Virtual Neanderthals : a study in agent-based modelling Late Pleistocene hominins in western Europe
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5. THE MODELLED HOMININS

5.1 Introduction

Developing a model is a trade-off between different interests. Predictive accuracy, computational needs and realism compete in the process of finding an acceptable balance when building models that are valid descriptions of the actual processes (Levins 1966). The main factor steering dispersal is the resulting population sum of births, deaths, immigration and emigration through time (assuming no transport technology is available). The parameters concerning hominin behaviour in HomininSpace are qualified in this chapter and include demographic parameters, energy needs, group dynamics and mobility factors. Together they implement a generic hunter gatherer model with parameters selected from ethnographical literature. Finding specific values for these parameters is the main aim of this study. The use of data on modern human hunter-gather societies as a model for Neanderthal parameterization in this study is based on the following:

- Similar **anatomies**. Both hominin species are bipedal and anatomically similar, with similar body proportions, size, weight and stature (Trinkaus 1986);
- Matching **behaviour** (Villa and Roebroeks 2014) with both species implementing hunting and gathering as a main subsistence strategy which is core to the underlying model of this thesis;
- **Compatible DNA**. Remaining Neanderthal DNA in modern human DNA suggests that offspring of mixed parents is viable and that offspring of mixed parenthood is able to reproduce (Green *et al.* 2010). This suggests that *Homo sapiens* could be a good model for and even be the same species as *Homo neanderthalensis* when this criterion forms a major part of the definition of species (Klein 2009b; Mayr 1950);
- Comparable **life histories** (Smith *et al.* 2007; Weaver and Hublin 2009; Smith *et al.* 2010) and mortality patterns (Trinkaus 2011);
- There appears to be no significant **ecological differences** between Neanderthals and early modern humans (Chase 1989; Marean and Kim 1998);
- Neanderthals shared symbolic thinking with early modern humans and are **cognitively indistinguishable**, based on retrieved material culture as discussed by Hoffmann *et al.* (2018);

In short, both species are generally considered 'sufficiently' similar (O'Connell 2006). It is assumed that "after having assessed similarities and differences further similarities can be inferred" (Bernbeck 1997, 86, Kowarik *et al.* 2012). Of course there are many differences between the two species. Where many Neanderthals probably got most of their energy from large herbivores, many modern humans likely extended their diet to include more aquatic resources (Richards and Trinkaus 2009), Neanderthals probably used more energy

in their daily activities (Verpoorte 2006; Churchill 2009 but see Heyes and MacDonald (2015)), etc. These differences are acknowledged, but assumed to be differences in degree and not in kind. Nevertheless, material evidence should be used to test or support the validity of a model based on ethnographic data (Isaac 1968). Within HomininSpace, archaeological data is used to verify the proposed models by comparing simulation results to material culture remains.

The archaeological record for the Neanderthals never revealed evidence for the use of the wheel, for boats, for the use of draft animals, for sleds, etc. (Wobst 1974, 152). These hominins had to walk and carry everything they owned with them. Planning for the future would not include stocking much food surplus, and distance covered and speed of movement would be limited (Lee and DeVore 1968, 12). Also, modern hunting and gathering populations are invariably influenced by the modern cultural environments around them with imported diseases, negative migration balances, access to domesticated flora and fauna, contacts with sedentary populations, etc. (Wobst 1974). For this and other reasons cultural uniformitarianism from the present to the past is doubtful in itself (Martelle Hayter 2011). The cultural criteria used by any anthropologist further colour any interpretation of the ethnographic record (Marks 2012). And even those hunter and gatherer populations that still exist today show great diversity in many aspects of life (Binford 2001; Kelly 1995; Lee 1968). As such, even when sharing a similar environment two cultures can be a world apart.

This chapter identifies the model parameters that describe the variability in the hominins in HomininSpace. Parameters are model elements that can be changed by assigning different values. A unique model is created by assigning a specific value combination to the parameters. The parameters form the hominin model of HomininSpace together with the variables and logic that is embedded in the source code of HomininSpace and that describes how the parameters are used. The parameters are summarized with their selection motivated and with more details provided in the remaining sections of this chapter.

Demographic model parameters are discussed in the Section 5.2. Energy is a basic requirement for any living individual, and Section 5.3 will discuss the modelled energy requirements of Neanderthals. Within the HomininSpace modelling system the energy is used for two major action categories: it steers hominin movements through the landscape in which they aim to maximize possible intake, and it enables procreation. The basic unit in HomininSpace is the hominin group. These groups of hominins can be created and can

also be removed from the simulation, by leaving the simulation area, through extinction or when merging with another group. Group interaction and mobility is discussed in section 5.4. Section 5.5 summarizes all parameters and other model elements of the model.

5.2   Demography

Demographic processes can enable dispersal. If sufficient new individuals are born, members of a species can disperse into new territories. The demographic process in HomininSpace is implemented as a statistical procedure. This means that the system does not track individuals, but accounts for demographics with births and deaths recorded for the group as a whole. This implementation is possible due to the fact that the basic agent in HomininSpace is the group (not the individual hominin) and prevents random effects from demographic stochasticity. This process mimics population statistics, but is implemented at the group level.

In every group there are three age categories that individuals can belong to: `pre-fertile`, `fertile` and `post-fertile` (a common biological categorization, see for instance an application in the modelling of *Lynx pardinus* by Gaona *et al.* (1998)). This limited categorization ignores any differences between infancy, childhood, juvenile and adolescence stages in the pre-fertile category (Bogin 1999), since the interest of this research is neither in growth nor in foraging efficiency, and also lumps energy requirements for this phase into one (average) constant. Gurven and Kaplan (2007, 322) have identified different death profiles for these three categories, and they found that from birth through childhood, for adults and for surviving individuals after 40 years of age a different average mortality rate can be calculated supporting this separation into three segments (compare however the four categories identified by White (2013)). HomininSpace implements a different mortality rate for each of three age categories.

There is no separation between males and females in HomininSpace and for each category 50% of the hominins are assumed to be female, with birth and death rates being applied to both sexes equally. This is rationalized by the fact that, especially in the fertile category, males will most likely run many risks when hunting whereas females have a high death rate when giving birth or from complications thereafter. Other causes of death include disease and illnesses, inter-group and intra group violence, and accidents. For different types of societies, including extant hunter-gatherers, Gurven and Kaplan (2007, 348) find an adult mortality rate of 1%. Hill *et al.* (2007) observe a higher percentage of adult

mortality rates of 2% for the Hiwi hunter-gatherers of Venezuela. The Hiwi experience more violence related deaths than other groups who mainly suffer from diseases and the authors suggest that the Hiwi might reflect Palaeolithic cultures better. Only about 50%-60% of all hunter-gatherer infants reach adulthood (Gurven and Kaplan 2007; Kelly 1995). This means an overall mortality rate of 4%, see Table 8.

Although empirical data (Gurven and Kaplan 2007, 325) suggests a decreasing mortality rate for the pre-fertile category and an exponentially increasing rate for post-fertile individuals (referred to as the 'Siler' model), the HomininSpace model implements a flat parameterized death rate for each age segment since there are no aging individuals in HomininSpace, only groups. As with all parameters this natural death rate is constant throughout the simulation period[20]. One of the disadvantages of working with a mortality rate is that the segment will never become empty since there is always a remainder. For instance, with a mortality rate of 15% almost 5% is still alive after 20 years. This unrealistic situation is solved via group extinction (see subsection 5.4.1).

Table 8: Different mortality rates (in %) and the compounded effects on a starting population of 100 with no replenishment. Bold rows are results after 15 and 20 years.

Perc / Year	1%	2%	3%	4%	5%	6%	7%	8%	15%
1	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
2	99.00	98.00	97.00	96.00	95.00	94.00	93.00	92.00	85.00
3	98.01	96.04	94.09	92.16	90.25	88.36	86.49	84.64	72.25
4	97.03	94.12	91.27	88.47	85.74	83.06	80.44	77.87	61.41
5	96.06	92.24	88.53	84.93	81.45	78.07	74.81	71.64	52.20
6	95.10	90.39	85.87	81.54	77.38	73.39	69.57	65.91	44.37
7	94.15	88.58	83.30	78.28	73.51	68.99	64.70	60.64	37.71
8	93.21	86.81	80.80	75.14	69.83	64.85	60.17	55.78	32.06
9	92.27	85.08	78.37	72.14	66.34	60.96	55.96	51.32	27.25
10	91.35	83.37	76.02	69.25	63.02	57.30	52.04	47.22	23.16
11	90.44	81.71	73.74	66.48	59.87	53.86	48.40	43.44	19.69
12	89.53	80.07	71.53	63.82	56.88	50.63	45.01	39.96	16.73
13	88.64	78.47	69.38	61.27	54.04	47.59	41.86	36.77	14.22
14	87.75	76.90	67.30	58.82	51.33	44.74	38.93	33.83	12.09
15	**86.87**	**75.36**	**65.28**	**56.47**	**48.77**	**42.05**	**36.20**	**31.12**	**10.28**
16	86.01	73.86	63.33	54.21	46.33	39.53	33.67	28.63	8.74

[20] In times of resource insufficiencies or extreme cold rates are doubled or more, up to a maximum of 100%.

17	85.15	72.38	61.43	52.04	44.01	37.16	31.31	26.34	7.43
18	84.29	70.93	59.58	49.96	41.81	34.93	29.12	24.23	6.31
19	83.45	69.51	57.80	47.96	39.72	32.83	27.08	22.29	5.36
20	**82.62**	**68.12**	**56.06**	**46.04**	**37.74**	**30.86**	**25.19**	**20.51**	**4.56**
21	81.79	66.76	54.38	44.20	35.85	29.01	23.42	18.87	3.88
22	80.97	65.43	52.75	42.43	34.06	27.27	21.78	17.36	3.29

Three years is the average length of time between births for hunter-gatherers (Kelly 1995, Table 6-7; Pennington 2001, 184). The HomininSpace model assumes that all fertile women bear one child every *n* year. This is implemented with a birth-rate of $\frac{100}{n}$% of all female adults giving birth to a single new-born[21]. Ethnographic data suggests that in general within a few years of reaching adulthood and after being married a first baby is born (Kelly 1995, 245-246; White 2013, 126). Population growth is exponential (Kremer 1993), and continues until carrying capacity levels of the environment are reached. In HomininSpace, for each year that population size exceeds carrying capacity, penalties are applied: growth rates are halved and death toll is doubled (cf. White 2013, 137).

When anthropologists compare nomadic populations with sedentary groups the birth interval for the nomadic way of life is longer and birth intervals are prolonged to at least four years (Short 1987). It appears that these intervals mainly depend on energy recovery after birth, which in turn depends on food quality and food availability (Valeggia and Ellison 2009). Fine-tuned birth and death rates are important elements of a realistic simulation for hominins. It might be possible to obtain more realistic birth rates from morphological features from hominin skeletons (e.g. Gunz *et al.* 2010), or from genetic profiles (Arenas *et al.* 2013). Since these rates are important for population distribution, comparing these rates to other species, modern humans in particular, is highly recommended (as done by Zubrow (1989), Skinner (1997) or Flores (1997)).

In most hunter–gatherer populations, fertility has a parabolic character with few births occurring after reaching an age of 40 (Pennington 2001, 175). During the fecundity period the average hunter-gatherer woman produces five to six children, but a mean of eight is not exceptional (Hewlett 1991, Table 2; Kelly 1995, 244; Pennington 2001, Table 7.2). Note that in HomininSpace it is assumed that hominin females give birth to one new born per delivery. A variety of factors may influence fertility (the number of children born),

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[21] Twins are a practical issue with HGs. Australian aboriginals immediately killed one of any new-born twins, since it is impossible to carry two infants while foraging. HomininSpace assumes only one new-born per pregnancy.

reproductive span (the period in which reproduction occurs) and birth-intervals, including ovarian function, contraception and abortion, infanticide, coital frequency, nutritional stress, and lactation (e.g., Hill *et al.* 2007; Kelly 1995; Pennington 2001; White 2013, 125). Most of these factors are culturally defined and thus impossible to quantify for the past while others did not exist for prehistoric hominins. Only nutritional stress is quantifiable and responded to as discussed above.

Population growth in the HomininSpace model depends on mortality and birth rates that are included as parameters in the model. They are applied at the end of every year. Distribution within the population segments is assumed to be uniform. Thus in each time step for each age segment the number of people in that age segment divided by the length of the segment move up to the next segment (with any deaths subtracted). Newborns, to be added to the first segment, are calculated using women of the `fertile` age segment. The mathematical model is given below (Equation 8). Base mortality rates and birth percentages are constant throughout the simulation period, assuming that health and fertility did not substantially improve or decline in the Late Pleistocene, although local resource shortages impact both. In the calculations that follow *Pre(t)* is the number of pre-fertile hominins at time *t*. *Fertile(t)* is the number of fertile hominins and *Post(t)* the number of post-fertile individuals. For each segment there is a specific mortality rate *dPre, dFertile* and *dPost.* The length of the pre-fertile segment is 15 and the length of the fertile segment in this example is 25. New population numbers for time *t+1* are calculated as follows, with *b* the birthrate in percentages[22]:

```
Pre(t+1)     = Pre(t)-dPre*Pre(t)-Pre(t)/15+(b/100)*(Fertile(t)/2);
Fertile(t+1) = Fertile(t)-dFertile*Fertile(t)-Fertile(t)/25+Pre(t)/15;
Post(t+1)    = Post(t)-dPost*Post(t)+Fertile(t)/25;
```
Equation 8: Calculating the number of hominins per segment for the next time step.

An example of results from these calculations is shown in Figure 20. These are taken from the spreadsheet '*HomininSpace Population Calculator.xlsx*' which implements the demographic model mathematically (see Supplementary Materials). Figure 21 contains seven graphs presenting population growth (or reduction) for different illustrative values for the demographic parameters. This figure uses the same initial sizes as in the spreadsheet in Figure 20 and serves to illustrate the effect of subtle changes to these parameters. Values for the selected parameters define the population through time and are
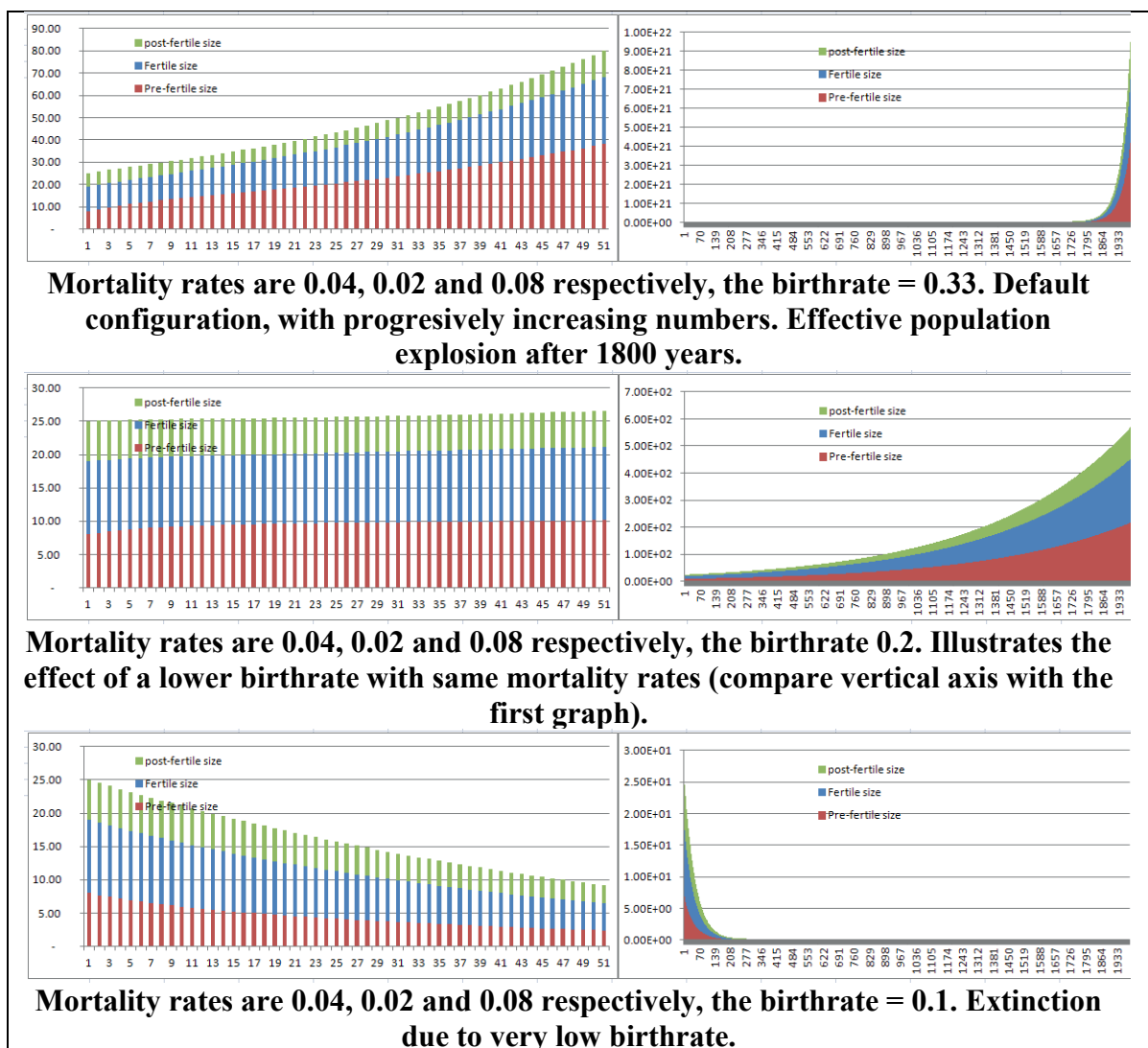
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[22] Based on the calculations shown in http://www.di2.nu/pop_sim.html, accessed June 2012.
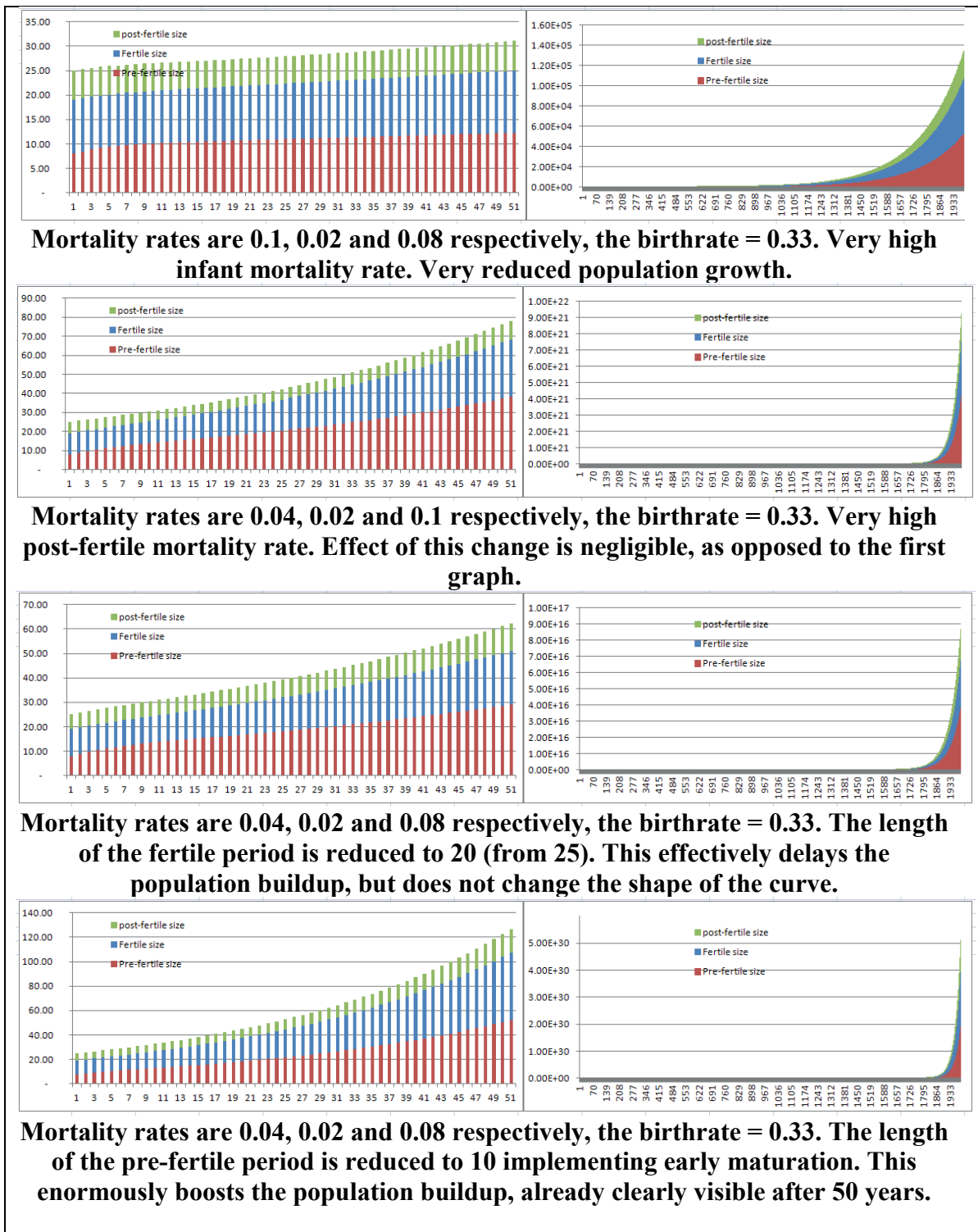
therefore included as parameters in the HomininSpace model (birthrate, segment sizes and mortality rates per segment).

Year	Newborns	Pre-fertile size	Pre-fertile deaths	Becoming fertile	Fertile size	Fertile deaths	Becoming post-fertile	post-fertile size	Post-fertile deaths	Total
0	1.82	8.00	0.32	0.53	11.00	0.22	0.44	6.00	0.48	25.00
1	1.79	8.96	0.36	0.60	10.87	0.22	0.43	5.96	0.48	25.80
2	1.79	9.80	0.39	0.65	10.82	0.22	0.43	5.92	0.47	26.54
3	1.79	10.54	0.42	0.70	10.82	0.22	0.43	5.88	0.47	27.24
4	1.79	11.20	0.45	0.75	10.88	0.22	0.44	5.84	0.47	27.92
5	1.81	11.80	0.47	0.79	10.97	0.22	0.44	5.81	0.46	28.58
6	1.83	12.35	0.49	0.82	11.10	0.22	0.44	5.78	0.46	29.23
7	1.86	12.87	0.51	0.86	11.26	0.23	0.45	5.76	0.46	29.89
8	1.89	13.35	0.53	0.89	11.44	0.23	0.46	5.75	0.46	30.54
9	1.92	13.81	0.55	0.92	11.64	0.23	0.47	5.75	0.46	31.21
10	1.96	14.26	0.57	0.95	11.86	0.24	0.47	5.76	0.46	31.88
11	2.00	14.70	0.59	0.98	12.10	0.24	0.48	5.77	0.46	32.57
12	2.04	15.13	0.61	1.01	12.36	0.25	0.49	5.79	0.46	33.28
13	2.08	15.55	0.62	1.04	12.62	0.25	0.50	5.82	0.47	34.00
14	2.13	15.98	0.64	1.07	12.90	0.26	0.52	5.86	0.47	34.74
15	2.18	16.40	0.66	1.09	13.19	0.26	0.53	5.91	0.47	35.51
16	2.23	16.83	0.67	1.12	13.50	0.27	0.54	5.96	0.48	36.29
17	2.28	17.26	0.69	1.15	13.81	0.28	0.55	6.03	0.48	37.10
18	2.33	17.70	0.71	1.18	14.13	0.28	0.57	6.10	0.49	37.93
19	2.39	18.14	0.73	1.21	14.46	0.29	0.58	6.17	0.49	38.78
20	2.44	18.59	0.74	1.24	14.80	0.30	0.59	6.26	0.50	39.66

Figure 20: Population calculations for a group with initial size 25: Pre=8, Fertile=11 and Post = 6. Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.33.

Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.33. Default configuration, with progresively increasing numbers. Effective population explosion after 1800 years.

Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate 0.2. Illustrates the effect of a lower birthrate with same mortality rates (compare vertical axis with the first graph).

Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.1. Extinction due to very low birthrate.

Mortality rates are 0.1, 0.02 and 0.08 respectively, the birthrate = 0.33. Very high infant mortality rate. Very reduced population growth.

Mortality rates are 0.04, 0.02 and 0.1 respectively, the birthrate = 0.33. Very high post-fertile mortality rate. Effect of this change is negligible, as opposed to the first graph.

Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.33. The length of the fertile period is reduced to 20 (from 25). This effectively delays the population buildup, but does not change the shape of the curve.

Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.33. The length of the pre-fertile period is reduced to 10 implementing early maturation. This enormously boosts the population buildup, already clearly visible after 50 years.

Figure 21: Population composition after 50 years (left) and after 2000 years (right) with unlimited carrying capacity. Graphs visualize typical exponential growth and are created with "HomininSpace Population Calculator.xlsx", see Supplementary Materials.

5.3   What does it take to be a Neanderthal - energy requirements

For practical reasons the model in HomininSpace parameterizes overall mean subsistence values differing per age segment, constant through time and space and averaged over sex. In the model a carrying capacity of X indicates how many kilograms edible meat are

available for consumption. It is assumed that hominins are capable of extracting that amount from the environment. These kilograms meat are converted into kcal and that gives a maximum to the amount of available energy. This does not mean the population will always be at maximum level (X*kcal/hominins). Instead mortality and birth rates for hominins are positively or negatively adjusted based on whether the population level and their energy usages are above or below the local carrying capacity (White 2013, 137). For every year with resource shortages a penalty is applied to birthrate (that is halved) and mortality rates (which are doubled). These rates return to normal when sufficient resources are found. When there is less than 10% of the required resources available, a group is immediately removed.

Energy requirements for modern humans are suggested to average 2000 kcal, but this number varies according to activity, sex, age, size, etc. (Kelly 1995, 101). Energy, obtained from digested food, is spent on movement, resting, sleeping, thermoregulation including diet-induced thermogenesis, daily activities, reproduction, digesting food, and maintenance and growth of the body (Snodgrass and Leonard 2009). Isotopic analysis of Neanderthal bones suggests that most of their protein intake came from animal protein and fat (Richards *et al.* 2000; Snodgrass and Leonard 2009) which does not exclude however consumption of additional types of food that are not reflected in the isotope data.

Neanderthal energy intake is estimated to be higher than that of modern day modern humans based on a larger body mass and more muscles, high levels of physical activity and intake of high protein diets, mostly meat (Aiello and Wheeler 2003; Churchill 2005; Klein 2009b; Snodgrass and Leonard 2009; Steegmann *et al.* 2002). Comparative research amongst modern day northern populations with similar lifestyles suggests an elevated Basal Metabolic Rate (BMR) as a response to colder climates. Higher energy requirements (intake and increased travel costs due to physiological properties) can influence mobility and will influence the effective foraging radius, the frequency that campsites are moved and investments in furniture and technology (MacDonald *et al.* 2009; Verpoorte 2006).

Energy supply is limited and must be extracted from the local environment (Bird *et al.* 2009). Some researchers suggest that an average Neanderthal would expend between 3000 and 5500 kcal/day, depending on physique, activities, age and sex (Churchill 2005; Churchill 2006; Sorensen and Leonard 2001). The mobility cost for reproductive women would be in the high end (Wall-Scheffler and Myers 2013). Sorensen and Leonard (2001) estimated energy requirements of 4000-7000 kcal for male Neanderthals, and 3000-5000

kcal for women. Snodgrass and Leonard (2009) suggested a similar amount for women but 4000-6000 for men. Steegmann *et al.* (2002) estimated 3360-4480 kcal were needed for male Neanderthals. And Froehle and Churchill (2009) distinguished cold and temperate climates, with energy use in temperate zones 3227-3527 for males, and 2297-2547 kcal for females. In colder periods energy use would amount to 4469-4877 kcal per day for men, and 3180-3190 for females. MacDonald *et al.* (2009) found 5020 kcal per day for male and 4590 kcal per day for female Neanderthals, based on BMR estimations from skin surface area. From body mass calculations they found values of 4450 kcal/day and 4230 kcal per day. They used the maximum relative amount of energy expenditure above basal needs for hunter-gatherers (MacDonald *et al.* 2009, 215). However, the assumed higher body mass of Neanderthals from which these estimates are reconstructed is contested (Heyes and MacDonald 2015). The exact energy needs are thus disputed but that Neanderthals need energy and extract it from the environment is a given fact.

Energy is derived from the sun and becomes available in a landscape as flora and fauna. Isotopic analysis of Neanderthal fossil material suggests that most of their food intake came from animal protein and fat (Richards *et al.* 2000; Snodgrass and Leonard 2009). Research has shown that Neanderthal diet in different periods and environmental conditions focused on medium to large terrestrial game (Hublin 2009; Salazar-García *et al.* 2013). Fish (Bocherens *et al.* 2013), small terrestrial and aquatic game (Archer and Braun 2013; Richards and Trinkaus 2009), birds (Fiore *et al.* 2016 but see Rufà *et al.* 2015) and vegetables (Henry *et al.* 2011) were all consumed by Neanderthals but meat was likely the main component of their diet (Hardy *et al.* 2015), maybe comparably limited in diet breath to some earlier hominins in Wallacea (O'Connor *et al.* 2017). Meat contains high quality protein and the essential nine amino acids that humans cannot make themselves and is one of the most successful ways of coping with energy needs in cooler environments (Steegmann *et al.* 2002, 571). Meat is denser than plant materials and contains some essential minerals, including iron, glucose and some vitamins (Kelly 1995, 105).

Meat can provide around 3000 kcal/kg (Diem and Lentner 1962) and is included as a parameter in the HomininSpace model. The calculations further assume a 60% available meat return on live animal weight (White 2006, 11), but see Lyman (1979) or Stewart and Stahl (1977) with lower percentages). Today butchery results deliver similar meat percentages. See for instance http://lovelivegrow.com/2011/01/how-much-meat-from-a-pig/, accessed 2 August 2013. Here a return percentage of 48% is mentioned, but larger animals tend to have larger percentages of usable meat and since blood and marrow in the

past probably had greater value than today the 60% quoted is likely not far off the useable percentage . In particular, in order to prevent protein poisoning from eating too much lean meat, maintain vitamin C levels, and to get essential carbohydrates and fats, a hunter could eat raw meat, plus internal organs like the liver and brain or extract marrow for the additional materials (see Speth (2010), also for other risks and limitations of high-protein intake). In certain cultures hunting large and dangerous animals serves social or symbolic purposes (Speth (2013) and references therein) but in HomininSpace all hunting is assumed to be subsistence related. This assumes that time and effort are optimally spent in hunting and gathering (see for example Dusseldorp (2009)).

5.3.1 Temperature tolerance

The Late Pleistocene is characterized by a generally lower annual mean temperature distribution compared to today. Exposure to extreme cold could have increased the energy requirements of Neanderthals compared to ethnographic data even further. The specific physique of the Neanderthals including shorter limbs and high muscularity offered only limited advantages for coping with cold temperatures (Aiello and Wheeler 2003; Snodgrass and Leonard 2009; Sørensen 2009). It is suggested that an elevated BMR might be related to colder climates (Churchill 2009).

Some of the energy requirements for preventing heat loss from the bodies of Middle and Late Pleistocene hominins must have been generated or sustained using external means which could include domestic fire and/or clothing. It is estimated that about 5477 Watt per month would be needed to warm and provide cooking fuel for a mixed group of about 25 Neanderthals (Sørensen 2009). This is about 1.5 kilogram of wood per day per individual, providing 4.8W/kg or 1136 kg wood per month for the group. Although wood supply can be limited in certain environments like grasslands and cold rugged areas (Pryor *et al.* 2016), the model in HomininSpace assumes that alternative fuels in the form of animal dung or bones were available and that heating through fire or furs was no limiting factor to the modelled hominins. Internal resistance to cold and cultural means to mitigate climate effects are combined into one model parameter, the *temperature tolerance*. This threshold is the minimum temperature where hominins still survive. If at any time the coldest reconstructed temperature falls below this threshold, the hominins will die. Benito *et al.* (2016) show that the coldest temperature is a good predictor of habitat suitability for Neanderthals.

5.4 Are Hominins social animals? - hominin groups

Hunting animals in groups requires cooperation and coordination of efforts (Marín *et al.* 2017). Living and hunting in social groups facilitates hunts with game driving, the final kill and the distribution of the meat afterwards. Most authors therefore assume that Neanderthals moved and hunted in groups (Radloff and Du Toit 2004; Kaplan *et al.* 2000 and the papers in the special edition of Quaternary International, Volume 297, 2013: "Worldwide Large-Scale Trapping and Hunting of Ungulates in Past Societies"). In these groups non-breeding females might have assisted male hunters (Biesele and Barclay 2001; Kuhn and Stiner 2006). Other foraging activities are also often more effectively done in groups (for instance bee honey extraction, see Mulder *et al.* (2000)).

However, there is hardly archaeological data supporting the theory that Neanderthals actually lived and foraged in groups, but extended family structures have been suggested for the genetically related individuals identified in El Sidron (Lalueza-Fox *et al.* 2011. Teamwork at collaborative tasks has been attested with chimpanzees suggesting a deep origin within the hominids (Melis and Tomasello 2013). For an evolutionary pathway to cooperative social behaviour in hominins see for instance Shultz *et al.* (2011) and Lehmann *et al.* (2007). The underlying model in this study assumes that hominins live in groups, comprised of individuals of different age categories. Maximum group size is a parameter in the model.

The model in HomininSpace assumes that whatever the composition in age and sex when sufficient resources are available in the area, each group is capable of finding and retrieving all resources necessary to meet its subsistence requirements. Differences in hunting and gathering behaviour between males and females (e.g. Bird and Bliege Bird 2005), or between adults and children (MacDonald 2007; White 2013) are of no influence on the foraging efficiency of the modelled group as a whole. With insufficient resources groups will suffer as described in the next subsection. Groups, when sufficiently repopulated, have the potential to live forever.

5.4.1 Group demographics - new groups, group extinction, merging of groups

A group moves through the landscape and interacts with the environment and other groups as a whole (cf. Agustí and Rubio-Campillo (2017)). Groups can procreate by splitting a new group from the mother group. When that happens a group is created consisting of fertile adults of both sexes to ensure healthy growth potential. Groups look for

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opportunities to split when the total group size exceeds a given, parameterized value. The default for this number is 50, the largest size for what Dunbar (1993) refers to as the overnight camp or band size, derived from ethnographical observations of traditional hunter-gatherers, but different group sizes have been observed (Hill and Dunbar 2003; Zhou *et al.* 2005; Hamilton *et al.* 2007; Layton and O'Hara 2010, 101). The model in HomininSpace assumes that groups exceeding the maximum size will split. In the HomininSpace model new groups can also be created in *core areas*. These are locations on the map in which, conditions permitting, new groups are created (see subsection 9.4.2). A newly created hominin group consists of 25 individuals, with 15 being of pre-fertile age (cf. Sørensen (2009)).

Groups can join other groups (merge). Especially when the group size is below a minimum threshold (this is a parameter) they will send a join request to other groups in the area around them aiming to avoid extinction (Soltis *et al.* 1995). When another group agrees to such a merger proposal the populations are added together and the joining group, now an empty administrative unit, is removed from the simulation. A group can refuse a join request because there are too few resources for their own number in the area, or when the group size already exceeds the maximum size[23].

Ethnographic research has shown that group extinction is a common process in hunter-gatherer societies, where groups are eliminated for a variety of reasons (Soltis *et al.* 1995, 477). The percentage of eliminated groups varies wildly across cultures and therefore the model in HomininSpace has adopted a viability criterion. Since death is a stochastic process in HomininSpace, and during each time step that a group is hungry only a percentage of a group dies, a minimum threshold has been established after which a group is considered extinct. The group cannot be sustained when the number of individuals falls below a parameterized minimum (Birdsell 1968; Wobst 1974). The default for this threshold is three fertile adults, considered the minimum size critical for regeneration and survival (Nabel *et al.* 2013). This number is however parameterized and if a group contains this number or less reproductive adults it is considered not viable and if it does not join another group that year it is removed from the simulation. Groups are removed from a simulation when they move out of the simulation area.

Newly created groups are not able to interact with other groups for several time steps after creation. Since a new group is always created within the foraging range of the parent group

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[23] Other reasons are easily found but have not been implemented, like different cultural affiliations or just chance.

any new group is always in direct competition for resources with other groups, and will most likely become "hungry" (see below). Such new groups are allowed to merge with other groups only after a certain number of years, to prevent an intense creation-hungry-merge cycle. The number of these years is included as a parameter. Although exact ranges are unknown, this modelled behaviour is partly based on the intrinsic mammal dispersal pattern that drives away all or some of one's offspring, to avoid inbreeding or competition for resources or members of the opposite sex (Dobson 1982). In humans most often young males are expelled, sometimes accompanied by fertile female companions. With mammals in areas with high population densities emigration rates increase, forcing groups to move away (Baker 1978). Such expansive behaviour is sometimes even actively promoted genetically, especially in frontier regions (Phillips, Brown, *et al.* 2006).

5.4.2   Social interaction - home range and foraging range

Each grid cell in HomininSpace can contain one group only. When a group is present this cell is referred to as the *home range* of the group and will be defended against other groups at all costs. Small groups defending their own home range stand a good chance even against much larger groups (Crofoot and Gilby 2012). Therefore, the model in HomininSpace prevents other groups from occupying an already claimed home range or even exploiting it in their foraging activities. Each grid cell, and thus also the home range, is implemented as an area of 10x10km or 100km^2. Such a limited area hardly ever produces enough resources to meet the subsistence needs of a group for longer periods. Members of the group will have to constantly leave the home range and forage outside the protected area. They will have to collect resources within the *foraging range* (FR) for that group. Since a time step in HomininSpace is one year, this is actually the *annual range* as generally referred to in the literature.

The FR is variable and recalculated for each individual group based on the characteristics of that group and the environment each year. The range is implemented as a square area around the home grid cell (not a circle!). FR gives the number of grid cells from the center to any side. The length of one side is two times the range plus one (see Figure 22 and below). The flexibility of the range reflects the ability of hominins to obtain resources from any environment. Foraging ranges can optionally be limited by a maximum size, included as a parameter in the HomininSpace model. For an example of modern day hunter-gatherer ranges see the values collected by Kelly (1995), table 4.1, or by Weaver and Steudel-Numbers (2005).

At the beginning of each simulated year the estimated required FRs for all groups are computed in random order. These ranges are based on the subsistence needs of the members of the group, the remaining available resources in the area (defined by the climate parameters and previous consumption), and the presence and subsistence needs of other groups that occupy nearby regions. To calculate the FR the number of individuals in each age segment is multiplied by the energy needs for members of that segment and added together. Then the available energy (usable meat) from the home range is subtracted. If there are still resources needed the foraging range is increased by one grid cell. The energy in each cell within the new foraging range is added together. If this is not enough to satisfy the needs of the group the FR is again increased and this process is repeated until the energy requirements are met or the maximum FR is reached (see Figure 22).
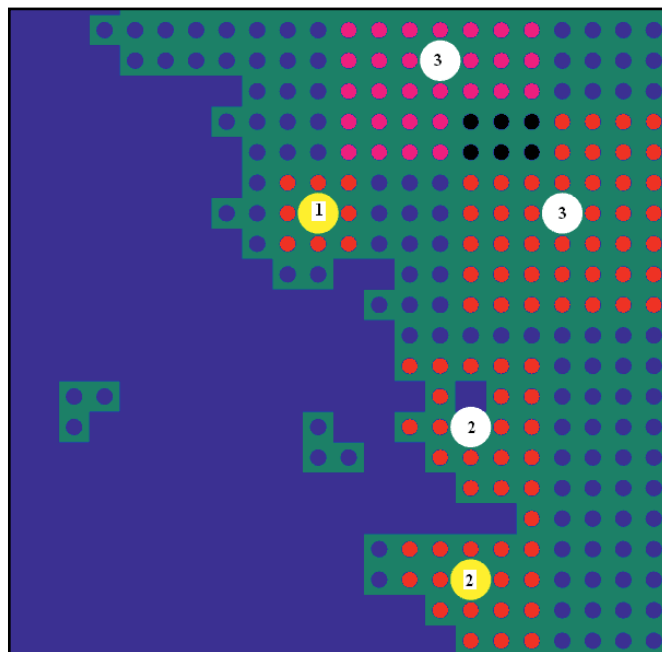
Figure 22: Foraging ranges and resource acquisition. Larger circles are home ranges with the value of the foraging range of the groups in the centre. A value of '2' means two grid cells in all directions (horizontal, vertical and diagonal) are included when foraging for resources. Black are shared grid cells.

When a FR is calculated that supplies enough energy all grid cells within that foraging range are 'claimed' by this group. That is, all grid cells have a counter for the number of claims, and within the foraging range all counters are increased by one. All grid cells that have received two or more claims can provide only that fraction of the available energy to each claiming group. The number of cells in a foraging range = $(2*range+1)^2$. So for range=0 the number of cells is 1, for range=1 the number of cells = 9, for range = 2

cells=25, for range=3 cells = 49, etc. If no maximum foraging range is set, the foraging area can theoretically include the whole map area.

Subsequently all groups consume the energy they need, in random order. Groups with not enough resources will consume all available energy in their foraging range. With insufficient resources (for instance because another group has consumed part of the claimed shared resources or because the foraging range is too small) a group is considered *hungry*. Hungry groups have penalties on birth rates and suffer from increased death rates. Groups are allowed to move through another foraging range in search for food (for a comparative example with hyena's see Hofer and East (1993)). The most likely situation in which a group A is deprived of resources is when group B claims cells in the FR *after* the computation of the foraging range for A.

5.4.3 Mobility

If the local climate deteriorates this will affect resource availability and influence hominin presence in the area. Generally, populations will decline, either through migration following preferred habitats or through local extinction of individual groups (Bradtmöller *et al.* 2012; Dalén *et al.* 2012; Hublin and Roebroeks 2009; Roebroeks *et al.* 2011). Net population dynamics in general are steered by four processes: immigration into the area, emigration out of that area, the rate of reproduction of the species under the given circumstances and the number of individuals that die per time unit. Climate change will cause geographical ranges for species to contract, expand, shift or stay the same depending on the climatic tolerances and environmental conditions (MacDonald *et al.* 2012; Stewart *et al.* 2010, 661).

Groups move through the landscape and available energy steers their direction. In the model of HomininSpace there are two types of hominin mobility strategies, referred to as *static* mobility and *dynamic* mobility. Hominins that follow the static mobility strategy will move through the landscape until they find an area that suits their subsistence needs. This is where they will stay even when resources are depleted (with insufficient resources groups will shrink and subsequently need fewer resources). There is one exception where static groups that have decided to stay can move, and that is when the group size is getting below the viability threshold. When the group is about to go extinct they have the possibility to join another group if such a group is in the area and if that group will take them. Dynamic mobility is characterized by constant movement, always directed towards the most favourable area within range. As groups tend to deplete the resources in the area

where they stay they will move almost every year towards other areas that have relatively more resources.

Movement for both strategies is identical. A group that is about to move will scan the environment for the best *habitat patches* in an area with a radius twice the foraging range. This factor two is derived from the radius leap-frog pattern described by Binford (1982) where residential moves between home bases are twice the foraging distances of a group. Habitat patches are defined as the sum of the available energy for each cell combined with its surrounding adjacent eight neighbours. When implementing movement it was found that hominin groups should not be attracted by the high productivity of single grid cells to avoid so called *death traps*: a grid cell with high productivity surrounded by cells with very low productivity. Groups that move onto such attractive cells will have problems sustaining themselves and quickly vanish. Examples of these death traps are small islands and promontories, both surrounded by mostly zero productivity sea cells.

When the cell with the highest productivity for this group is found, the group moves onto that cell, the new foraging range for this location is computed and for each cell in the new foraging range the presence of the group is recorded (claim on resources). Thus other groups will have to share the surplus of resources of those cells with this group. There are no separate locomotion costs (Alexander 2002) associated with these residential moves since they are included in the energy budgets for each individual. The single move in each time step is in effect the net displacement of all residential moves that year. Thus an effect of energy requirements on frequency of displacement or duration of stay (Verpoorte 2006) is not included in the HomininSpace model.

Groups will never move onto sea or lake patches, and they will not move onto a cell that is already occupied by another group. When the borders around the simulation area are activated, they also never move to a grid cell located near any border. If these borders are not activated groups can leave the simulation completely.

5.5   Overview: building blocks for the underlying model

Table 9 summarizes the model elements in the HomininSpace model as identified in this chapter. The default values are provided for illustrative purposes and have been discussed elsewhere (Scherjon 2015a). HomininSpace identifies three age categories for hominin species: each individual is either pre-fertile, fertile or post-fertile. Model variables included in this table can be one of two types:

- *Parameters*: variables that can be given a value and that control the behaviour of the agents or the system in a certain way. These are read from the parameter input file, the naming of the variables in the table below is consistent with that file;
- *Constants*: constant values, the same for all simulations; these can be modified only by changing the source code and recompiling the executable that runs the simulations.

Table 9: Variables on hominin behaviour included in the HomininSpace model.

Name	Type	Description	Default value
CohortSize_PreFertile	parameter	The size of the pre-fertile segment.	15
CohortSize_Fertile	parameter	The size of the fertile segment (the length of the post-fertile segment is not limited).	25
DeathRate_PreFertileCohort	parameter	Mortality rate for the pre-fertile segment per group.	4
DeathRate_FertileCohort	parameter	Mortality for the fertile segment per group.	2
DeathRate_PostFertileCohort	parameter	Mortality for the post-fertile segment per group.	8
BirthRate	parameter	Birth-rate in a percentage of the fertile category per group (a value of 33% means one child per three years for each female).	33
Subsistence_PreFertileCohort	parameter	Energy needs for an individual in the pre-fertile segment in kcal.	3,000
Subsistence_FertileCohort	parameter	Energy needs for an individual in the fertile segment in kcal.	4,000
Subsistence_PostFertileCohort	parameter	Energy needs for an individual in the post-fertile segment (in kcal).	3,500
Years_Before_Group_Maturity	parameter	Period in years before newly created groups can interact with other groups (for instance to join).	5
GroupSize_BeforeMerge	parameter	Minimum size (threshold) for the group. If the size of the groups falls below this number the group will attempt to merge, if possible.	3
GroupSizeFertile_BeforeMerge	parameter	Minimum size for the fertile category. If this segment contains fewer individuals, the group will also attempt to merge.	3
GroupSize_BeforeSplit	parameter	Maximum size of a group. If the number of individuals exceeds this number the group will split into two groups.	50
Calories_Per_Kg_Meat	parameter	The amount of kcal that can be extracted from one kilogram of meat.	3,000
Temperature_Tolerance	parameter	Minimum temperature that can be sustained by the hominins. If the coldest temperature during a year falls below this value the hominins die.	-18
Max_ForagingRange	parameter	Maximum annual foraging range. Groups cannot forage outside this range.	15
Penalty growthrate	constant	Penalty applied to the growth rate when subsistence requirement are not met.	0.5

Penalty mortalityrate	constant	Penalty applied to all mortality rates when subsistence requirement are not met.	2
FemaleMale	constant	The percentage of females in the population.	50
usableMeat	constant	The percentage of one kilogram of animal that is usable meat for meeting subsistence needs.	60
maxGroup size	constant	The maximum size for a group before offspring is created, in individual members.	50
newGroups prefertile	constant	The size of the pre-fertile segment in newly created groups (from core areas).	8
newGroups fertile	constant	The size of the fertile segment in newly created groups (from core areas).	11
newGroups postfertile	constant	The size of the post-fertile segment in newly created groups (from core areas).	6
Homerange	constant	The number of grid cells that are considered by a group as their territory.	1
ViableGroup-size	constant	If the number of individuals in the group falls below this number the group is removed.	3
Scanning modifier	constant	The scanning range is defined by default as two times the annual foraging range. Within scanning range the hominins are aware of resource availability.	2
Factory ScanningRange	constant	The radius (in grid cells) of the area that a factory must monitor when creating new groups.	30
openBorders	constant	Defines if borders are open or closed. If True (open), hominins can leave the simulation area.	False