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**Demographic uniformitarianism: the theoretical basis of prehistoric demographic research and its cross-disciplinary challenges**

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**Abstract**

*A principle of demographic uniformitarianism underpins all research into prehistoric demography (palaeodemography). This principle*—*which argues for continuity in the evolved mechanisms underlying modern human demographic processes and their response to environmental stimuli between past and present*— *provides the cross-disciplinary basis for palaeodemographic reconstruction and analysis. Prompted by the recent growth and interest in the field of prehistoric demography, this paper reviews the principle of demographic uniformitarianism, evaluates how it relates to two key debates in palaeodemographic research and seeks to delimit its range of applicability to past human and hominin populations.*

**Keywords:** Prehistoric demography; Uniformitarianism; Population dynamics; Life History; Archaic hominins

1. **Introduction**

Like many historical sciences, prehistoric demography relies on a doctrine of uniformitarianism for some of its foundational principles. Uniformitarianism is the adherence to the axiom that processes that occurred in the past (and so cannot be directly experienced) were nonetheless likely to resemble those that are observable in the present day. The utility of a principle of uniformitarianism in prehistoric demography is clear when one considers the database available from which to study the demography of past non-literate societies (palaeodemography). Data derive from a wide range of disciplines but are frequently sparse and inform on a limited selection of demographic parameters **[1-5].** Furthermore, these data provide only proxy measures of the demographic variables of interest. Multiple inferential stages are required to turn the data into meaningful statements about prehistoric demography and issues of equifinality abound. A clear underlying theoretical framework, such as that provided by a uniformitarian principle, aids in the reconstruction of prehistoric demographic patterns, providing clear constraints on interpretations of past demographic trends and processes, and justifying the use of estimates for population characteristics and model parameters derived from recent populations to supplement the sparse prehistoric demographic database.

Despite providing the basis for all prehistoric demographic research, sustained discussion of demographic uniformitarianism is rare outside of the sub-field of skeletal palaeodemography. As the field of prehistoric demography grows, so does the necessity to ensure that the field’s underpinning theoretical basis—and the impact this has on the generation, analysis, and interpretation of prehistoric demographic data—is clear and secure.

1. **Defining demographic uniformitarianism**

The uniformitarian principle was first articulated by geologists in their efforts to understand the mechanisms responsible for the formation of the Earth. As utilised in the historical sciences, the principle argues that there is continuity between processes and causative mechanisms that occurred in the past and those that are observable in the present. There are clear links between uniformitarianism and other heuristic principles of philosophical and scientific argument, such as Occam’s razor (the law of parsimony) and analogical reasoning (comparisons that use similarities between independent systems as evidence for the existence of hidden causative commonalities: **Figure 1**). Uniformitarian principles were utilised during the development of demography as a science during the 19th century, underpinning theories of the drivers of, and constraints on, population growth rates **[7]** and large-scale patterns of migration **[8]**. More recently, the argument that demographic parameters derived from historical records of human populations can be used as guidelines for constraining demographic models of prehistoric communities was expressed forcefully by Howell **[9]**.

**[Figure 1 near here]**

Howell argued that model life tables and fertility schedules ―which are constructed on the principle that patterns of age-specific variation in mortality and fertility vary in biologically constrained ways across different populations ―could be used to interpolate and smooth fertility and mortality data obtained for prehistoric populations. Howell’s uniformitarian assumption was that prehistoric populations occupied essentially the same demographic parameter space observed amongst historically documented populations. She cited Simpson **[10]** and other authorities in support of the argument that demographic aspects of human life histories, including fertility span and longevity, were evolved species-wide attributes. Howell also pointed out that the application of uniformitarianism enables the prediction of otherwise unobservable population characteristics, such as family size and kinship structure, with implications for the role of cultural transmission. Accordingly, the principle of uniformitarianism may also inform on the social, as well as the biological, elements of past demography. However, as Howell makes clear, demographic uniformitarianism does not assume that demographic behaviours have remained the same throughout history but that the basic biological processes relating to fertility and mortality are similar, that they respond to variations in the social and natural environment in the same way, and that these similarities act as constraints and impose limits on demographic behaviours.

1. **Uniformitarianism in prehistoric demographic research: two key debates**

The implications of the uniformitarian assumption vary depending on the demographic parameter addressed and the palaeodemographic proxy used. Below, we discuss the implications of the uniformitarian principle for two key debates in palaeodemographic research.

1. *Population dynamics and the “Forager Population Paradox”*

It has long been recognised that there is a stark contrast between the observed population growth rates of recent hunter-gatherers (mean of ~1% per annum **[11]**) and long-term prehistoric growth rates estimated via palaeodemographic methods which are typically close to zero for foraging populations **[12-13]**. Explaining this discrepancy (the “forager population paradox” **[14]**) by presuming that current hunter-gatherer population growth rates are unrepresentative of the past violates the uniformitarian assumption, as long-term population stationarity is only possible via a combined fertility and mortality schedule outside of, or at the extreme limit of, the known range of human variation **[12-14].** A more convincing solution is that long term population growth followed a ‘saw-tooth’ pattern, with brief crashes followed by longer periods of recovery **[15-16]**; a pattern supported by genetic data indicating multiple instances of sharp reductions in prehistoric population sizes (e.g. **[17]**). In a foraging population with a typical 1% per annum growth rate, the time for recovery from a catastrophic episode causing 50% mortality is only 70 years. Even higher growth rates of up to 3% per annum, and consequent shorter recovery times, have been reported for post-catastrophe indigenous populations in South America, although these high growth rates may be partially accounted for by immigration and group fusion **[18].** Such rapid recovery times are too short to be visible by any palaeodemographic method, including the comparatively high-resolution method of summed posterior probability distributions of sets of radiocarbon dates (SPDs) **[19, 20]**. A difference in scale, rather than in demographic regimes, best explains the discrepancy between past and present embodied in the forager population paradox.

What are the implications of this for the reconstruction of prehistoric population growth rates? The uniformitarian assumption relates primarily to underlying mechanisms, not specific parameter values derived from recently observed populations (although the former heavily constrains the latter).Due to the imprecision of radiometric dating, growth rates calculated from palaeodemographic data record only the longer term and slower time-averaged rate across crash and recovery cycles. They are therefore not directly comparable to growth rates recorded in ethnographic and historical contexts which represent ‘instantaneous’ per annum measures along this continuum of growth and decline. While the uniformitarian assumption likely holds in most prehistoric contexts, this difference in scale means that caution is required when using ethnographic data to interpret models of prehistoric demography, and does not support the simple transference of growth rates from ethnographic to prehistoric contexts; growth rates recorded for recent foragers are not realistic long-term estimates for either the population from which they derive or past hunter-gatherers. Tallavaara **[21]** further argues that population dynamics derived from palaeodemographic proxies can only be directly interpreted in terms of what controls the long-term mean population size. In the case of prehistoric hunter-gatherers, the primary population limiting factor would be the density-independent variable of environmental productivity **[21]** leading to debate as to how to combine palaeodemographic results with shorter-term density-dependent growth models derived from population ecology **[22]**, as well as how to infer underlying fertility and mortality rates **[23]**.

1. *Age structure of mortality and fertility* *and longevity in prehistory*

Under natural living conditions human populations exhibit regular patterns of age-specific fertility and mortality rates that are strongly age-structured and are likely to be evolved versions of patterns that are common to the great apes **[24, 25].** Female age-specific fertility rates follow a unimodal peaked distribution between maternal ages of 15 and 50 years, with peak fertility rates being higher and occurring earlier in farming populations than in foraging populations **[26].** The distribution of the risk of death in human populations is bimodal with peak mortality rates in the first year of life, declining to a minimum in adolescence and early adulthood before rising exponentially in later adulthood. These three additive components of human age-specific mortality rates (i.e. juvenile, adult and an age-independent constant risk of death) are represented well by the Siler model **[27].** Variation in the overall risk of mortality, together with variation in the relative contributions of juvenile versus adult mortality risks, underlie much of the populational variation in attritional mortality that is captured by model life tables.

The reconstruction of patterns of mortality and fertility for prehistoric populations is challenging. Fertility leaves few visible traces on the skeleton but can be measured indirectly through its effects on the age distribution of mortality: the latter is constrained by the age distribution of the living population, which in turn is highly sensitive to changes in fertility **[28-30]**. The variation of mortality risk with age can be inferred from representative samples of human skeletal remains, subject to assumptions about the stability of the age structure of the living population and its average rate of growth. Although survivorship declines with age, the exponential rise in the risk of death at older ages should result in the elderly being well represented in skeletal assemblages. However, when ages at death are estimated for samples of skeletal remains using traditional osteological age indicators, the resulting distribution of age often appears to show an excess of individuals in the young and middle age categories and a corresponding marked deficit of individuals aged above 60 years. This abnormal pattern deviates from the strongly age-structured pattern of human mortality described above; it is neither observed in data from model life tables, nor apparent in demographic data from extant foraging and subsistence farming populations, and at face-value implies the inapplicability of the uniformitarian assumption to all prehistoric contexts **[31]**.

This common deviation of prehistoric age-at-death distributions from uniformitarian expectations has long been recognised as the likely result of unrepresentative skeletal samples (the result of selective burial and/or differential preservation) and biases in many osteological age estimation methods that affect particularly the oldest age categories **[26, 32-34]**.Some of these biases stem from identified methodological problems, for example the prediction of age from calibrations against biased reference samples or the use of point age estimates rather than posterior probability distributions. Another potential source of departure from the age distributions predicted by model life tables could arise from the contribution of catastrophic mortality, which elevates the risk of death across all age categories: as young adults comprise a large segment of the living population, they tend to be over-represented in catastrophic death assemblages. For these reasons, considerable caution needs to be exercised when interpreting age distributions estimated from human skeletal remains.

Furthermore, regardless of overall levels of mortality, all censused human populations contain a proportion of individuals who live to advanced ages, providing evidence for the evolution of delayed senescence and hence increased longevity in humans as part of the distinctive slow *Homo sapiens* life history pattern. Thus, the underrepresentation of older people in prehistoric skeletal assemblages is problematic not only for accurate reconstruction of the age-specific risk of death, but also for understanding longevity in past populations. Above, we argued that the apparent deficit of older people in the skeletal populations of prehistoric *Homo sapien*s is best explained by biases in preservation and methodological limitations of palaeodemographic analysis. We now return to the key point that demographic uniformitarianism argues for continuity in the evolved mechanisms underlying human demographic processes and pose the question as to why a longer life span was selected for among *Homo sapiens*.

Importantly, selection for a longer lifespan has implications for fertility as well as mortality. Cessation of reproduction in females long before the end of life is highly unusual in mammals **[35]**, and a long post-reproductive lifespan is one of the life history traits that distinguishes modern humans from all other primate species. In non-human primates, as is the case in nearly all mammalian species, the approach to maximal lifespan and an irreversible decline in female fertility occur in tandem. In humans, the relative invariance in the timing of menopause, observed both across living human populations and throughout the historical record, together with the lack of evidence for recent secular trends in age at menopause, suggest that humans have retained a hominoid pattern of fertility. The menopause is therefore more likely to be a consequence of selection for longer lifespan, rather than of selection for a shorter reproductive span **[36]**. Due to their later physiological maturation, human females start giving birth about 5 years later than great apes **[37]** although with shorter birth intervals in humans even foraging populations achieve higher total fertility than do great apes.

One argument is that selection for a longer lifespan enabled older generations, especially post-reproductive females, to enhance the survival chances of their offspring and descendants. This “grandmother hypothesis” is shorthand for a range of evolutionary scenarios that explain the evolution of long post-reproductive lifespans through the selective advantage conferred by grandmothers to their kin - essentially by providing surplus resources to daughters of reproductive age **[38, 39]**. The extension of post-reproductive female lifespan predicted by the grandmother hypothesis is effectively equivalent to the length of a generation (around 25 years in modern humans) because the fitness benefits conferred by the grandmother diminish sharply when the grandmother’s own offspring terminate their reproduction **[40]**. When in human evolution did this occur? The pattern of female fertility in modern humans described above appears remarkably plesiomorphic, broadly resembling the ancestral hominoid condition in its age distribution, though with the ability to achieve higher total fertility through maintaining shorter inter-birth intervals. We infer that the modern human pattern of female fertility may also have characterised earlier species in the *Homo* lineage. O’Connell et al. **[38]** associated the extension of lifespan required by the grandmother hypothesis with the evolution of *H. erectus*/ *H. ergaster*, in particular correlating extended longevity with this species’ larger brain and body size, and its delayed maturity compared to *Australopithecus*. One prediction from this hypothesis is that the abbreviated hominin lifespans calculated from skeletal data for Middle Pleistocene hominins (*H. heidelbergensis* and *H. neanderthalensis* – see below) are likely to be incorrect.

**4. Prehistoric demography in the absence of the uniformitarian assumption: the palaeodemography of archaic hominins**

Howell **[9]** explicitly excluded non-*Homo sapiens* in her argument for human demographic uniformitarianism. However, the archaeological and palaeoanthropological records of the genus *Homo* extend millennia beyond the initial appearance of *Homo sapiens* in most regions of Africa, Europe, and Asia, and these populations are the subject of a growing body of cross-disciplinary palaeodemographic research **[41-47].** The anatomical and behavioural contrasts between all archaic forms of *Homo* on the one hand, and *Homo sapien*s on the other, indicate wider biological differences which render the assumption of demographic uniformitarianism in its strictest form problematic for these populations. This conclusion leads to two further questions which lack easy answers: 1) what is the extent of these biological differences, and how do they relate to the key demographic variables of fertility and mortality? 2) what are the implications of these biological and demographic differences for cross-disciplinary research into the palaeodemography of archaic hominins?

The answer to the first question usually begins by seeking to establish when the ‘modern human’ (i.e. *Homo sapiens*) life history pattern emerged. The life history of extinct hominins is inferred from indirect proxies related to rates of maturation and longevity (body mass, brain size, and dental development) **[48-49].** At a minimum, we can state that the modern human life history pattern emerged within the *Homo* clade **[50].** However, accurate measurement of archaic hominin life history variables is complicated by fragmentary and small fossil sample(s) and the evidence is often conflicting **[51-52].** This is the case even for the archaic hominins of the Middle and Late Pleistocene for whom comparatively large and well-preserved fossil collections exist. For example, comparative analysis of body size, brain size, and dental development indicates that the life history of Neanderthals (*Homo neanderthalensis*) was consistent with that of *Homo sapiens* **[49]**; a finding supported by a recent study of the growth pattern of the El Sidrón Neanderthal child **[53].** However, other studies have suggested a Neanderthal developmental rate both faster **[54-56]** and potentially slower **[57]** than those of *Homo sapiens*. While on balance, the data suggest that later archaic hominins (*H. heidelbergensis, H. neanderthalensis*) probably had a pace of development within the *Homo sapiens* range, there were likely nonetheless subtle differences related to other aspects of their physiology **[53, 58-59].**

The implications of these biological and life history differences for method and theory in prehistoric demography have been most firmly addressed by practitioners of the skeletal palaeodemography of archaic hominins. As is the case in later prehistory, age-at-death distributions of site-specific and pooled skeletal samples typically do not conform to expectations of age-specific attritional mortality distributions derived from recent populations **[42, 46, 60-62].** As shown in section 3b, where the demographic uniformitarian assumption holds we can, with reasonable confidence, interpret this pattern in terms of unrepresentative sampling and inaccuracies in age estimation. However, in the absence of the uniformitarian assumption, no such cross-checks hold, leading to some fierce debates as how to interpret these palaeodemographic profiles.

The age-at-death distribution of the Middle Pleistocene pre-Neanderthal hominin fossils from the site of Sima de los Huesos (SH) (Burgos, Spain) is an excellent case in point. These SH hominins all derive from the same lithostratigraphic unit at the site and their taphonomic condition is relatively homogenous, suggesting that they belong to the same biological population **[63]**. However, the assemblage produces a mortality profile with almost no infants and children, a preponderance of adolescents and young adults, and very few older adults (35 years +) (**Figure 2).** Wolpoff and Caspari **[62]** propose that this distribution reflects an attritional profile consistent with the life history and survivorship rates of Middle Pleistocene hominins; an interpretation that they also apply to the age-at-death distribution of the later Krapina Neanderthals from Croatia. Life history data from the SH hominins provides mixed support for this scenario. The pattern and timing of dental development of the SH hominins falls within the range of variation of *Homo sapiens* **[64].** On the other hand, calculations of the rate of wear of the anterior teeth (incisors and canines) indicate that these would have been completely worn down by the age of 50 and may have been an important limiting factor on their potential longevity (maximum life expectancy) **[65].**

**[Figure 2 near here]**

Nonetheless, as is the case with the age-at-death distributions of prehistoric *Homo sapiens*, the Sima de los Huesos profile is unlikely to be an accurate reflection of demographic reality. Ages of the juvenile hominins in the SH assemblage were undertaken using modern human standards for dental development, which as previously mentioned, probably overlap with dental development schedules for *H. neanderthalensis* and *H. heidelbergensis*. However, the ages of the adult individuals were estimated using the Miles method, which produces a calibration of the amount of dental wear in adults based on the wear rates observed in the juvenile component of the assemblage. As with other skeletal age estimation methods, the Miles method requires adjustment to avoid the under-estimation of age at death in older adults **[66]**,so the estimated ages of some of the adult SH individuals may be too low. The likely presence of much older adults in the SH assemblage is further suggested by the state of the articular surfaces on the SH pelvis 1 specimen **[67]**. Although the age at death of the SH1 specimen was estimated to fall in the open-ended age category of >45 years, unbiased age estimations based on uniform priors developed for modern human populations (e.g. **[68]** would suggest a median estimated age for this specimen of between 60 and 70 years. It is furthermore highly likely that the potential for a longer life span was present before many individuals regularly reached it **[48]**, and small skeletal samples are unlikely to include the necessarily outlying individuals who died at extremely old ages **[69].** In the case of the SH hominins, arguments for a maximum life span of ~50 years are further weakened by the predicted life spans of *H. habilis* (52-56 years) and *H. erectus* (60-63 years) **[70],** derived from the allometric relationship between body size, brain size, and longevity among mammals **[71].**

Sampling may also be an important factor in the age-at-death distribution of the SH hominins. The assemblage does not neatly correspond to either an attritional or a catastrophic profile ([**61 cf. 62**]), but a scenario whereby a catastrophic event impacted a subset of the population is plausible (an exploratory hunting party of young, mobile individuals separated from their larger group; **[60, 72]**), and instances of catastrophic mortality may have been more common in early population history than usually suspected **[26].** The role of biological differences between the early members of the Neanderthal clade at Sima de los Huesos and the modern-day *Homo sapiens* from whom our palaeodemographic models and methods derive should not, however, be excluded from interpretation. Even minor differences in rates of development between archaic hominins and *Homo sapiens* —compounded by differences in diet, health and economic conditions **[73]** —could impact estimates of age-at-death (albeit not the relative distribution of individuals across categories).

In other branches of the palaeodemography of archaic hominins, the methodological and theoretical implications of the absence of the uniformitarian principle are less keenly felt but are nonetheless highly relevant. In archaeological demography, the applicability of methods and standards developed from the study of ethnographic and historical populations to pre-modern (i.e. pre-*Homo sapiens*) hominins has long been questioned (e.g. **[74]).** The impact of life history differences on demographic reconstructions and interpretations based on these data —which are primarily used to study changes in relative population size and growth **[3-5]**—are, however, indirect and hard to take into account, despite both these variables being determined by underlying fertility and mortality rates. Within this branch of prehistoric demographic research, other biological differences between archaic hominins and *Homo sapiens* have a greater impact. The large body mass, and resultant high energy demands of Neanderthals, for example, is a particularly important biological difference between them and *Homo sapien*s **[75-76]**. High energy requirements and the challenges of obtaining enough food to meet these, particularly in the lack of evidence for food storage, are often cited as potential restrictions on the maximum size of Neanderthal living-groups [**77-78]**, fertility rates, and local population densities **[79]**, and would need to be taken into account in palaeoecological estimates of potential environmental carrying capacity. Within environmental carrying capacity models, the key implication of the higher energetic requirements of Neanderthals is that if foraging from a central place, the effective foraging radius (the area at a distance from camp at which the required amount of energy is equal or more than the net return) would have been smaller than for *Homo sapiens*, meaning that Neanderthal groups would have depleted local resources more quickly and needed to move camp more frequently **[78].** This higher mobility—which has a key biological component— also complicates estimates of relative change in population size based on archaeological site counts (e.g. **[80]**) raising questions about the exact relationship between site quantities and population size (a relationship that is often assumed to be linear, but is in reality unknown), and the possible differences in this relationship between different hominins. More broadly, life history differences, combined with other wider biological and cognitive differences (such as body size, energy expenditure, and brain size) would also have had important implications for population structure, living group size and composition, with attendant repercussions for the emergence of key human social behaviours such as alloparenting, division of labour, and intergenerational cooperation **[81].**Dennell **[82]** posits an important role of these biological differences in the pattern and speed of migration and colonisation of new environments of *Homo erectus* and *Homo sapiens* during the Out of Africa 1 and 2 events respectively.

**5. Conclusion: challenges and lessons for the use of the uniformitarian principle in cross-disciplinary prehistoric demography**

The assumption of demographic uniformitarianism is a core principle in palaeodemography. This assumption provides the basic framework for palaeodemographic research across a range of disciplines, allowing for the construction of theoretically plausible models and parameters against which to test and examine palaeodemographic data, and providing the justification for the use of data from ethnographic and historical populations to supplement sparse prehistoric records.

The principle of demographic uniformitarianism is well-accepted. Critics have questioned whether the use of the uniformitarian assumption is a form of “self-fulfilling prophecy” **[83]** that prevents the possibility of identifying unusual or unrecorded demographic behaviour in the past, either because prehistoric populations lived in environments that have no modern analogue, or because there is greater variation across human biological and life history parameters than is frequently supposed**,** particularly between Pleistocene and Holocene populations **[84-85]**. While this possibility cannot be rejected outright, the null hypothesis should be that reconstructions of population dynamics and structures should fall within the known envelope of human responses, at least when analysing *Homo sapiens* populations. As life history parameters are subject to strong evolutionary constraints, patterns of age-specific fertility and mortality, and their subsequent effects on population size and dynamics, should vary in predictable, easily modelled, and fairly constrained ways **[26]**.

Debate continues as to how far back in evolutionary and prehistoric time we can extrapolate human demographic and life history parameters comparable to those of recent historical and contemporary populations. The inapplicability of the assumption of demographic uniformitarianism in its strictest form complicates palaeodemographic research into archaic hominin populations, even for the more recent hominin species. Conversely, contradictions between expectations based on the uniformitarian assumption and palaeodemographic data do not automatically mean that the palaeodemographic data is best interpreted as representative of vastly different demographic regimes; issues of sampling and poor preservation are even more pertinent in these stages of early prehistory. The non-applicability of a strict principle of demographic uniformitarianism has far-reaching implications for the study of the demography of archaic hominins across multiple disciplines. It reduces the comparability of palaeodemographic data from archaic hominins—both in terms of comparison with each other, and with *Homo sapiens*— even if derived using the same method. It also means that greater caution must be taken in the use of values for absolute population estimates and model parameters derived from recent populations to supplement the prehistoric database, as the baseline justification for the use of these values is undermined. Understanding the evolution of human life history traits, and their impact on the demography of archaic hominins is one of the most important challenges of palaeodemography **[26]**.

The principle of uniformitarianism features less heavily in areas of prehistoric demographic research which focus on variables (such as population size and density) that are not directly subject to uniformitarian principles, and which are usually interpreted in relative, rather than absolute, terms. Nonetheless, as discussed in section 4, many palaeodemographic proxies contain assumptions about factors such as mobility and social structure that are, in part, influenced by biology, life history, and demographic parameters. In genetics, the estimation of effective or breeding population size from patterns of genetic variation **[86]** requires an assumption of average generation length- an attribute that likely varies between hominin species due to its relationship with life history parameters such as age at first birth and rate of senescence. Although containing a cultural component, demography is, at its core, the product of biological processes. The principle of biological and demographic uniformitarianism that provides the theoretical scaffolding for palaeodemography should be borne in mind by all who work in cross-disciplinary prehistoric demographic research.

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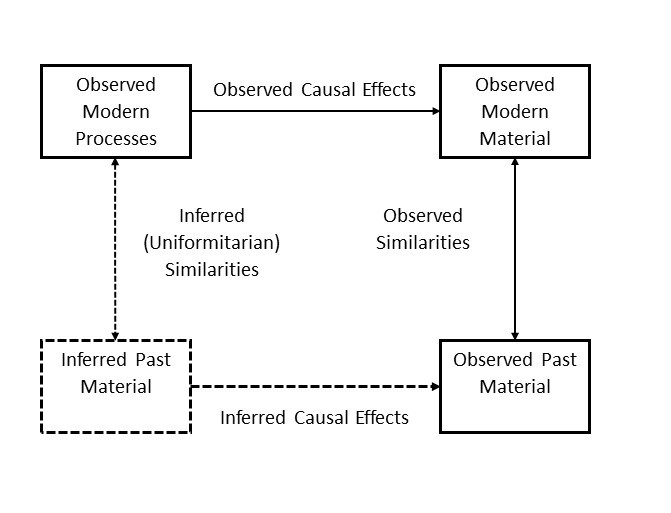
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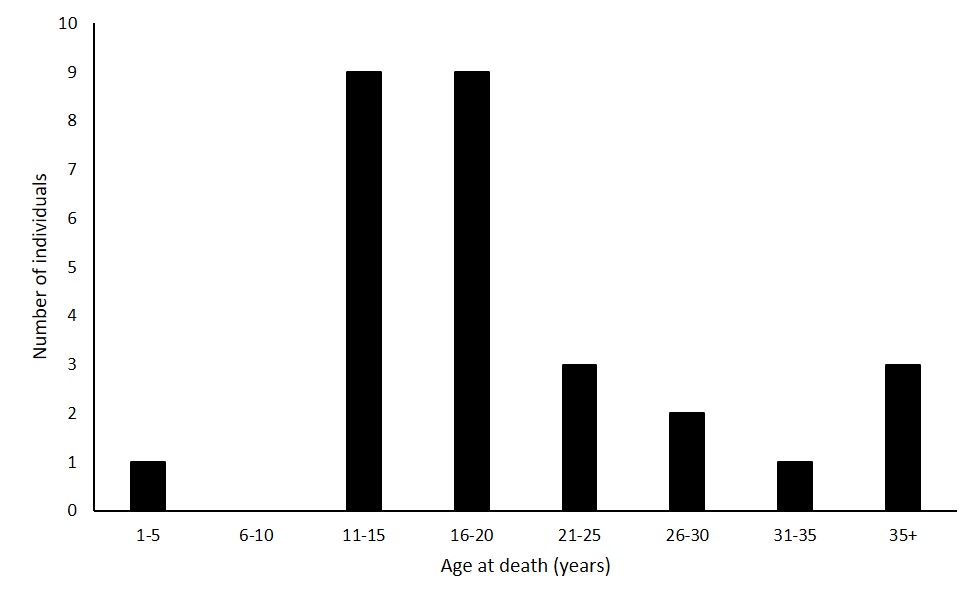
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**Figures**

**Figure 1.** Role of uniformitarianism in simple analogical reasoning. The uniformitarian principle underpins the argument that similarities between modern and ancient materials can be explained by inferring that unobservable past processes and their effects would have resembled processes observable in the present day (after **[6])**

**Figure 2.** The age-at-death distribution of the 28 Middle Pleistocene hominins from the site of Sima de los Huesos, Spain. Redrawn from **[61]**