the largest brain size $b^{\max}$
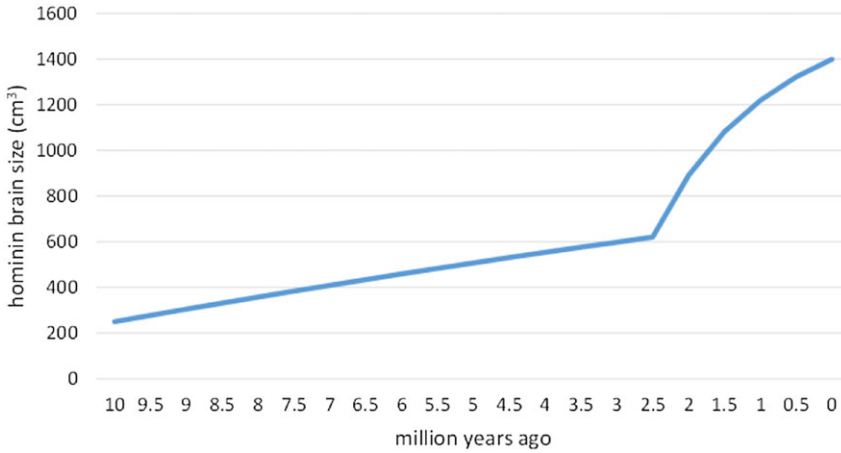
**Figure 1.** Simulated trend of hominin brain size.

would dominate the population by having the highest hunting-gathering productivity $\theta(b^{\max})$ and the highest population growth rate. Suppose we now modify the hunting-gathering productivity function as $\theta(s_{i,t}b_i)$ to be increasing in $s_{i,t}b_i$, where $s_{i,t} \equiv N_{i,t}/N_t$ is the population share of family $i$ and captures a scale effect of relative population size on hunting-gathering productivity. For example, a larger family group may be able to occupy a more fertile area of land for hunting-gathering purposes. In this case, the population growth rate of family $i$ in ([12]) becomes

$$g_{i,t} = \frac{\gamma}{\rho}\left[\theta(s_{i,t}b_i)l^\alpha \left(\frac{Z}{N_t}\right)^{1-\alpha} - \kappa\right] - 1, \tag{22}$$

which shows that the relative population size $s_{i,t}$ now plays a role. The family that dominates in the long run may no longer be the one with the largest brain size $b^{\max}$. Instead, the initial population share $s_{i,0}$ also matters. Specifically, the family with the largest $s_{i,0}b_i$ dominates the population in the long run as its population share $s_{i,t}$ rises over time and eventually converges to unity (i.e., $s_{i,t} \to 1$). In other words, a human species with a relatively large brain size (e.g., the Neanderthals) may not survive in the long run because its initial population size is relatively small.

### 4.2 Body mass

Our model assumes that a larger brain size carries a benefit to productivity but requires higher subsistence consumption. Considering the evolution of human body mass, Lagerlof (2007) and Dalgaard and Strulik (2015) also assume that a higher body mass has a positive effect on productivity but requires higher subsistence consumption. Therefore, one natural question is how the evolution of human body mass differs from the evolution of human brain size.

Empirically, Lagerlof (2007) documents that the average human body mass increased from 61.8 kg roughly 1.8 million years ago to 76.0 kg about 36-75 thousand years ago.[23] This 23% increase in human body mass is significant but not as much as the increase in human brain size, which more than doubled in the last 2 million years. Therefore, the increase in human brain size is not a mere reflection of a higher human body mass. Rather, human brain size has increased relative to human body mass.[24]

Theoretically, if we modify the hunting-gathering productivity function as $\theta_i = \theta(B_i)$ and the subsistence requirement function as $\kappa_i = \kappa(B_i)$, which are both increasing in the body mass $B_i$ of

family $i \in \{1, \ldots, m\}$. Then, this alternative model could generate the same implication that the average human body mass rises over time. However, given that the increase in human brain size is quantitatively more prominent in the data than the increase in human body mass, it is arguably more important to apply an evolutionary growth model (like the one in this study) to the evolution of human brain size than that of human body mass.[25]

## 5. Conclusion

In this study, we have developed a hunting-gathering Malthusian growth model with heterogeneity in human brain size, which gives rise to natural selection and brain size evolution. We find that if the cognitive advantage of a larger brain dominates its higher metabolic costs, then the average human brain size increases over time, which is consistent with the rising trend in brain size of archaic human species. Furthermore, we have used our evolutionary growth-theoretic framework to show how an improvement in hunting-gathering productivity (e.g., the discovery and use of fire) could give rise to an expanding brain size in human evolution. Quantitatively, our Malthusian model is able to replicate the trend in hominin brain evolution over the last 10 million years. In the modern time, as the human society evolves away from the Malthusian equilibrium, there will emerge additional factors that determine human brain size. For example, medical technological progress (such as the invention of cesarean section) can overcome the limitation in the size of human birth canal in allowing for further growth in human infant brain size. Therefore, introducing medical technological progress to the Malthusian growth model could be an interesting extension for future research.

Finally, we conclude with the following discussion. Our growth-theoretic analysis assumes that the range of human brain size is exogenous. It is the population share that changes endogenously over time, which in turn gives rise to an endogenous evolution of the average brain size. One can endogenize the range of brain size, for example, by assuming that the average brain size has a spillover effect on its range, such that each family's brain size in the next generation grows by the same proportion as growth in the average brain size across families in the current generation. We leave this extension to future research.

## Notes

**1** See DeSilva et al. (2021) for data on a rising trend in human brain size starting over 2 million years ago. They also find that there may have been a brain size reduction since 3000 years ago; however, a subsequent study by Villmoare and Grabowski (2022) questions the validity of this recent reduction in human brain size.

**2** Existing evidence suggests that both *Homo neanderthalensis* and *Homo sapiens* evolved from *Homo heidelbergensis*, rather than *Homo neanderthalensis* evolving into *Homo sapiens*.

**3** Another exception is *Homo floresiensis*, who lived in the island of Flores, Indonesia from possibly 190,000 to 50,000 years ago and had a small brain size of about 420 cm³, which was likely due to island dwarfism.

**4** See van Valen (1974) and Lynn (1990) for estimates of the cognitive advantage of a larger human brain size. See Gonzalez-Forero and Gardner (2018) for estimates of the metabolic costs of the human brain.

**5** See Hansson and Stuart (1990) and Rogers (1994) for early economic models of natural selection of agents with different time preferences but not in a Malthusian environment. See also Robson (2001) for a survey of this related branch of the literature.

**6** See Collins et al. (2014) for an interesting quantitative analysis of the Galor–Moav model.

**7** See Ashraf and Galor (2018) for a comprehensive survey of this literature.

**8** Chu, Peretto and Furukawa (2024) explore the endogenous transition of human society from multiple states to a unified empire in an agricultural Malthusian economy.

**9** Appendix A considers a more general land-division rule.

**10** It is useful to note that $g_{i,t}$ simply depends on $N_t$ (instead of $N_{i,t}$) due to $Z_{i,t} = s_{i,t}Z$ in ((10)).

**11** Here, we assume that the initial level of population is below the steady-state equilibrium level.

**12** The approximation $N_{t+1} \approx N_t$ implicitly assumes that the brain size of an individual family has a negligible effect on the total population growth rate $g_t$. In general, $\Delta s_{i,t}/s_{i,t} = (g_{i,t} - g_t)/(1 + g_t)$.

**13** See for example, Galor (2022, p. 16-17).

**14** A related interpretation can also be applied to the cost parameter $\overline{\kappa}$.

**15** If the inequality in ([16]) is reversed, then brain size would eventually converge to $b^{\min}$ instead. However, if initial population $N_0$ is sufficiently small, then the positive effect of $b_i$ may still dominate but only initially.

**16** See Fonseca-Azevedo and Herculano-Houzel (2012), Galor (2022, p. 17) and Ofek (2001, p. 73).

**17** Here, we assume that at least one of the families $i \in \{1, \ldots, m\}$ has this brain size $b^*$.

**18** Here, we assume that the average brain size at time 0 is below $b^*$.

**19** See Figure 1 of DeSilva et al. (2021).

**20** In other words, at larger values of $\rho/(\gamma\overline{\kappa})$, the trend of human brain size from 2.5 million years ago becomes more linear and less consistent with DeSilva et al. (2021).

**21** In Appendix A, we also consider a more general land-division rule.

**22** We would like to thank a referee for suggesting this extension.

**23** Since then, the average human body mass has fallen back to 58.2 kg in recent times.

**24** Grabowski (2016) argues that the increase in human body mass may be the result of a larger brain size.

**25** We would like to thank a referee for this suggestion.

**26** Chu (2023) also adopts this conflict success function to explore the Neanderthal extinction.

**27** See for example Fa et al. (2013).

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## A. Appendix A

In our baseline model, we consider a simple land-division rule in ([10]). In this appendix, we consider a more general land-division rule given by[26]

$$Z_{i,t} = \frac{(N_{i,t})^\phi}{\sum_{j=1}^m (N_{j,t})^\phi} Z,$$ (23)

which nests ([10]) as a special case with $\phi \to 1$. Here, we consider another parameter space given by $\phi \in [0, 1)$. This parameter $\phi$ captures the elasticity of the relative land ratio $Z_{i,t}/Z_{j,t}$ with respect to the relative family size $N_{i,t}/N_{j,t}$. In this case, all families with different brain sizes survive in the long run. To see this result, we use ([23]) to modify ([12]) as

$$\frac{\Delta N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho} \left[ \theta_i l^\alpha \left( \frac{Z_{i,t}}{N_{i,t}} \right)^{1-\alpha} - \kappa_i \right] - 1 = \frac{\gamma}{\rho} \left[ \theta_i l^\alpha \left( \frac{(N_{i,t})^\phi}{\sum_{j=1}^m (N_{j,t})^\phi} \frac{Z}{N_{i,t}} \right)^{1-\alpha} - \kappa_i \right] - 1.$$ (24)

If $\phi = 0$, then the steady-state population size of any family $i \in \{1, \ldots, m\}$ is

$$N_i = \left( \frac{\gamma \theta_i l^\alpha}{\rho + \gamma \kappa_i} \right)^{1/(1-\alpha)} \frac{Z}{m},$$ (25)

which is increasing in hunting-gathering productivity $\theta_i = \theta(b_i)$ and decreasing in the subsistence requirement $\kappa_i = \kappa(b_i)$. Therefore, a larger brain size $b_i$ has a positive effect on the steady-state population size of family $i$ via a higher level of hunting-gathering productivity $\theta_i$ and also a negative effect via a higher subsistence requirement $\kappa_i$.

If $\phi = (0, 1)$, then the steady-state population size of family $i \in \{1, \ldots, m\}$ is given by

$$N_i = \left( \frac{\gamma \theta_i l^\alpha}{\rho + \gamma \kappa_i} \right)^{1/(1-\alpha)} \frac{Z}{\sum_{j=1}^m (N_j/N_i)^\phi},$$ (26)

where the relative family size is given by

$$\frac{N_i}{N_j} = \left[ \frac{\theta_i/(\rho + \gamma \kappa_i)}{\theta_j/(\rho + \gamma \kappa_j)} \right]^{1/[(1-\alpha)(1-\phi)]}.$$ (27)

Therefore, $N_i$ continues to be increasing in hunting-gathering productivity $\theta_i$ and decreasing in the subsistence requirement $\kappa_i$. As before, a larger brain size $b_i$ has a positive effect on the steady-state population size of family $i$ via a higher level of hunting-gathering productivity $\theta_i$ and a negative effect via a higher subsistence requirement $\kappa_i$. Interestingly, larger brain sizes $b_j$ of other families $j$ now have a negative effect on the steady-state population size of family $i$ via their higher level of hunting-gathering productivity $\theta_j$ and a positive effect via their higher subsistence requirement $\kappa_j$.

More importantly, for $\phi \in [0, 1)$, the steady-state population size of all families $i \in \{1, \ldots, m\}$ remains strictly positive. In this case, even human species with the smallest brain size $b^{\min}$ continue to survive in the long run. This counterfactual outcome deserves attention as it allows for the possibility of trade in different food products between different human species. For example, there is evidence that Neanderthals hunted large mammals whereas early *sapiens* hunted smaller preys.[27]

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