

Demography and the extinction of the European Neanderthals

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Suggested causes for the sudden extinction of Neanderthals in Europe, starting around 35 ky BP, comprise food shortage, climatic effects and violence from Modern Humans. I use demographic modelling with reconstructed fertility and death rates to model the population development from the early appearance of Neanderthals in Europe some 260 ky ago. Such long-range modelling poses strong constraints on the most sensitive parameter choices and thereby strengthen the conclusions reached: that because the Neanderthals survived the maximum glaciation near the end of the previous (Saalian) ice age, it is unlikely that the adverse climatic development up to the recent (Weichselian) maximum glaciation should have caused extinction. Examination of skeletal remains from the last period of Neanderthal European presence does not provide evidence for violence and killing by Modern Humans. Further, the Neanderthal population numbers and density of prey animals do not support food shortage as an important cause for population reduction, and it is concluded, that reasons other than the suggested ones must be sought. A probable candidate is an infectious disease, presumably transmitted by the incoming Modern Humans, as the main cause of the Neanderthal demise.

Keywords: Neanderthal, population, demography, ice age, food shortage, climate sensitivity, disease, extinction

Introduction and methodology

The population development during the Neanderthal presence in Europe can be modelled by simple demographic modelling, once birth and death rates are known. The variation of birth rate with age of the mother is similar for most hunting societies and has been adopted for Neanderthals (Hassan, 1981), leaving the overall fertility as an important parameter to vary. The death rate is reconstructed by assessment of the known perils of the Neanderthal hunting society. The primary input for such reconstruction is the age at death, determined from skeletal remains found. The following death rate components are considered:

1. Shortage of food
2. Occupational hazards including accidents
3. Poison (through food, skin, inhalation)
4. Birth complications
5. Genetic disease or defect
6. Epidemic diseases
7. Endemic diseases
8. Climate enhancement of disease rate
9. Natural disasters
10. Attack by animal predators
11. Violence by other humans

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The basic demographic model employed is a first order difference equation expressing the population change in terms of birth and death rates (the basic components of which are shown in Fig. 1, as function of the age of the person, male or female), with a time step equal to one year.

Occupational deaths were not insignificant, particularly for the members in a Neanderthal group taking part in hunting expeditions. As indicated in Fig. 1 (lower panel), the impact would be largest for young male hunters and decreasing with accumulated hunting experience. For the female population, the risk of death in connection with childbirth is known to have been high and is here taken as a fixed fraction of the actual number of births. Infant death at birth or during early infancy had a very high rate, as in all societies lacking ways to deal with birth complications. The remaining death rate due to endemic diseases and other causes mentioned above, except climate and food shortage, are increasing with age as indicated in Fig. 1.

With these parameters, the model gives a population age distribution similar to that of other reconstructions (Hassan, 1981). The life expectancy at birth is 19 years for males and 17 years for females, and for those who reach age 18 the life expectancy is 18 years for males and 14 years for females (because now the males have become better at dealing with hunting accidents but the females still face a number of years with risky childbirths). The data from age distribution of skeletal remains has a very high death rate in the age range of 40-60 years (Hassan, 1981). It has been diminished because it is thought to reflect a higher probability of finding human remains near the settlements and thus may overestimate death rates of age groups preferentially working around the base site, relative to age groups that if killed may be buried away from home and be less likely to be found by excavations. However, this has little effect on the model results due to the smallness of the upper age bracket population.

Two additional terms are considered. One expresses the increased death rate due to food shortage. It is assumed to set in for European Neanderthal hunter populations above 12 000 and to grow linearly as shown in Fig. 2. For Modern Human hunters, the curve starts at a population of 20 000, due to their wider choice of prey. The other is a climate-dependent addition to the death rate. It is assumed to be the product of the age profile given in Fig. 3 and a temperature-dependent parameter, given in Fig. 4. The latter is zero when the temperature is 10 °C and increases quadratically for both cold and hot annual average temperatures. Finally, a set of calculations is carried out with inclusion of the possibility of migration between the regions of Northern, Middle and Southern Europe added. Details are given below.

Food shortage

Because the Neanderthal population size was low throughout their European presence, as judged from the number of identified settlements, starvation due to lack of prey animals is unlikely to have played a major role. The human population density is estimated to have stayed below an average of 0.025 cap./km² and although climate variations moved the preferred prey (large herbivores) around, the Neanderthals were nomadic and simply followed the assemblage of prey. Prey animals such as horse, mammoth, rhinoceros and various deer species were probably never threatened species until the Modern Humans surpassed a population size of about 10 000, sometime after 30 ky BP (Ugan and Byers, 2008; Surowell *et al.*, 2009). The demographic model is used to test this assertion, by an option to add a food constraint that makes the death rate increase if the population surpasses 0.025 cap./km² (or some 12 000 people for the populated part of Europe). Fig. 5 shows the model output for Southern Europe (separate population values for males and females) for different overall fertilities F (the total number of children for a female living through her entire fertile period). For the highest value of F shown, the food shortage constraint comes into play. The initial population, in Fig. 5 taken as 100 male and 92 female, is also a parameter. If there is no food shortage and no mi-

gration, a given curve displaces unchanged up and down with start value (on the logarithmic scale). With migration in the model, changing start values will change behaviour such as the time for initiating a given migration event. The selected reference value of $F = 7.613$ will contain the total population below the value where food shortage becomes significant, for any reasonable values of the remaining parameters. As there is no evidence that the European Neanderthal population ever exceeded 10 000, prey shortage can at most have played a brief and local role.

Climate change

The death rate influence of climatic changes is modelled specifically, because of its central place in the discussion of why the Neanderthals disappeared at around 35 ky BP (with a small group surviving to 28 ky BP near Gibraltar) (Jiménez-Espejo *et al.*, 2007). The additional climate-related death rate is assumed to mainly affect the very young and the very old (as today, cf. Fig. 3), and to increase quadratically with the deviation of the annual mean temperature from 10 °C (Fig. 4). Fig. 6 shows the population development evolving for different regions of Europe, when calculated on this basis and with the same initial population value. The calculation reflects the different ambient temperatures in the different regions, which are based on the following assumptions:

The temperatures indicated in Figs. 5-8 are reconstructed from Greenland ice-core measurements. From 0 to 122 ky BP, the NGRIP reconstruction is used (Huber *et al.*, 2006) and from 122 to 250 ky BP a reconstruction is made based on GRIP ^{18}O data (Johnson *et al.*, 1997), adjusted to have the same mean and standard deviation as NGRIP for the first 122 ky, which are also covered by GRIP. The temperatures are annual means and they have been shifted by a constant amount for the entire time-interval, to give a mean temperature today of 8.5 °C for Neanderthal sites in Northern Europe (e.g. Hamburg region), 10.5 °C for Middle Europe (e.g. Ulm) and 13.5 °C for Southern Europe (e.g. Toulouse).

The dependence on the amplitude of the climate term is shown in Fig. 7, for Southern Europe. The strength of the climate sensitivity, which is the amplitude of the term given in Fig. 4, is taken as 10^{-5} times the constant C . Fig. 7 shows the population development for different C 's (with F fixed at 7.613, the value also used in Figs 6 and 8). It is seen to vary the depth of the population decline at the late Saalian glaciation. An increase of the term by 50% causes even the Southern European Neanderthals to go extinct during the maximum cooling of the previous Saalian ice age, while reducing the term by 30% relative to the reference value makes the population size reach such high levels that food constraints come into play. The reference case ($C = 1$) shown in Fig. 6 makes the Saalian maximum glaciation reduce population in Southern Europe considerably more than the reduction during the recent glaciation maxima at 75 and 30 ky BP, where the Southern European population stays rather high. In other words, if the Neanderthals survived the Saalian minimum they should also have survived the Weichselian minima.

Interpretation of parameter variation results

The considerations underlying the choice the parameters can now be summarised: Too small a C or too high an F causes the European Neanderthal populations (and particularly that in the South) to grow more than can be consistent with the number of Neanderthal sites found (even if the fraction found may diminish with the time passed since the use of the site). Too large a C or too small an F makes the population extinct (even in the South) already during the late Saalian period, leaving no possibility of reproducing the development during the Weichselian period. Too large a C cannot be compensated by a large F , because then population will grow from the smallest possible just before the Eem to one that is much too big around 40 ky BP. The reason for this behaviour is that the over-

all fertility level is taken as time-independent, while the climate term is varying with time (through temperature). That population may hit the food shortage ceiling is not the main point, because even before it does that, the population has become larger than what can be reconciled with data (Bocquet-Appel *et al.*, 2005). The introduction of Modern Humans in Fig. 6 from 45 ky BP eventually makes the Neanderthal population decline modestly due to Modern Humans, for which a 1% lower mortality is assumed, winning the prey competition.

One remaining problem is the slow (although exponential) population re-growth after the late Saalian minimum, making it impossible to account for the similar Eem populations in all three regions of Europe (Wenzel, 2007). The climate dependence necessarily makes the end-of-Saalian North European population lower than the Middle European one, which again is lower than the South European one (Fig. 6). The solution to the problem is to allow groups of Neanderthals to migrate between regions, whether to explore possibly better hunting territories or to flee from advancing low temperatures. Migration is considered in the following section.

It is of course possible or even likely, that the birth and death rates did not stay constant for the entire period as assumed. However, it is extremely unlikely that death rates should have systematically risen over time relative to birth rates, unless some totally unknown cause is invoked. The probable development would be that even if the Neanderthal society were a rather stationary until the late modernisation observed from around 43 ky BP, any persistent changes would have been in the direction of reducing the death rates. This could be by midwives learning from circumstances of childbirth deaths to take precautions that would reduce this most important component of the death rate, or it could be by learning to find and use herbal medicine.

Adding migration to the model

Migration of Neanderthals in response to changes in temperature and environment is now added to the demographic model. The extended model assumes that the population moves north or south when the thresholds of 0° and -5° C are passed in the appropriate direction, and at a rate of $0.003 \times P \times \Delta T$, where P is the population and ΔT the deviation of the annual average temperature from the threshold value.

More precisely, the Neanderthals move north, if the annual average temperature of the region they move into is above 0 °C, and at a rate increasing if the temperature is higher. The migration is further assumed to proceed only if the population density of the region being moved into is lower than that of the region left. Confirmation of better hunting conditions at higher latitudes would be obtained by seasonal explorations (of which many traces are left). Conversely, the Neanderthals would be fleeing south from the Northern or Middle European region if the temperature drops below -5 °C. Below this annual average temperature, occurrence of permafrost sets in and may limit prey availability. This situation would induce a southward migration of the entire population in the affected region. The results of this modification to the model are shown in Fig. 8, both for the Neanderthals and for a Modern Human population arriving in Europe at about 45 ky BP.

Now the modest Neanderthal population during the Saalian stays mostly in Southern Europe, except for the period 240 to 220 ky BP and later a couple of brief periods, where they venture north to both Middle and Northern Europe. However, the interglacial warming starting at 140 ky BP causes all of Europe to become populated, with only brief relocations south at the temperature depressions during the interglacial period (around 130 ky BP). The 125 ky BP populations in the three regions now match those of the observed Eem settlements. Despite subsequent temperature decreases, the population of all three regions largely continues to rise until 80 ky BP, because the temperature variations do not generally lead to levels below the -5 °C threshold.

The Neanderthals who migrated away from Northern Europe around 40 ky BP never moved back and the population in Middle Europe has according to the model entirely moved South by 28 ky BP, due to temperatures more and more frequently being below the assumed threshold for Middle European occupancy. During the same period, the Modern Human newcomers show a similarly increased preference for Southern Europe (lower panel of Fig. 8). The Modern Humans have been assumed to have a 1 % lower death-rate from hunting accidents and childbirth, which, however, is enough to ensure their population growth during the period from 45 ky to 15 ky BP, where the Neanderthals in Southern Europe experience a modest 20% decline in population, to 2500. After 15 ky BP, the Neanderthal population would again have risen, had it not been for the actual extinction not predicted by the model. The conclusion drawn from this more detailed model with migration is thus the same as for the simple model without migration, that climate is not the cause of the dwindling Neanderthal population between 35 and 28 ky BP.

Other contributions to Neanderthal death rate

Natural disasters can cause perturbations in death rates. Two very significant volcanic eruptions took place during the Neanderthal presence in Europe. The Toba eruption at 75 ky BP (Ambrose, 1998) is the largest ever recorded, resulting in globally elevated atmospheric dust concentrations for over 10 ky (Ruth *et al.*, 2003). The *Campanian Ignimbrite* eruption at 40 ky BP (Fedele *et al.*, 2008) led to ten times lower accumulated dust levels in the Greenland ice-cores (Ruth *et al.*, 2003) but was still large compared to eruptions in recent millennia. The dramatic lowering of European temperatures following these events is taken into account in the population model presented here, and as seen in Fig. 8 causes populations in both Middle and Northern Europe to flee into the Southern region (in the *Campanian Ignimbrite* case presumably avoiding for a time the areas East of the eruption site in Southern Italy). There could be additional indirect effects from these eruptions, say on vegetation and thus perhaps on faunal prey numbers and availability. However, e.g. the woolly mammoth, one of the preferred Neanderthal prey species, seems to have been continually present in Northern Europe during the period around 40 ky BP (Aaris-Sørensen, 2006).

On the list of reasons for death there remains two: violence and epidemics. Violence is a basic trait of Modern Humans (*homo sapiens sapiens*). Not only in the most recent century with two world wars, hundreds of local wars and millions of violent crimes, but also in material from archaeological excavations, the number of deaths caused by wounds inflicted by weapons is quite significant (Walker, 2001). So did the Modern Humans invading Europe from about 45 ky BP just kill the Neanderthals? The answer seems to be no. There are no unambiguous signs of violent death caused by other humans found in skeletal remains of the latest Neanderthals, and with a single exception, all earlier Neanderthal injuries can be interpreted as inflicted by animals during hunt (Berger and Trinkaus, 1994; Keeley, 2004; Bennike, 2006; for a dissenting view see Vencl, 1999). This might indicate that Neanderthals were more peaceful than the Modern Humans, or one may suggest a scheme where violent kills within or among human groups only manifests themselves for population densities above a certain level. In any case, Modern Humans are not invariably violent, and in this case seem to have coexisted peacefully with Neanderthals for more than 8 000 years.

As regards epidemics, it has been claimed that the low population density in the European Neanderthal society makes epidemic spread of diseases unlikely (Armelagos *et al.*, 2003). However, the large mobility implied by migration and by huge hunting territories, as well as the need for members of each group (typically with about 10 adults) to visit other groups in an extended mating network (needed for reasons of countering fluctuations in availability of females and incidentally for reducing inbreeding problems) may weaken this argument. Given the time scale of the Neanderthal demise (probably more than a thousand years), it is little relevant if the impact on death rates of a

novel disease is epidemic or endemic. The Modern Human intruders could have introduced such a new disease.

The idea of newly arrived Modern Humans bringing with them diseases that they themselves had already gained a level of adaptation to, but for which the Neanderthals had no defence, is not far-fetched, as it has repeatedly been invoked as contributing to the often dramatic indigenous population decline following European colonisation (16. century Aztecs and Mayas in Mexico, Incas in Peru, 18. century American Indians in New England) (Whitmore, 1991; Acuna-Soto *et al.*, 2004; Gilcrist, 2009). If the Neanderthals were open to contact with the modern newcomers, as the explosive cultural developments for both Neanderthal and Modern Human communities during the period of coexistence suggests, then extinction by transmission of a viral or bacterial disease could be plausible, including the timing of extinction starting in Eastern Europe and moving towards the south-west.

This suggestion has become testable, because of the current ability to extract the DNA from late Neanderthals and sequence it, despite heavy fragmentation of the double-spirals. Genetic material from some viruses or other infections will show in the code segments extracted from the Neanderthal genome, and one will be able to compare it to that of known infective diseases, of which presently some 200 (bacterial ones) have had their DNA sequenced (Fournier *et al.*, 2007). Identifying diseases such as tuberculosis in ancient populations has already been done for 5-6 ky BP Egyptian DNA (Crubézy *et al.*, 1998; Zink *et al.*, 2001; and in Chile by Guhl *et al.*, 1999) and thus could also be done when the ongoing sequencing of a 38 ky BP Neanderthal from Vindija Cave in Croatia is completed (Noonan *et al.*, 2006). One might argue that Neanderthal DNA from 35 ky BP or more recent would be better, but if the extinction proceeded from East to West, Vindija would be in the early bin and possibly quite relevant.

Conclusions

The demographic models presented here essentially select all required parameter values from the known behaviour of the Neanderthal population size around the Eem interglacial period and then proceeds to predict the behaviour 85 ky later. The main conclusion is that it is highly unlikely, that hunting-prey decline or climatic variations killed the Neanderthals. Eliminating climate as a cause has also been suggested by an entirely different approach, doing statistical analyses of an underdetermined machine-learning algorithm with the climates of actually occupied sites as input (Banks *et al.*, 2008). Inspection of the Neanderthal genome-mapping data for traces of infectious disease is thus suggested as highly worthwhile.

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Fig. 1. Reconstructed generic birth and death rates of European Neanderthal population. The upper panel shows total birth and death rates by sex as function of age, and the lower panel shows the main components of the death rates.

Fig. 2. Model of reduction in population caused by food shortage. Note the logarithmic population scale, implying a linear relation between population and food shortage-related death rate.

Fig. 3. Age-dependence of climate-related part of death rate.

Fig. 4. Temperature-dependence of climate-related part of death rate.

Fig. 5. Parameter variation: Influence of varying the overall fertility (F) on Neanderthal male and female population development in Southern Europe. Other parameters are at reference value.

Fig. 6. Neanderthal (N) and Modern (M) population as function of time, for Northern Europe (NE), Middle Europe (ME) and Southern Europe (SE), using reference values of all model parameters and selecting initial population sizes leading to a total of 750 people in the mid-Eem period. In this calculation, there is no migration: the regions are treated independently and started with the same initial population. The death rate contributions from childbirth and hunting accidents are 1% lower for Modern Humans than for Neanderthals. The underlying temperatures are estimated from Greenland ice-core data (see text) and the plotted ones pertain to Northern Europe.

Fig. 7. Parameter variation: Influence of varying the overall strength of the climate-related death rate (C) on Neanderthal male and female population development in Southern Europe. Other parameters are at reference value.

Fig. 8. Neanderthal (top panel) and Modern (bottom panel, with temperatures indicated for Northern Europe) populations as function of time, for calculation including migration between regions as a response to climate change as well as to hunting options. Curves are labelled as in Fig. 6 and it is seen that Middle and Northern Europe are only populated in periods. As discussed in text, parameter choices are made to reproduce late Saalian and Eemian behaviour. The subsequent 120 ky of population development constitute the model implications.

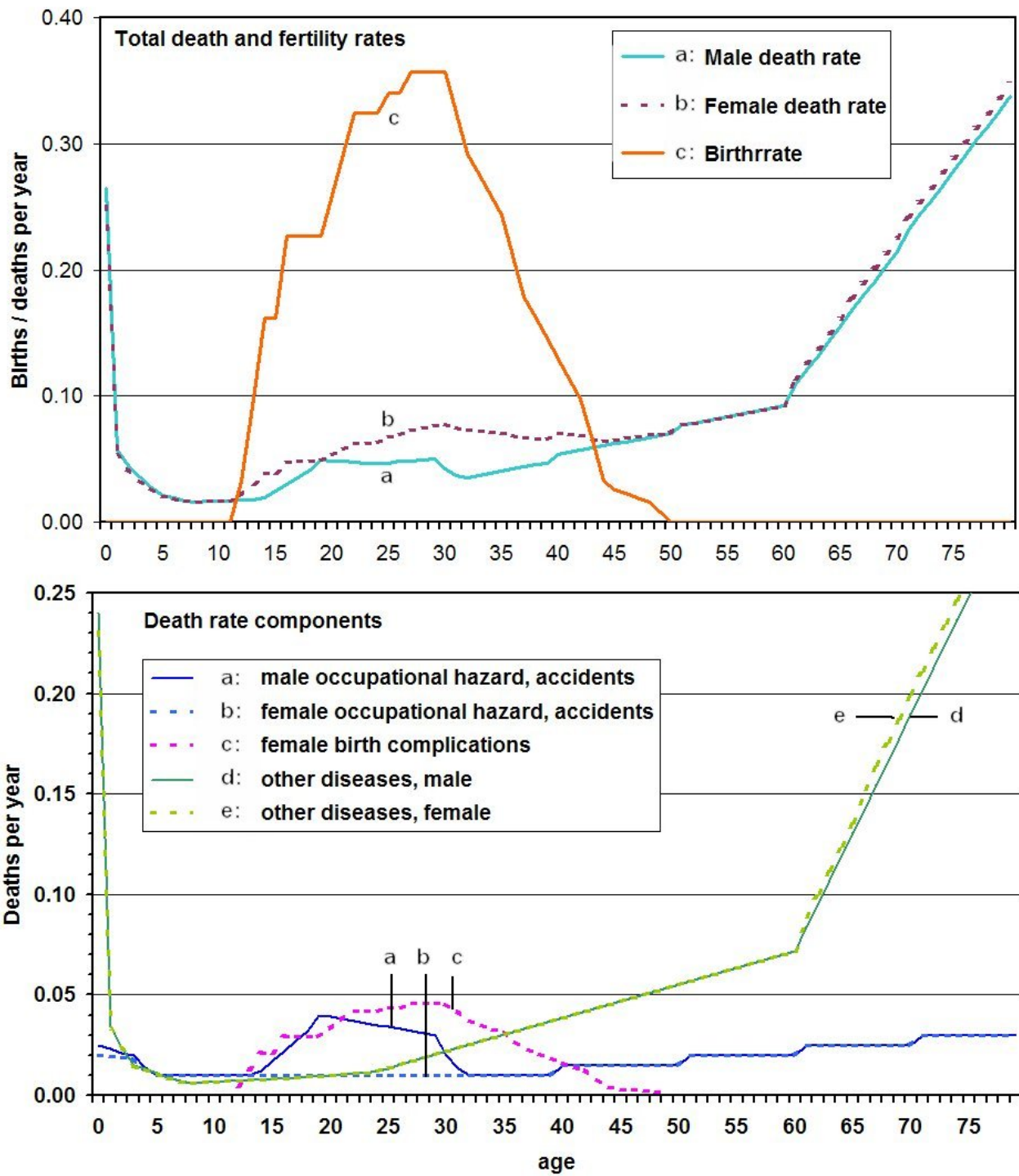


Figure 1.

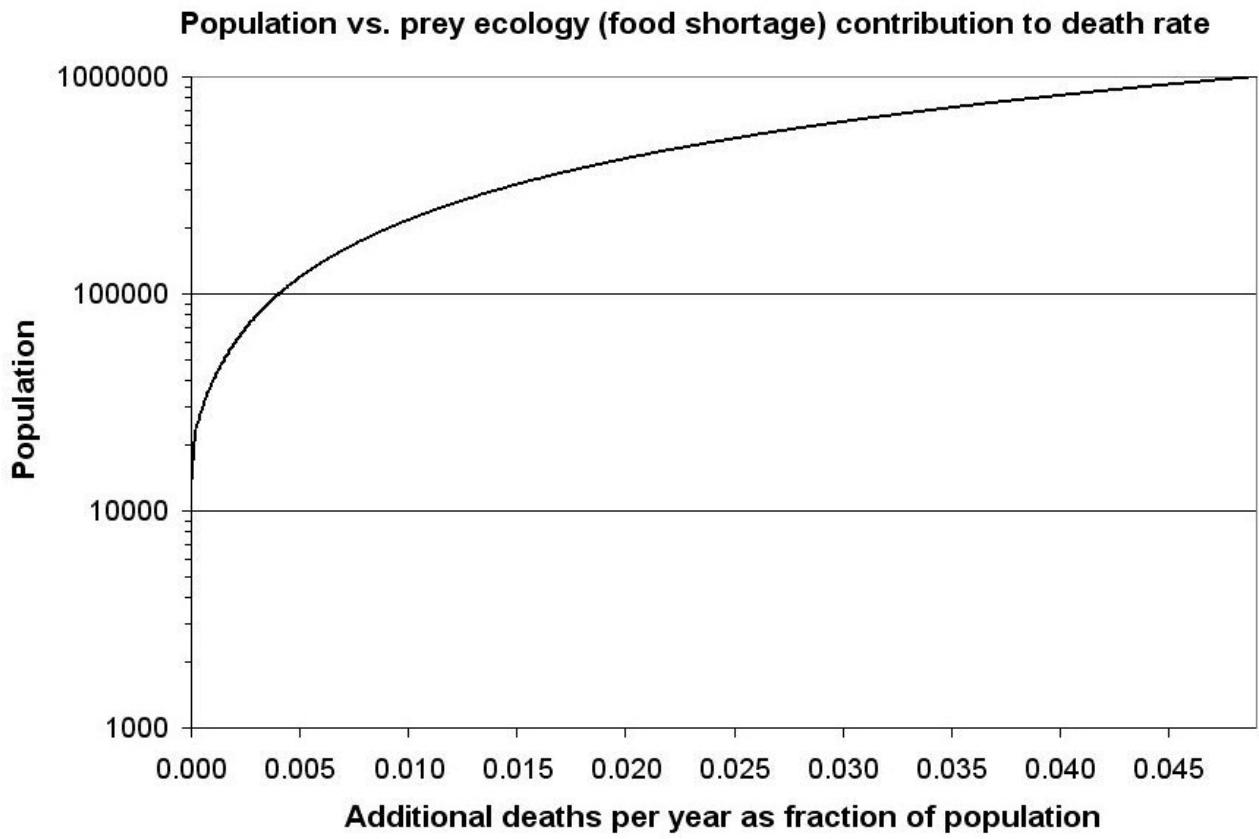


Figure 2

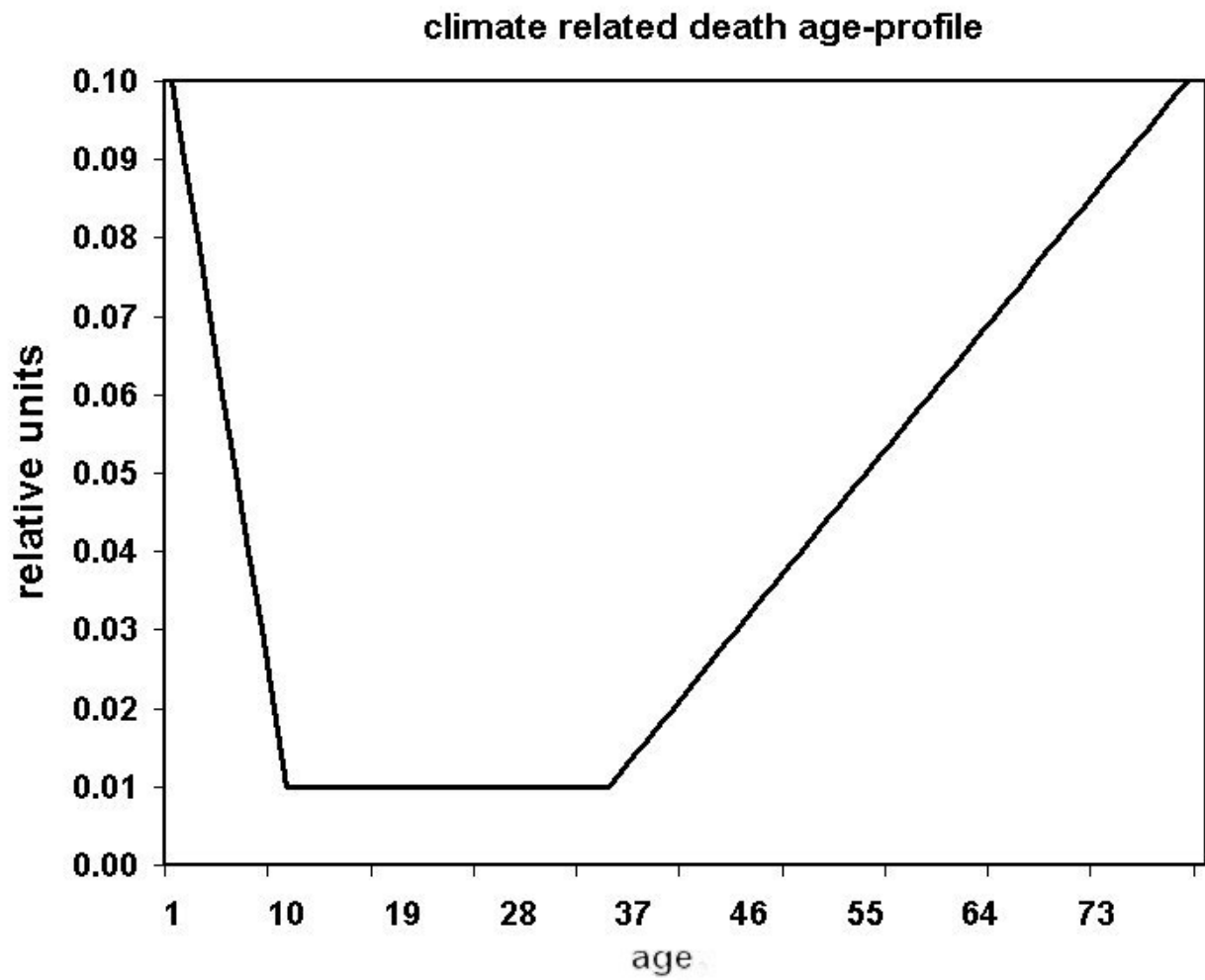


Figure 3

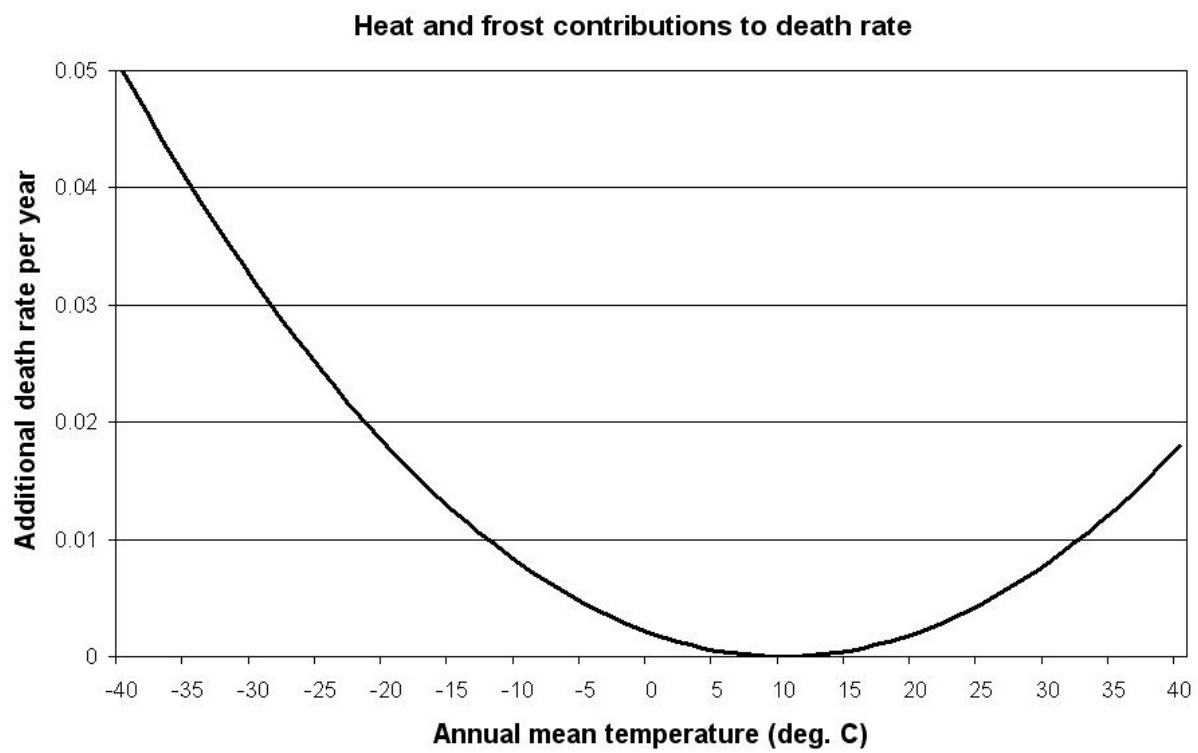


Figure 4

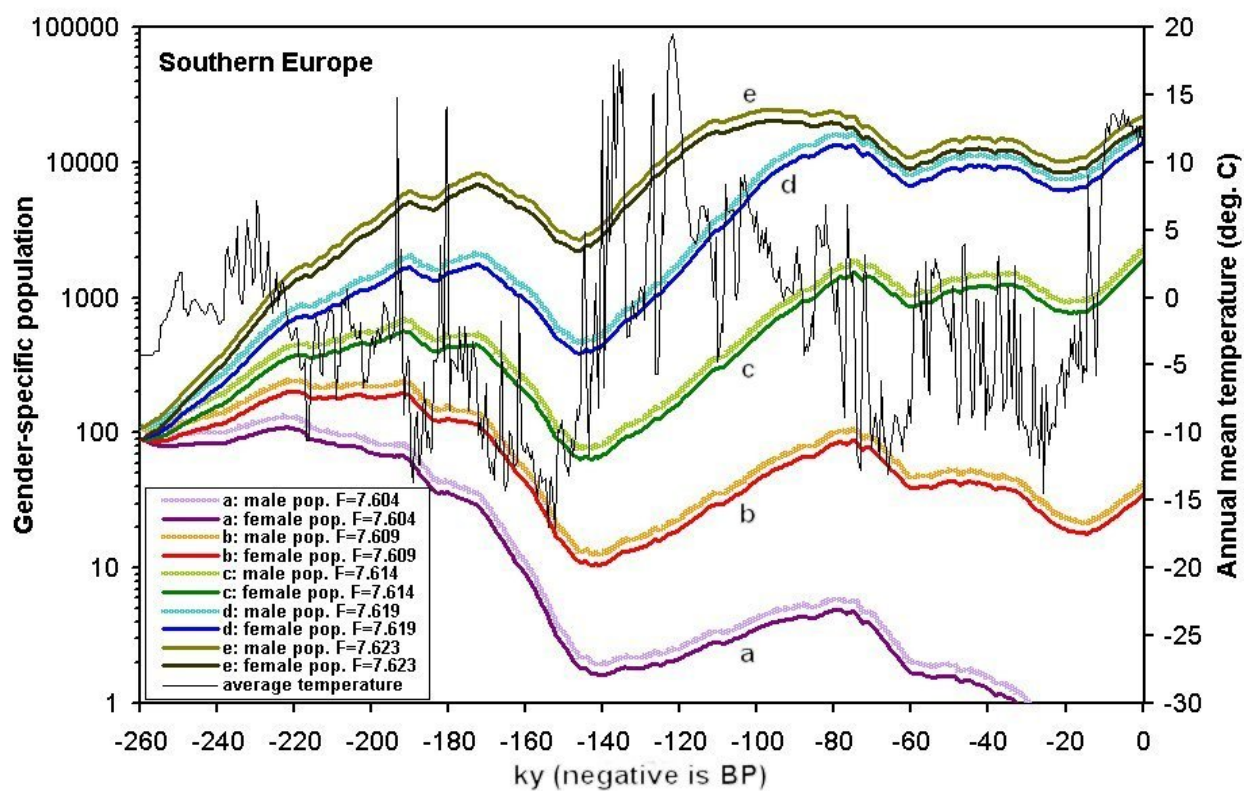


Figure 5.

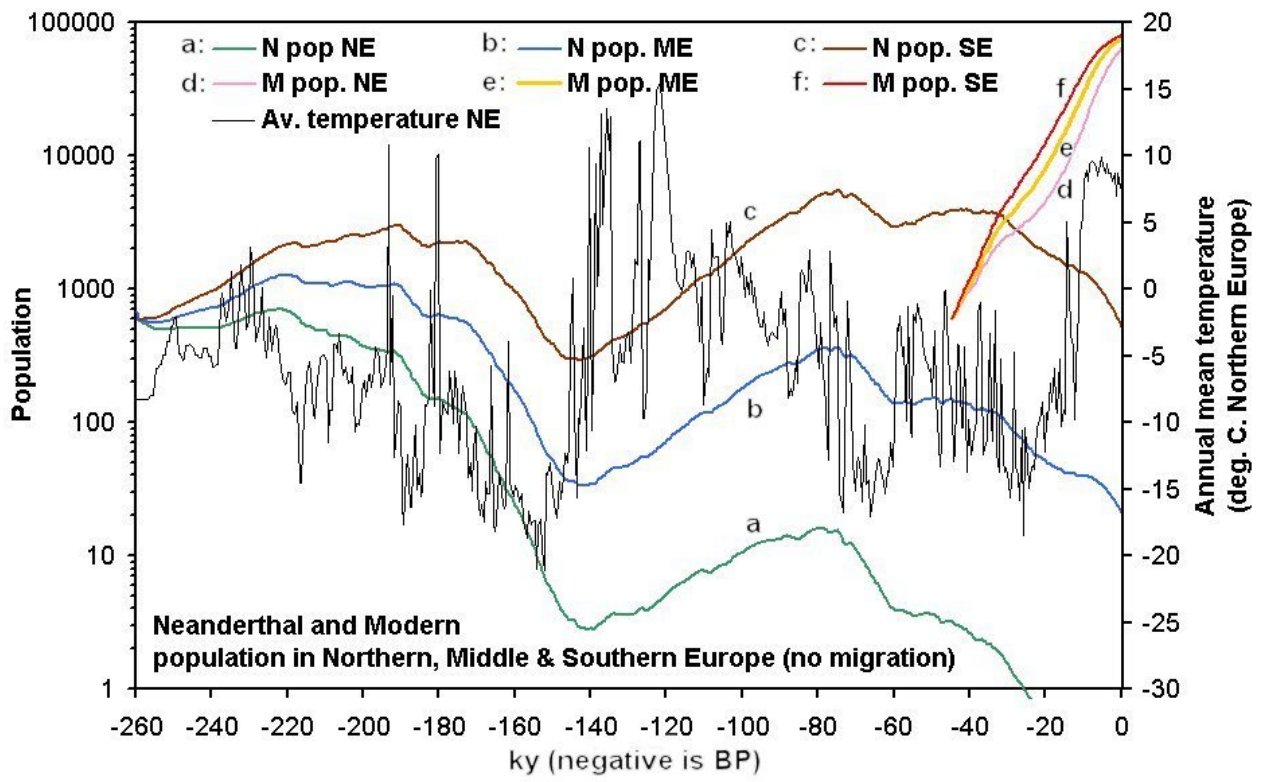


Figure 6.

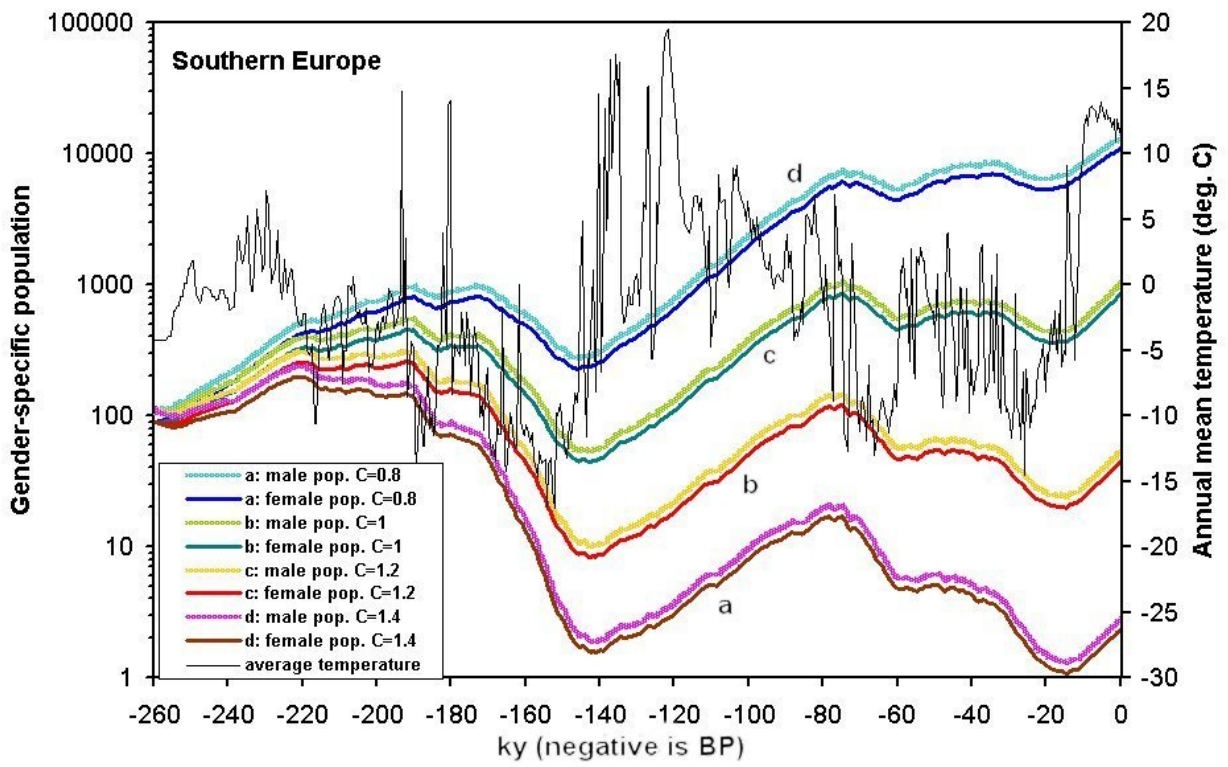


Figure 7

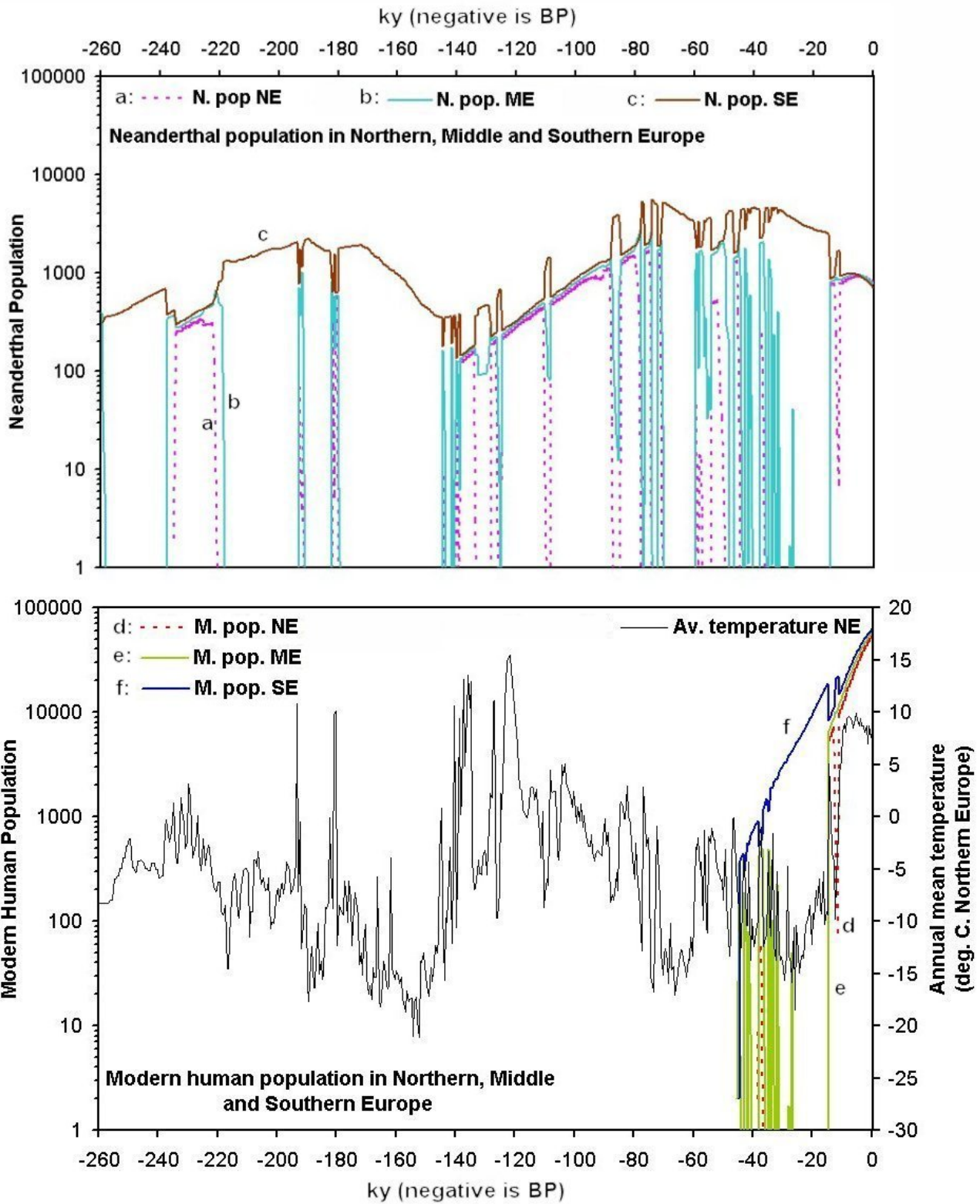


Figure 8