

Persistence in Neanderthal models

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1. Introduction

The persistence of Neanderthals and their subsequent replacement or partial absorption by modern humans is viewed by many as one of the more intriguing enigmas of palaeoanthropology. How they survived as a species, how they survived the hardships of severe ice ages, and why their peculiar morphological signal suddenly disappears from the archaeological record are still uncertain aspects (Hajdinjak et al. 2018; Hublin 2017). Many suggestions have been put forward to explain their disappearance and our relative success (Vaesen et al. 2021), including competition with more competitive modern humans (e.g. Richards and Trinkaus 2009; Wall-Scheffler 2012), environmental conditions (e.g. Golovanova et al. 2010; Müller et al. 2011), or demographic factors (e.g. Mellars and French 2011; Vaesen et al. 2019). However, most of these hypotheses remain largely untested because many aspects of the daily life of Neanderthals are still poorly known (Anwar et al. 2007).

Computer-based simulation techniques are well suited to explore explicit models of ideas about the past, and are used for hypothesis exploration, theory building, and method testing (Lake 2014). Here, we address the patterns of presence and absence of Late Pleistocene Neanderthals in western Europe (Scherjon 2019) by presenting results from simulations made with ‘HomininSpace’, an agent-based model designed to simulate hominin dispersals and persistence. The HomininSpace simulation tool explores different hypotheses about Neanderthals and their behaviour in a reconstructed environment with changing sea-levels and varying climate. In each simulation, the modelled presence of hominin agents is compared against the archaeological record by computing matches between the simulated and archaeologically documented presence of Neanderthals (cf. Janssen 2009).

Neanderthals are the most frequently modelled non-sapiens hominin species, with simulation studies regularly addressing their replacement by modern humans (e.g. Barton and Riel-Salvatore 2012; Greenbaum et al. 2019). However, in general Neanderthals are constructed as a less capable and inferior hominin with, for instance, a lower birth rate (Zubrow 1989), higher mortality rates (Flores 1998; Sørensen 2011), or lacking a ‘population pump’ (Kolodny and Feldman 2017). Not surprisingly, these studies have confirmed that if such inferiority is assumed and implemented using selected model parameter values, Neanderthals would indeed have been likely to go extinct (e.g. Flores 2011; Gilpin et al. 2016; Horan et al. 2005). Such an outcome does not prove that Neanderthals were less capable than modern humans, but merely the obvious that if handicaps are modelled, the impeded species will suffer (Vaesen et al. 2019).

Since many details from the daily lives of Neanderthals are unknown (including exact birth rates, energy requirements, and foraging modes), HomininSpace constructs hominin models by autonomously running simulations while assigning key parameter values for a generic hominin dispersal model. This model consists of parameters from demographic, subsistence, and social domains (see below). Due to the number of parameters and the wide range of possible values for each model parameter in HomininSpace, the total parameter value space is huge, and the sheer number of possible unique models is enormous—almost 400 million if we conservatively assume that each parameter can take only three values out of its possible range: the minimum, medium and maximum value. A range of hypotheses and combinations thereof can be tested in the system where plausible values for the model parameters are found using a ‘genetic algorithm’ (GA), a technique borrowed from the artificial intelligence toolset to explore big datasets (Coello-Coello 2002; Forrest 1993; Grove 2014). The system can traverse the parameter space created by the set of all possible parameter value combinations to find those parameter values that will result in a simulation that matches well with the archaeological data given the selected hypotheses (Calvez and Hutzler 2006). First, a database of radiometrically dated archaeological Neanderthal sites for western Europe has been constructed for the simulation period (130-50 ka) to enable this comparison. Then, each simulation is validated against the presence and absence of Neanderthals through time in that database. The validation result (the qual-

ity of match with the archaeological data) for each simulation is compared against all other simulations to assess the explanation value of the implemented hypotheses. Noteworthy, each model also produces a viability score, a population level measurement of the potential to persist.

Population persistence in a simulation for a given period is the presence of at least one agent (group of Neanderthals) at the end of the model run. In order to address the ability of modelled Neanderthal populations to persist over time and through hardships, we use the conservation biology principles of representation, redundancy, and especially resilience (the '3Rs') (Smith 2011). First, representation is often taken as the breadth of genetic diversity. However, since HomininSpace does not model diversity between agents (they vary between complete simulations), the presence in different ecological settings or habitats has been considered (Smith et al. 2018). To assess the correlation between agents and habitats, simulations that include delimited habitats are compared to simulations with the same settings in which habitats have been replaced by an energy continuum. These show that there are no substantial differences, which suggests that the modelled Neanderthals were present in all habitats. Therefore, representation is directly linked to validation results. Second, redundancy is the number and spatial distribution of populations, with high values illustrating the ability to withstand large scale catastrophes. In HomininSpace, the number of individuals is irrelevant, only the resulting geographical distribution through time (since the archaeological record only provides presence data, no population densities). By definition, populations that survive until the end of the simulation period prove that sufficient redundancy is present in that model. This suggests that the persistence of modelled populations in HomininSpace depends primarily on their resilience over time (Crawford et al. 2020). Finally, in order to quantify resilience, we use the variable ViabilityIndex (see below).

The purpose of this paper is twofold. This paper will first describe the model, detail which parameters are included, and summarise the simulation method used to test many different hypotheses. Elsewhere (Scherjon 2019), we have discussed the simulation results in detail and provided interpretations and suggestions about some of the hypotheses that were implemented. Second, we will focus on the resilience of the created Neanderthal models based on the best results from the different configurations. We will show that the

flexibility offered by a model that incorporates variables from different domains achieves the resilience that enabled Neanderthals to withstand the most severe environmental hardships of the end of the Pleistocene in western Europe.

2. The model

The model underlying the HomininSpace simulation system consists of two major elements: (1) the environment and (2) the hominins. The environment consists of a topography that varies through time and that utilises current geography, bathymetry, and reconstructed global sea-level changes to calculate available landmass. Net Primary Production (NPP), the amount of energy remaining in vegetation from the process of photosynthesis after respiration, is considered a crucial factor driving population density (Tallavaara et al. 2018). An energy availability landscape derived from estimated NPP values is created using current and past distributions of key climate parameters, such as temperature and precipitation (see Scherjon 2019 for further details). Regarding the second element, the modelled agents represent hominin groups that forage through the environment, extracting energy from the landscape according to group size and energy requirements. The simulation period for all simulations starts at 130kya and ends at 50kya. We know that in this period Neanderthals were the only species in the area (Higham et al. 2014) and also that the strong disturbances of both the Eemian and the subsequent cooling of the last Glacial Period are included to test agent performance in extracting energy during varying climatic conditions.

The model is implemented in the Repast Symphony (version 2.2) simulation system (REPAST). REPAST creates the simulation environment, keeps track of model variables, executes turn-based model runs, and visualises simulation results. In REPAST, source code is primarily written in Java or in any other supported programming language. Furthermore, external libraries can be connected, and debugging of the agent-based models is facilitated (Macal and North 2009; North et al. 2013). Variation in models (behavioural change) is created by assigning different values to model parameters. Parameters (see Table 1) were selected as candidates for variation either because exact values are disputed in the current literature (birth rate, energy requirements for sub-

sistence, temperature tolerance, foraging range), they are directly related to other parameters (mortality or death rates), or they were found important to agent dynamics and interaction (cohort sizes, number of years before group maturity) (Scherjon 2019). The assigned values uniquely identify simulations for all parameters combined with the seed value for the random number generator. This combination is henceforth referred to as a ‘model’.

3. The simulations

The search for optimal solutions in simulated systems is computationally expensive, especially with an extensive environment and a large number of parameter combinations. HomininSpace is one of the first systems to employ a GA-based search and optimisation method that identifies models that match well the archaeological record while efficiently exploring the parameter space (Grimm and Railsback 2005; Grove 2014; Revay and Cioffi-Revilla 2018). The model parameter values are adjusted until an experimental optimum is reached with no substantial improvement in the simulation results for newly generated models (Calvez and Hutzler 2006). Due to the nature of the GA method, local optima are thus explored in the parameter space. The search ends when 100 new combinations have been tried that fail to score better than the maximum found so far.

In each simulation run, results are validated by comparing the modelled presence of agents representing groups of hominins against the empirical archaeologically attested presence in the past (Barton et al. 2011). From the literature, a database has been constructed with archaeological sites for which archaeological finds have been radiometrically dated to the simulation period (see Table 2). Sites without proper dating or with dates outside the simulation period were not included. Each of these absolute dates (D) with associated standard deviations (SD) is translated into time intervals defined as $[D+SD, D-SD]$. All matches between simulated and archaeologically attested presence are counted and used in calculating the simulation score. When, during a simulation, an agent moves onto a grid cell with a site that has a time interval, and when the current time step falls in that interval, the score is increased. The increment is reversed proportional to an interval’s length, with matches to shorter intervals contributing more to the final score than agents visiting

longer intervals. The final simulation scores can be used to compare individual simulations, assuming that a higher score means a better match with the archaeological record, and the better matching model is a more accurate description of the hominins living in the past.

The simulation area is divided into grid cells of 10km², and each archaeological site is connected to the enclosing grid cell. 83 archaeological sites with 470 dated finds are included in the database and distributed on the map—Table 2 provides a list of all the sites with the constructed intervals. Then, the simulation score (MatchedIntervalCoverage) is calculated by summing all interval scores for all sites (fig. 1). The theoretically maximum possible score for the chosen study area and period is 39,200, that is when all sites are continuously visited and all intervals fully matched.

In a typical GA, a population of potential solutions evolves within the solution space towards higher fitness function values (Forrest 1993). These are nature-inspired numerical optimisation techniques that operate in a virtual laboratory. The basic elements that compose evolutionary algorithms are a population of individuals to work with, a string with manipulable values that define individuals (referred to as the genes or the chromosome of that individual), and a fitness function that calculates how well adapted an individual is within the modelled environment (Michalewicz 1992).

In HomininSpace, an initial population of possible solutions ($n = 1500$) is constructed by assigning parameter values randomly from the domain of each parameter. Then, the user creates a specific scenario by selecting a combination of hypotheses to be explored. Each hypothesis has a switch that can be used to (de)activate specific model functionality that implements the hypothesis. Hence, simulations run for all the 1500 models in the initial population and, from these simulation results, high scoring models are selected with promising parameter combinations. Seven new models are generated through recombination ($n=4$) and single point mutation ($n = 3$) (fig. 2). Simulations are run for these new, evolved models that, alongside their results, are then added to the population. This process continues until no further improvement in the simulation score is found.

The following hypotheses can be incorporated into a scenario: (1) a preference for habitats; (2) a mobile or more residential mobility character; (3) the use of coastal resources (fig. 3); (4) using a maximum foraging range; (5)

crossing of open waters; (6) the presence of population core areas producing new hominin groups; and (7) the use of absence data. It is worth mentioning that a scenario can include more than one hypothesis. For instance, if the scenario includes coastal resources and the crossing of open waters, the best performing models will optimally use the extra resources from the coastlines where the ability to cross open water helps their dispersals match as many archaeologically attested Neanderthal locations and intervals. If the best model from this scenario outperforms the best model from a similar scenario, but without coastal resources, it can be argued that, all else being equal, Neanderthals would indeed have included shells and sea mammals in their diet (Fa et al. 2016). Thus, the archaeology from the research area and simulation period is used to autonomously calculate the best matching model for the given circumstances using the GA to evolve new models that produce more matches.

4. Analysis of the results

Each scenario was given a simple name and, for 18 scenarios, the best performing model was searched. For each scenario, at least 2000 simulations were executed; for some, many more were executed before convergence was achieved. Table 3 lists the maximum score achieved by the best model in each scenario, together with the number of needed simulations.

Table 4 lists the best performing models for scenario *Habitat-C* and it illustrates the effectiveness of the modelling system, with the best three scores from the initial population of 1500 models on top (generated with random parameter values), and the best three evolved models (created by the GA) below. For instance, the best-evolved model (*Evolved 1*) features a staggering annual mortality rate of 12% for the post-fertile cohort and an almost impossible high birth rate of 50, meaning that females reproduce every second year. The second-best model (*Evolved 2*) illustrates another approach with a more relaxed, but still high, birth rate of 43, contrasted by a relatively high mortality rate of 3% for the pre-fertile cohort (i.e. many children do not reach adulthood). Interesting features in this model are the lowered subsistence requirements for all three cohorts. Note that the best three evolved models have almost the same value for the MatchedIntervalCoverage (score) and therefore match the archaeological data equally well (see fig. 4 for an illustration of a good scoring

model).

The ViabilityIndex, which is the theoretical number of individuals remaining when a default hominin group (standard size 25) is followed for 100 years, given birth- and death rate values, is also included in the model. For instance, for model *Evolved 2*, the ViabilityIndex is equal to 30,712 (see Table 4), meaning that the population of 25 individuals will grow to 30,712 after 100 years. The ViabilityIndex gives a rough indication of the viability of a population without considering resource availability and can be used to assess the ability to persist.

When analysing the results in Table 3, we can identify two clusters of scenarios: those where the best models score around 30,000, and those that score substantially less. The names belonging to this last cluster are given in italics in this table and include, for instance, *Habitat-B* and *Habitat-D*. The cause for the lower scores is easily identified, as all these scenarios include absence of Neanderthals from the UK for certain periods; an absence that must be matched during the simulations. If only presence data is used in any model, theoretically an always omnipresent species would provide the maximum match with the data. In HomininSpace there is a clear tendency to achieve a maximum score with large populations; for instance, an increase in the birth rate will produce more agents, which therefore will allow a better match with the archaeology (e.g. see *Evolved 1* in Table 4). However, genetic data analysis has shown that Neanderthal population size was consistently small (Prüfer et al. 2014). In addition, excavation results highlight that, at least in many locations, Neanderthals were not always present at all sites all the time (e.g. see Discamps et al. 2011 for a general overview, or Bertran et al. 2013 for an example).

Modelling efforts and interpretation of simulation results where only presence data is matched must consider the inherent tendency of the system to simply create as many agents as possible to achieve maximum match with the data. One way to avoid this is to include absence data. As to our case, there is one large area for which the absence of hominins has been postulated for an extended period of time: the whole of Great Britain during MIS 5 and MIS 4 (Ashton 2002; Wragg Sykes 2017). The initial breach of the chalk barriers formed the Strait of Dover sometime during MIS 12, which since then has allowed a rising sea-level that has periodically isolated Britain from the main-

land of Europe (see Ashton et al. 2018). This assumed absence is implemented for an interval of 107 ka +/- 35 kyr, which represents most of the simulation period. To achieve absence for this period, evolution in the system attempts to slow down the spread of the Neanderthals. It does so in different ways, for instance, by reducing the birth rate, increasing death rates, or increasing subsistence requirements. However, this also means that many presence intervals are not met. In the current implementation of HomininSpace, avoiding absence violations is more important than reaching presence intervals. Thus, in these scenarios with absence activated, high scores are very difficult to obtain.

5. Discussion

In almost all scenarios with absence included, the ViabilityIndex of the evolved models is less than 100. The persistence probability of these modelled populations is extremely low, except for scenario *Energy C* where *Evolved 1* has a ViabilityIndex of 427 but a simulation score of 6273, which is a poor match with the archaeological data. All these populations, even with such low values for the ViabilityIndex, managed to survive in generally very low population densities and often remaining in the south of the simulation area, which automatically results in fewer matches with the archaeological data. If the absence test is not included, the system will attempt to spread Neanderthals everywhere, at any point in time, to maximise the match with the archaeological data, for instance via an increase in the birth rates to unrealistic levels. However, we know that Neanderthals were not everywhere as they are absent from the archaeological record in specific areas for specific time periods.

In all other scenarios, the GA creates more successful evolved individuals with values for ViabilityIndex that are high to extremely high, suggesting good persistence capabilities. The scores for all these evolved models are very similar, especially when we consider the uncertainty introduced into the model by using one standard deviation when calculating the match with the archaeological record. In other words, the HomininSpace simulation system can find values for the model parameters that allow Neanderthal populations to survive in varying and often difficult circumstances.

In order to obtain successful Neanderthal models, the system aims for resilience via the model's parameter values since a key element of a successful

model is survival at the end of the simulation period. The autonomic parameter value optimisation of the GA is consistently capable of using the flexibility in the model to realise persisting Neanderthal populations that vary depending on the tested hypotheses. Non-persisting models are eliminated from the system, while populations that disperse successfully are used to create models that produce more matches with the archaeology.

Both the test for absolute absence with very low scores and the system's tendency to create Neanderthals everywhere with very high scores produce unrealistic Neanderthals that have physically impossible parameter values or unlikely large population sizes. Alternatively, the system created other, more realistic Neanderthals, but their scores were not as high. With the GA being able to efficiently explore the huge parameter space, future efforts will be directed at a reconciliation of these two opposing forcing powers in the HomininSpace modelling system.

6. Conclusions

HomininSpace was designed to contribute to the discussion about dispersal and persistence of past hominins. Many parameters, some of which influence subsistence requirements, that effect population persistence and validated presence, were identified. Parameter values have been modified with a genetic algorithm, an Artificial Intelligence method aimed to find good scoring models through optimization techniques inspired by evolution. These models were used to address a set of hypotheses on Neanderthal behaviours in the landscape. The system autonomously explores the parameter space and finds a diverse set of models that are capable of persistence throughout the simulation period combined with an optimal dispersal through the geographical and archaeological dataset. The results have underlined the importance of absence data in model validation, and with the inclusion of data about the absence of Neanderthals in England, HomininSpace becomes a virtual laboratory where hominins evolve to match the archaeology with a novel implementation of representation, with redundancy where needed, and especially while showing resilience.

Access to the ABM model

Both the model and a copy of the detailed model description, including a design document following the Overview, Design and Details protocol can be obtained through the NSF funded Computational Model Library of the Network for Computational Modeling for Socio-Ecological Sciences (CoMSES).

Acknowledgements

I thank Wil Roebroeks, Kathy MacDonald, and Alexander Verpoorte (Leiden) for fruitful discussions about all aspects of this study. The paper profited from very constructive comments by one anonymous reviewer, and from extensive suggestions made by the Editors. This study was partly financed by the ‘NWO Spinoza prize’ awarded to Wil Roebroeks by the Netherlands Organization for Scientific Research (NWO).

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$$\text{MatchedIntervalCoverage} = \sum_{k=1}^{\text{CSTs}} \sum_{n=1}^{\text{\#intervals}} \frac{\text{visitCount}}{\text{length}}$$

Fig. 1. Combining the interval scores for all sites (CSTs) to compute the simulation score.

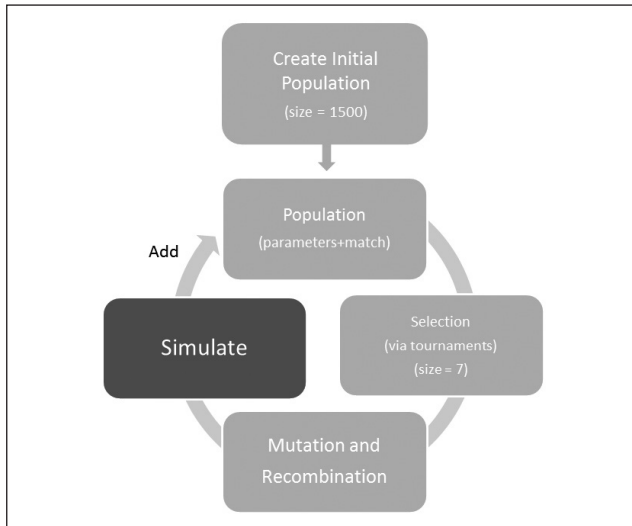


Fig. 2. Illustration of the genetic algorithm.

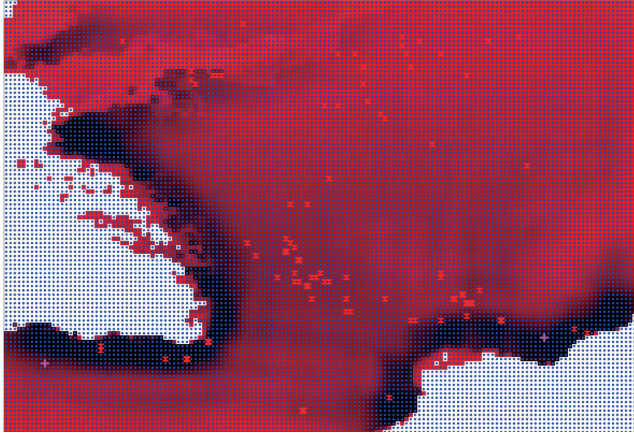


Fig. 3. Density map illustrating the attractiveness of coastal resources. The darker colours are areas where hominin groups spend most of their time.

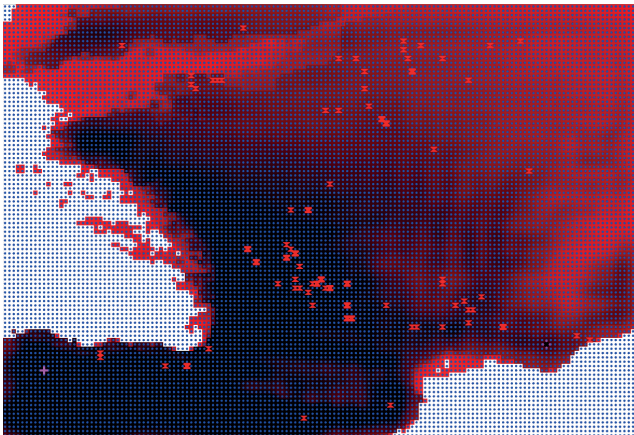


Fig. 4. Map showing population density through time for a model with a high MatchedInterval Coverage value.

Tab. 1. The 16 parameters of the HomininSpace model (Scherjon 2019: Tab. 13).

Name	Description
<i>BirthRate</i>	The number of females that conceive this year (a value of 33% means one child per three females, or one child every three years for a female).
<i>DeathRate_PreFertileCohort</i>	Death rate for the pre-fertile segment per group, the percentage that does not survive.
<i>DeathRate_FertileCohort</i>	Death rate for the fertile segment per group, the percentage that does not survive.
<i>DeathRate_PostFertileCohort</i>	Death rate for the post-fertile segment, the percentage that does not survive.
<i>Subsistence_PreFertileCohort</i>	Energy needs for an individual in the pre-fertile segment of a group in kcal.
<i>Subsistence_FertileCohort</i>	Energy needs for an individual in the fertile segment of a group in kcal.
<i>Subsistence_PostFertileCohort</i>	Energy needs for an individual in the post-fertile segment of a group in kcal.
<i>Years_Before_Group_Maturity</i>	Period in years before a newly created group can interact with other groups (join) or settle.
<i>GroupSize_BeforeMerge</i>	Groups can merge with other groups if their total size is smaller than this value.
<i>GroupSizeFertile_BeforeMerge</i>	Groups can merge with other groups if their size of the fertile segment is smaller than this value.
<i>GroupSize_BeforeSplit</i>	A group can procreate by splitting in two, thereby generating a new group. This value is the minimum size before a group can split.
<i>Temperature_Tolerance</i>	Minimum temperature that can be sustained by the hominins. If the coldest temp in a year falls below this value the group of hominins dies.
<i>CohortSize_PreFertile</i>	The size of the pre-fertile segment in a group, with age boundaries in years.
<i>CohortSize_Fertile</i>	The size of the fertile segment in a group in years. Note that the length of the post-fertile segment is not limited, but chances of survival decrease progressively with age.
<i>Calories_Per_Kg_Meat</i>	The number of kilocalories that can be extracted from one kilogram of meat.
<i>Max_ForagingRange</i>	Maximum annual foraging range from the current location. Groups cannot forage outside this range (in grid cells).

Tab. 2. 83 alphabetically ordered archaeological sites that are used for validation of the simulation results. Combined, these sites have 370 intervals (adapted from Scherjon 2019: tab. 12).

Checkpoint	Intervals
Abauntz	40000 - 54000
Abri Bourgeois-Delaunay	130000 - 166000, 91000 - 116000, 111800 - 128670, 77060 - 79280, 107000 - 117000, 65000 - 121000
Abri des Canalettes	68500 - 78500
Abri des Pecheurs	49000 - 59000
Abri du Brugas	57200 - 68800
Abri du Maras	81000 - 99000, 53000 - 57000, 40000 - 52000, 69000 - 95000
Abri Suard	111000 - 141000, 217000 - 287000, 45000 - 57000, 94000 - 108000
Ange	59700 - 161800
Anse de Query	114720 - 136360
Artenac	96650 - 119000, 122200 - 123200, 64000 - 70000
Ault	45000 - 65000
Barbas I	117000 - 175000
Baume Vallee	71000 - 86000
Beauvais 1	51600 - 59600
Berigoule	61300 - 122100, 49800 - 97600
Biache-Saint-Vaast	162000 - 188000, 112000 - 166000
Boxgrove	72000 - 142000
Cantalouette II	55000 - 66870
Caours	109000 - 139000, 108700 - 124500, 105000 - 131000
Champlost	52500 - 60900
Chez-Pinaud Jonzac	55300 - 80700, 67000 - 95600, 59500 - 82700, 40200 - 75300, 56100 - 79200, 56000 - 75200, 36400 - 79600, 47900 - 89300
Combe Brun	56600 - 69600, 105000 - 131000
Combe Grenal	40000 - 48000, 54000 - 68000, 55000 - 69000, 61000 - 75000, 91000 - 126000
Combe-Capelle Bas	48000 - 57000, 48300 - 57500, 49100 - 64700, 33900 - 61600
Coudoulous I	88200 - 112600, 110100 - 146200, 127700 - 152000, 119000 - 161000, 40300 - 65300, 61800 - 67600, 99600 - 138300
Cova de l-Arbreda	74300 - 93700
Covalejos Cave	87857 - 95857
Croix du Canard	74900 - 83700

Tab. 2. (Continued)

El Castillo	58500 - 79900, 54300 - 84400
Estret de Trago	65600 - 141000, 67500 - 122000, 37200 - 46200, 42900 - 58800, 38400 - 47600, 41500 - 50700
Fermanville-La Mondree	63700 - 75700
Fonseigner	44900 - 55500, 47300 - 58300, 49600 - 63200
Fresnoy-au-Val	99300 - 114300
Gouberville	108000 - 148000
Grossoeuvre	122000 - 138000
Grotte de Coudoulous II	39000 - 51000, 34600 - 85700, 23300 - 56600, 79100 - 97400, 78000 - 102600, 86900 - 147500
Grotte des Barasses II	98000 - 124000, 43000 - 53000, 53000 - 66000
Grotte du Figuier	43000 - 61000
Grotte du Lazaret	53000 - 175000
Grotte Vaufrey	110000 - 140000, 102000 - 116000
Grotte XVI	53600 - 74500
Havrincourt 1	61200 - 71500, 50800 - 65200
Igue des Rameaux	34800 - 53500, 34500 - 69200, 129300 - 158600, 75600 - 102200
Jupiter	45000 - 55000, 58000 - 78000, 90000 - 132000
Kents Cavern	72000 - 142000
La Butte d-Arvigny	97000 - 141000, 56000 - 116000, 59000 - 87000, 42000 - 94000, 75000 - 125000
La Chapelle aux Saints	44000 - 60000
La Ferrassie	56000 - 66000, 53000 - 57000, 41800 - 57800, 41800 - 59600, 58500 - 78800, 79500 - 100300
La Folie	55300 - 60100
La Quina	39400 - 46600, 40300 - 58000
La Roche a Pierrot	29700 - 52000, 33100 - 43600, 38100 - 46700
La Rochette	49100 - 55900
La Roquette II	52900 - 61500
Le Moustier	32400 - 45200, 35500 - 53900, 36300 - 53800, 37700 - 42900, 36500 - 45300, 36600 - 51000, 38000 - 45200, 37300 - 44500, 38700 - 53300, 38200 - 48200, 44800 - 55800, 50800 - 60800, 40700 - 49500
Le Prisse	78700 - 89900
Le Rescoundudou	62500 - 201000

Tab. 2. (Continued)

Le Rozel	92000 - 112000, 102000 - 124000, 97000 - 117000, 104000 - 126000
Les Canalettes	60800 - 88400
Les Cottés	46100 - 55300
Les Forêts	85300 - 103900
Les Pradelles	53000 - 62200
Lezetxiki	109000 - 153000
Mauquenchy	69800 - 84200, 75400 - 90600
Ormesson	46800 - 53000, 41400 - 48200
Payre	117000 - 147000
Pech de l-Aze I	24000 - 60000, 66000 - 196000
Pech de l-Aze II	60000 - 162000, 102000 - 158000, 120000 - 155000, 113000 - 161000, 37300 - 133000, 47800 - 63000, 51000 - 66300, 35900 - 101400, 40700 - 84700, 49900 - 85000, 63200 - 90400, 105000 - 133000
Pech de l-Aze IV	40000 - 59600, 41000 - 57000, 61900 - 78500, 61900 - 97800, 79600 - 118000, 46000 - 76000
Pie-Lombard	62300 - 77700
Pont-des-Planches	45000 - 60900, 41100 - 54800
Port Racine	62000 - 81000, 55000 - 88000
Roc de Marsal	45000 - 52200, 48900 - 57100, 46900 - 53900, 42600 - 60700, 52000 - 82000
Saint Germain-des-Vaux	55100 - 87600
Saint-Amand-les-Eaux	45860 - 52540
Sainte-Anne	96200 - 129700, 82700 - 97500, 80800 - 102300
Saint-Hilaire-sur-Helpe	89600 - 108200
Saint-Illiers-la-Ville	97200 - 112800
Savy	48000 - 54000
Scladina	110000 - 150000
Seclin	80000 - 106000
Sous les Vignes	40300 - 47800
Villiers-Adam	99000 - 121000
Walou Cave	78500 - 105800, 38000 - 57000

Tab. 3. Summary of all simulation results.

Scenario name	#simulations	MatchedIntervalCoverage
Habitat-A	2,148	30436
Habitat-B	3,102	13758
Habitat-C	2,008	30206
Habitat-D	2,618	19168
Habitat-E	2,42	27948
Habitat-F	2,24	17486
Habitat-G	2,043	31016
Habitat-H	2,192	31119
Habitat-I	2,355	31142
Habitat-J	2,21	30954
Energy-A	2,089	30522
Energy-B	2,278	29896
Energy-C	2,118	6273
Energy-D	2,012	26112
Energy-E	2,176	30651
Energy-BR	2,127	28125
Energy-CR	2,079	3301
Energy-ER	2,037	30439
Total number of simulations:	40,252	18 scenarios

Tab. 4. Example: the best performing models for scenario Habitat-C (adapted from Scherjon 2019: tab. 29).

	ScenarioNumber	matched-Interval-Coverage	BirthRate	DeathRate PreFertileCohort	Death-Rate_ FertileCohort	Death-Rate_ Post-FertileCohort	Subsistence_ PreFertileCohort
Standard 1	1365	28532	43	3	1	12	2000
Standard 2	39	26593	47	5	1	11	2750
Standard 3	486	26542	49	2	2	12	2750
Evolved 1	2008	30206	50	1	1	12	3500
Evolved 2	1952	30001	43	3	1	2	2000
Evolved 3	2002	29877	49	3	1	8	2500

	Subsistence_ FertileCohort	Subsistence_ PostFertileCohort	Years_ Before_ Group_ Maturity	Group-Size_ BeforeMerge	GroupSize_ Before Merge	Group-Size_ Before-Split	Temperature_ Tolerance
Standard 1	5000	3250	2	4	2	16	-17
Standard 2	3250	3750	5	5	2	56	-28
Standard 3	4750	4250	5	2	1	56	-23
Evolved 1	3250	5000	8	1	1	16	-22
Evolved 2	2475	3250	7	4	2	14	-25
Evolved 3	4000	4675	4	4	2	14	-25

	CohortSize_ PreFertile	CohortSize_ Fertile	Calories_ Per_ Kg_ Meat	Max_ ForagingRange	ViabilityIndex
Standard 1	9	37	2700	12	28722
Standard 2	12	23	3000	10	4053
Standard 3	8	25	2550	10	41287
Evolved 1	9	33	2750	14	138160
Evolved 2	9	37	3150	15	30712
Evolved 3	9	37	2750	10	73985