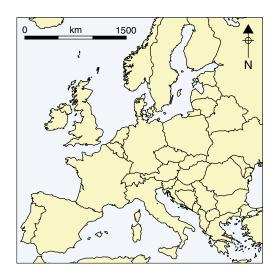
Populations headed south? The Gravettian from a palaeodemographic point of view

Andreas Maier^{1,*} & Andreas Zimmermann²



The Gravettian is known for its technological innovations and artisanal craftwork. At the same time, continued climatic deterioration led to the coldest and driest conditions since the arrival of Homo sapiens sapiens in Europe. This article examines the palaeodemographic development and provides regionally differentiated estimates for both the densities and the absolute numbers of people. A dramatic population decline characterises the later part of the Gravettian, while the following Last Glacial Maximum experienced consolidation and renewed growth. The results suggest that the abandonment of the northern areas was not a result of migration processes, but of local

population extinctions, coinciding with a loss of typological and technological complexity. Extensive networks probably assured the maintenance of a viable population.

Keywords: Western Europe, Central Europe, Gravettian, palaeodemography, migration/local extinction, cultural complexity, minimum viable population

Introduction

The Gravettian (33 000–25 000 cal BP) is known for its flourishing artwork (e.g. Mussi et al. 2000; Jaubert 2008) and high technological standards, illustrated by the Obłazowa boomerang (Valde-Nowak et al. 1987), by ceramics, and by evidence of cordage items, basketry and textiles such as those from Pavlov I and Dolní Věstonice (Soffer 2000; Soffer & Adovasio 2004). While cultural life prospered, the Gravettian community had to cope with continuous environmental deterioration. Shortly after 33 000 cal BP, summer insolation in

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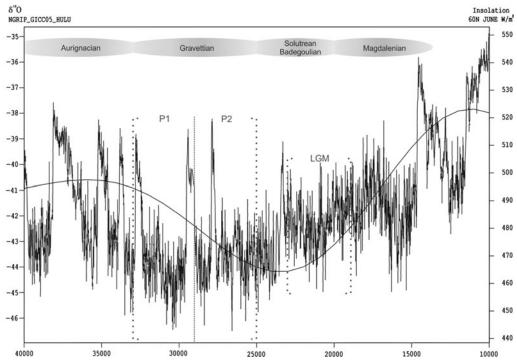


Figure 1. The climatic conditions during the Gravettian. Temperatures are indicated by the δ^{18} O curve. Insolation (smooth curve) is given in watts per square metre for 60°N. Time on the x-axis is given as cal BP. Data from CalPal 2012 (Weninger et al. 2012).

northern latitudes started to decline, coinciding with the inception of glaciation processes that culminated in the peak ice-sheets of the Last Glacial Maximum (LGM) (Clark *et al.* 2009). This decline in insolation continued steadily, attaining its lowest level for the entire Upper Palaeolithic shortly after 25 000 cal BP (Figure 1). Judging from the δ^{18} O values recorded in the NGRIP GICC05 ice-core (Björck *et al.* 1998; Rasmussen *et al.* 2006), temperatures throughout most of the Gravettian were lower than in any other period of the Upper Palaeolithic, including the LGM (*c.* 24 000–18 000 cal BP; *sensu* Mix *et al.* 2001). The continuous decrease in solar energy probably led to a progressive decline in net primary productivity and, consequently, to a reduction in animal biomass (cf. Binford 2001: 58–113). Together with the advancing glaciers, this trend presumably affected living conditions in higher latitudes particularly strongly.

The objective of the investigation presented here is threefold: first, we analyse the extent to which climatic conditions affected Gravettian populations throughout Western and Central Europe by estimating absolute numbers of people and population densities for two chronological phases in ten different regions. In contrast to previous palaeodemographic studies, where the Gravettian is treated either as a spatial and temporal unit (Bocquet-Appel & Demars 2000; Bocquet-Appel *et al.* 2005), or where internal variability is studied only in smaller areas and with regard to relative values (French & Collins 2015), our approach allows us to discuss the population dynamics of the Gravettian on a large spatial scale in more

detail. Second, we try to assess whether abandonment by migration or local extinction was a more probable cause for the desertion of certain areas during the later part of the Gravettian; and third, we explore to what extent observable population dynamics affected the complexity of the technological and typological spectrum of Gravettian hunter-gatherers.

Material and methods

The database for this study (Maier & Zimmermann 2016) was compiled during an extensive literature survey, and comprises 654 assemblages. Although not necessarily exhaustive, it is considered statistically representative. The chronological boundaries (33 000–25 000 cal BP) are in good accordance with other chronological definitions of the Gravettian (Jöris & Weninger 2004; Klaric 2008; Jacobi *et al.* 2010; Kozłowski 2015), although slightly older dates are sometimes reported, e.g. from Willendorf II (Haesaerts & Teyssandier 2003).

Temporal division and sorting of the assemblages

We divided the Gravettian into two phases of equal duration: P1 (33 000-29 000 cal BP) and P2 (29 000-25 000 cal BP) (Figure 1). This allows for the observation of population dynamics while ensuring a sufficiently large number of assemblages per phase to obtain reliable results. Recorded assemblages were then allocated to one of these phases using both absolute dates and typological data. Absolute dates are available for 219 assemblages, with 146 dated to P1 and 73 dated to P2 (see Table S1 in online supplementary material), an imbalance of 2:1 in favour of P1. The remaining 435 assemblages were allocated according to their artefact typologies. The typological structure of the Gravettian is particularly well suited for such a task, as it comprises a relatively large number of widely accepted, chronologically successive sub-stages, with characteristic typological features. To assess for typological shifts around the chosen threshold of 29 000 cal BP, we compiled a set of radiocarbon dates from selected sites with a good chronological control pertaining to the time frame shortly before and after 29 000 cal BP (Figure 2 & Table S2). In Western Europe, Bosselin and Djindjian (1994) identified six consecutive typological stages for the Gravettian: the Fontirobertian, Undifferentiated Gravettian, Noaillian, Rayssian, Laugerian (A and B) and Protomagdalenian. Prior to or contemporaneous with the Fontirobertian were the Bayacian (Rigaud 2008) and the Belgian facies called Maisière-Canal (Otte & Noiret 2007; Jacobi et al. 2010). When reliable radiocarbon dates are taken into consideration (Figure 2 & Table S2), the 29 000 cal BP boundary coincides well with the transition from the Noaillian/Rayssian to the Laugerian in Western Europe (Figure 2; cf. Klaric 2008). In Portugal, early and late Gravettian phases occur before and after 29 000 cal BP (Bicho et al. 2015: 500). In Central Europe, the 29 000 cal BP threshold roughly marks the transition from the Pavlovian to the Willendorf-Kostenkian (Jöris & Weninger 2004). Typologically, this coincides with the appearance of shouldered points during the later phase (Svoboda 2007).

In the valleys of the Prut and Dniester, the appearance of shouldered points (Noiret 2004: 448) and the disappearance of bifacial points (Nuzhnyi 2009) are seen as fairly

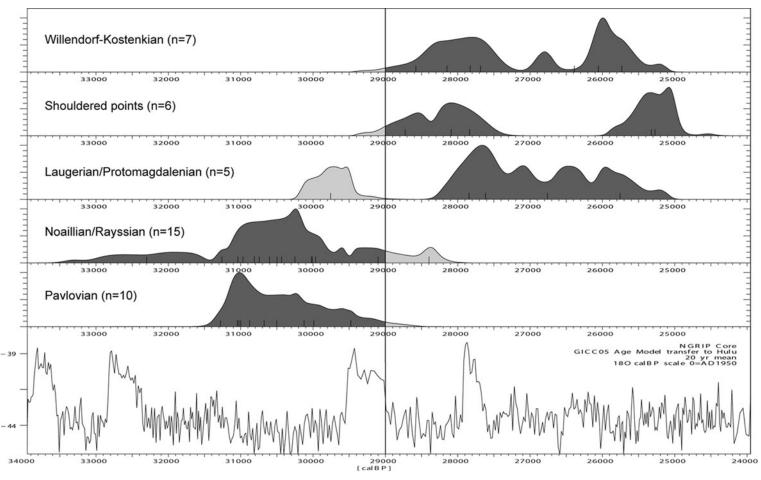


Figure 2. Radiocarbon dates from different Gravettian facies and different regions with standard deviation \leq 200 around 29 000 cal BP (CalPal-Multigroup-compilation with CalPal 2012; Weninger et al. 2012). As the slope of the calibration curve at around 29 000 cal BP is particularly steep, any bias introduced should lead to a 'peak' in the summed probability distributions at this position, emphasising the reliability of the observed gaps. n = number of dates included in the sum calibration. P1: 33 000–29 000 cal BP; P2: 29 000–25 000 cal BP. For details on dates, see Table S2.

precise chronological markers. The earliest ¹⁴C dates for shouldered points are reported from layer 7 at Molodova V. Unfortunately, the dating of this layer spans between 30 500 and 24 500 cal BP (Figure 2 & Table S2). Most dates are, however, younger than 29 000 cal BP. When radiocarbon dates from the archaeological horizon with the earliest shouldered points at Mitoc-Malu Galben are taken into account—so-called 'Gravettian IV' (Noiret 2009: tab. 7)—the signal becomes clearer, pointing towards an occurrence of shouldered points after 29 000 cal BP. Thus it can be stated that around 29 000 cal BP, clearly discernible typological shifts may be observed throughout the investigated area, allowing a typological attribution of assemblages to either side of this threshold: P1 or P2. Nevertheless, typological classification is always plagued with uncertainties, and may lead to incorrect allocations. For the reasons explained above, however, in the case of the Gravettian, it is considered reliable enough not to bias the overriding temporal distribution significantly.

Typological attribution increases the assemblages associated with P1 to 347 and P2 to 163, maintaining a ratio of about 2:1. The remaining 144 cases were not attributable by typological means and were excluded from further analysis. They are, however, plotted on our maps for an assessment of potential spatial distortions. For the protocol of demographic estimates, see Maier *et al.* (2016), and for more details generally, see the online supplementary material.

Results

To account for differences in site density between Western and Central Europe (perhaps caused by different subsistence and land-use patterns), the Optimal Isolines (OIs; comprising areas of equal site densities—for explanations and definition, see the online supplementary material) have been determined individually. For P1, the OI in the western part is found at a radius of 41km Largest Empty Circle (LEC; this serves as a density measure, the larger the LEC, the lower the density—for explanations and definition see the online supplementary material), and at 44km LEC for the eastern part, whereas for P2 it is found at a radius of 50km LEC (west) and 33km LEC radius (east) (Figure S2). The resulting settlement areas, together with the raw material catchments, are depicted in Figures 3 and 4. Departing from these data, population densities have been calculated at both regional and continental scales, resulting in the values given in Tables 1 and 2.

The estimated total population for the investigated area (continental scale) ranges roughly between 1700 and 3700 people for P1, and 700 and 1550 for P2. During P1, the highest regional number of people (300–1000) can be found in south-western France, whereas the lowest regional number is estimated for Provence (70–100). The highest density of people (given in people per 100km² (P/100km²)) is estimated for the Prut region (1.7–2.7 P/100km²) and Belgium (1.0–2.5 P/100km²), whereas the lowest density is calculated for the Middle Danube area (0.3–0.7 P/100km²). During P2, the Middle Danube is estimated to have had the highest number (130–460) of people, and the Prut region the lowest (30–110). At the same time, population density in the east (0.5–1.9 P/100km²) seems to have been higher than in the west (0.5–1.0 P/100km²). The median estimates of total population dropped from about 2800 to 1000 people, while the population density within

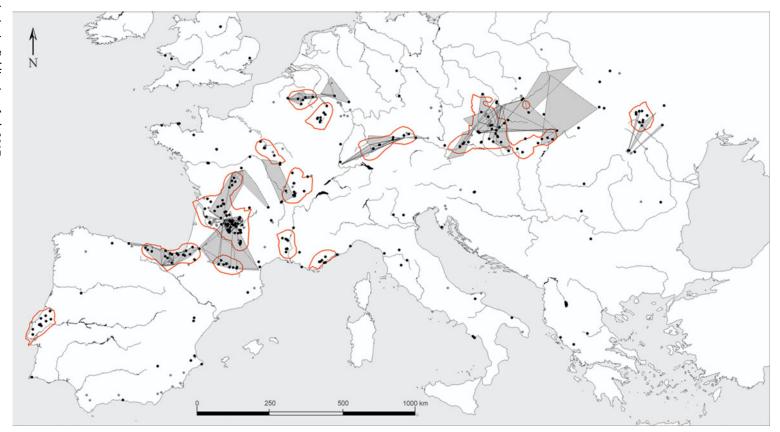


Figure 3. Map of settlement areas and raw material catchments for P1. Black dots: sites attributed radiometrically or typologically to P1; grey dots: sites lacking chronological attribution (excluded from calculations); grey polygons: P1 raw material catchments; red lines (Optimal Isolines): Western Europe 41km LEC radius, Eastern Europe 44km LEC radius (cf. Figure S2).

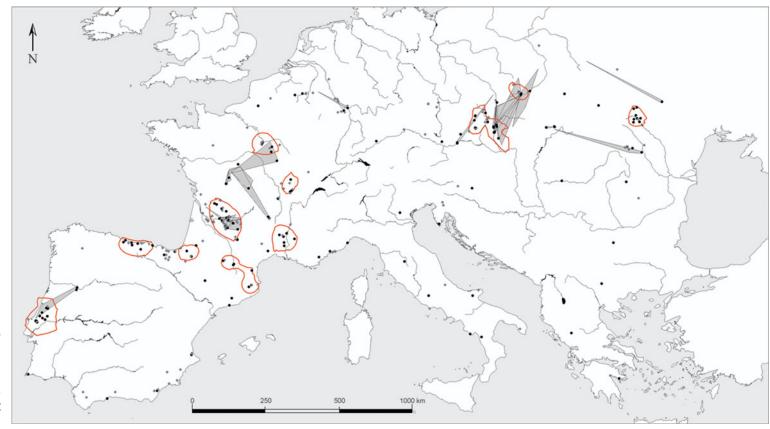


Figure 4. Map of settlement areas and raw material catchments for P2. Black dots: sites attributed radiometrically or typologically to P2; grey dots: sites lacking chronological attribution (excluded from calculations); grey polygons: P2 raw material catchments; red lines (Optimal Isolines): Western Europe 50km LEC radius, Eastern Europe 33km LEC radius (cf. Figure S2).

Table 1. Regionally differentiated palaeodemographic estimates for the earlier Gravettian (P1).

Region	Q	OI	\mathbf{A}_{RM}	\mathbf{A}_{OI}	$N_{\rm g}$	P	D_s	A_{m}	D_{m}
Portugal (N-Spain inserted)	1		3001	12493	4.2	179	0.014		
_	2	41	3451	12493	3.6	156	0.012		
	3		4110	12493	3.0	131	0.010		
N-Spain	1		3001	21 270	7.1	305	0.014		
	2	41	3451	21 270	6.2	265	0.012		
	3		4110	21 270	5.2	223	0.010		
SW-France	1		2563	60 201	23.5	1010	0.017		
	2	41	3265	60 201	18.4	793	0.013		
	3		8273	60 201	7.3	313	0.005		
Burgundy (SW-France inserted)	1		2563	25 308	9.9	425	0.017		
	2	41	3265	25 308	7.8	333	0.013		
	3		8273	25 308	3.1	132	0.005		
S-Rhône (N-Spain inserted)	1		3001	9693	3.2	139	0.014		
	2	41	3451	9693	2.8	121	0.012		
	3		4110	9693	2.4	101	0.010		
Provence (N-Spain inserted)	1		3001	6507	2.2	93	0.014		
	2	41	3451	6507	1.9	81	0.012		
	3		4110	6507	1.6	68	0.010		
Belgium	1		1735	19731	11.4	489	0.025		
	2	41	2586	19731	7.6	328	0.017		
	3		4368	19731	4.5	194	0.010		
Upper Danube	1		2800	20 361	7.3	313	0.015		
	2	44	4677	20 361	4.4	187	0.009		
	3		5023	20 361	4.1	174	0.009		
Middle Danube	1		5791	56723	9.8	421	0.007		
	2	44	8360	56723	6.8	292	0.005		
	3		16078	56723	3.5	152	0.003		
Prut	1		1592	10753	6.8	290	0.027		
	2	44	2064	10753	5.2	224	0.021		
	3		2536	10753	4.2	182	0.017		
Total	1				85	3664		2 000 000	0.0018
	2			243 039	65	2780		2 000 000	0.0014
	3				39	1670		2 000 000	0.0008

Notes

Q: quartiles of raw material catchments; OI: selected Optimal Isoline (km); A_{RM} : area of raw material catchments in km² according to Q1–Q3; A_{OI} : area encircled by the Optimal Isoline in km²; N_g : number of groups; P: absolute number of people; D_s : population density (people/km²) within the settlement areas (OIs); A_m : area of the considered map section in km²; D_m : population density (people/km²) across the map section.

the considered map section (approximately 2 000 000km²) dropped from 0.0014 to 0.0005 persons per km².

Discussion

Our estimates for the Gravettian indicate low population numbers. Bocquet-Appel and Demars (2000) and Bocquet-Appel *et al.* (2005) also estimate absolute numbers of people

Table 2. Regionally differentiated palaeodemographic estimates for the later Gravettian (P2). For abbreviations, see notes to Table 1.

Region	Q	OI	A_{RM}	A _{OI}	N_{g}	P	D_s	\mathbf{A}_{m}	D _m
					, -				
Portugal (N-Spain inserted)	1		4159	18 798	4.5	194	0.010		
	2	50	5075	18 798	3.7	159	0.008		
	3		7941	18 798	2.4	102	0.005		
N-Spain	1		4159	15 900	3.8	164	0.010		
	2	50	5075	15 900	3.1	135	0.008		
	3		7941	15 900	2.0	86	0.005		
SW-France	1		4159	32 920	7.9	340	0.010		
	2	50	5075	32 920	6.5	279	0.008		
	3		7941	32 920	4.1	178	0.005		
Burgundy (SW-France inserted)	1		4159	14951	3.6	155	0.010		
	2	50	5075	14951	2.9	127	0.008		
	3		7941	14951	1.9	81	0.005		
S-Rhône (N-Spain inserted)	1		4159	11 853	2.9	123	0.010		
	2	50	5075	11 853	2.3	100	0.008		
	3		7941	11 853	1.5	64	0.005		
Provence (N-Spain inserted)					_				
Belgium					_				
Upper Danube					_				
Middle Danube	1		2217	23 692	10.7	459	0.019		
	2	33	5927	23 692	4.0	172	0.007		
	3	55	7933	23 692	3.0	128	0.005		
Prut	1		2217	5696	2.6	110	0.019		
	2	33	5927	5696	1.0	41	0.017		
	3	33	7933	5696	0.7	31	0.007		
Total	1		7933	2020	36.0	1546	0.00)	2 000 000	0.0008
iotai				122.010					
	2			123 810	23.6	1013		2 000 000	0.0005
	3				15.6	671		2 000 000	0.0003

for the Gravettian. The time frame is set slightly differently, ranging from about 31 000 to 23 500 cal BP and is not further subdivided. Their estimates range between 1879 and 30 589 people with an average value of 4776 for Western and Central Europe (Bocquet-Appel *et al.* 2005), or 7771 for Western Europe (Bocquet-Appel & Demars 2000), and thus are significantly higher than our estimates, even for the older phase. The generally higher estimates, and particularly the maximum value of about 30 500 people, are probably the result of neglecting the empty areas between the site clusters. This, in our view, results in a clear overestimation of the Gravettian population.

Our calculations indicate a reduction in the number of people from P1 to P2 of about 60 per cent. This view is supported by the results of other analyses, such as the study by French and Collins (2015) that shows a considerable population decline in south-western France during the late Gravettian. These findings have a strong impact on our view of the Gravettian and thus deserve a critical evaluation. As mentioned above, there is already a strong imbalance in the database between sites attributed to P1 and P2. Before approaching

further interpretations, it is thus crucial to discuss possible biases in the compilation of the database that might distort our calculations in favour of P1.

A biased data set?

When only typologically attributed assemblages are considered, there is a ratio of 2:1 in favour of P1. This might indicate a better typological visibility of assemblages of the earlier phase. Indeed, at least in Western Europe, P1 comprises a number of typologically recognisable facies, characterised by several distinctive components, such as Font-Robert points (Fontirobertian), fléchettes (Bayacian), Noaille burins (Noaillian) or Raysse burins (Rayssian). The later phase, however, only includes the Laugerian and Protomagdalenian, whose typological composition is less distinctive. The P2 assemblages may, therefore, be less visible in terms of typology than their P1 counterparts. Assuming, however, that the remaining 144 assemblages, attributable to neither P1 nor P2, are mainly unrecognised assemblages of the later phase seems untenable for three reasons. First, an imbalance between earlier and later Gravettian sites has already been recognised on a regional scale (e.g. French & Collins 2015). Second, the distinctive types of P1 are not necessarily present in every assemblage, and smaller assemblages in particular probably present a chronologically undiagnostic typological spectrum; the 'Undifferentiated Gravettian' of P1 is equally hard to recognise typologically, as are the Laugerian and the Protomagdalenian. Third, if only radiometrically dated sites are considered, then the ratio between P1 and P2 remains at 2:1.

Given that taphonomic loss usually has the effect of younger sites being preserved in higher proportions than older ones (Surovell & Brantingham 2007), the probability of finding sites from P2 should generally be higher than finding sites from P1. This assumption gains further credence given the increased likelihood of P2 sites being preserved as a consequence of the substantial loess accumulation in the later Gravettian. While P1 sites may share comparably favourable preservation conditions, they are more susceptible to becoming deeply buried and thus archaeologically invisible because of their earlier formation. Since typological invisibility does not explain the imbalance in the number of radiometrically dated sites, these observations are a strong argument in favour of a general decrease in the number of sites during the later Gravettian. Therefore, even if P2 assemblages might be less visible by virtue of their typological composition, we consider our database to be statistically representative.

Migration or population breakdown?

Having excluded sampling error as a major factor in the calculation of our estimates, we can now explore their significance for the questions raised at the beginning of the article. In order to assess whether migration or population breakdown (local extinction) led to the abandonment of certain areas, it is necessary to take a closer look at the different regions, as not all areas were affected equally. There seems to be a general trend that settlement areas located farther north and closer to glaciers were more strongly affected demographically.

In Britain, Belgium and the Upper Danube region, the population drops to extremely low levels, and even zero during P2 (see also Straus 2000: 76; Jacobi et al. 2010; Pettitt & White 2012: 419–22). In Provence, it drops to a level too low to be measurable using our method. Only in the most southerly settlement area, in Portugal, does the population seem to have remained roughly stable (Figure S3). This geographic variation strongly supports the hypothesis that climatic cooling together with the decrease in insolation were the major factors driving population decline. Given the fact that almost all settlement areas experienced a reduction in population during P2, including those adjacent to areas displaying a complete population breakdown, it must be assumed that people from Britain, Belgium and the Upper Danube area did not leave their settlement areas to migrate southwards, at least not in large numbers. Rather, it seems that populations in these three areas broke down and suffered extinction. Interestingly, a similar conclusion is reached by Roebroecks et al. (2011) for Neanderthal populations in northern latitudes during the pronounced cooling of MIS 4.

If substantial migration had taken place, a rise in population should be observable in the adjacent areas. The possibility that a few individuals joined neighbouring groups whose overall numbers had decreased despite the arrival of newcomers cannot be excluded. A strong, logistically organised subsistence strategy, predicated on a wide raw material procurement range, and only a few base camps per year, would probably result in an underestimation of the population (Kretschmer et al. 2016). The reported raw material catchments do not, however, indicate an increase in size (cf. Figures 3 & 4). Even if they did, it is unlikely that such an increase, even in an extreme case, would result in complete archaeological invisibility in such a way that it might be mistaken for evidence of a population breakdown. Our inference does not mean to imply that hunter-gatherer subsistence would have been impossible under these circumstances, but rather that the ever deteriorating conditions, particularly during the later phase, were a major problem for the adaptive capacities of Gravettian people. Thus, migration does not appear to have been a response of Gravettian hunter-gatherer groups when faced with climatic deterioration. Rather, at many locations the population decreased until eventually it entered a so-called 'extinction vortex', i.e. a self-enhancing process, where interaction between different factors such as inbreeding, environmental and demographic stochasticity, and also behavioural failures cause a population to become extinct (Gilpin & Soulé 1986).

Observations have shown that some populations decline directly from more than 100 individuals to extinction and that "time-to-extinction scales logarithmically with population size" (Fagan & Holmes 2006: 56). There seems to be a trend that "key aspects of a population's dynamics should deteriorate as extinction nears" (Fagan & Holmes 2006: 52) because major factors, such as inbreeding, environmental and demographic stochasticity, and year-to-year declines gain importance in small populations. Moreover, observations suggest that a given population size "a few years before extinction was somehow less valuable to persistence than the same population size several years earlier" (Fagan & Holmes 2006: 58). Thus, a certain number of individuals prior to or at an early stage of the extinction process can be enough to ensure the survival of a population, while the same number of individuals at a late stage of the process may be too small to prevent extinction.

The surviving hunter-gatherer groups seem to have responded differently. Within all settlement areas in Western Europe, a drop in population density (D_s) is observable, indicating that people were more dispersed across the landscape, perhaps in response to less abundant resources. In the east, however, we see a dramatic drop in density for the Prut region, but, at the same time, a slight increase for the Middle Danube area. The latter could point towards a slight aggregation of the remaining population. The lack of very large sites during P2, such as the P1 sites of Pavlov I, Dolní Věstonice I or Předmostí I, which seem to have been settled year-round (Fišáková 2013), could, however, point to increased residential mobility as a reaction to the altered resource situation.

Minimum viable population and a bottleneck situation

The later phase of the Gravettian seems to have been the rock bottom of demographic development since the arrival of modern humans in Europe (see Figure S4). Given the extremely low number of people in Western and Central Europe (700–1550) between 29 000 and 25 000 cal BP, it might seem questionable whether this number of people was sufficient to provide a minimum viable population (MVP), i.e. "all members of the population, whether or not they are members of the reproductive age cohort" (Smith 2014: 21). The lowest estimate for a MVP for modern humans is set at about 1500 individuals, comprising around 770 individuals in the reproductive age cohort (Hey 2005; Smith 2014; but see Traill *et al.* 2010). The effects of inbreeding can, apparently, be avoided even at numbers lower than this: Smith (2014: 19) states that "any population over 100 or so will be sufficient to avoid drift-related inbreeding effects", although Traill *et al.* (2010) see 500 adult individuals as a minimum threshold. The numbers we present are minimum estimates, but despite being relatively low compared to the MVP numbers noted here, our estimates are still within the range of a viable population.

Nevertheless, the dramatic drop in population size certainly led to a loss in genetic variability. This assumption is in accordance with the finding of a genetic bottleneck described by Posth *et al.* (2016) that led to the loss of mtDNA haplogroup M in the European population. They see this loss as having occurred during the LGM. Our results, however, support the possibility of an even earlier bottleneck, namely during the late Gravettian. The LGM, in contrast, seems to have been a phase of climatic amelioration, with warmer temperatures than during the late Gravettian, increasing insolation, demographic consolidation and renewed population growth (Figures 1 & S3; Maier *et al.* 2016). In particular, south-eastern Spain shows a pronounced increase in population, with estimates of between 200 and 900 people living there during the LGM.

Large-scale and long-distance mating and communication networks can, to a certain extent, counteract the effects of decreasing populations by connecting otherwise small communities to larger meta-populations. People in Western and Central Europe certainly maintained contact with populations in bordering regions. Southern Spain, Italy, the Balkans and the regions north and east of the Black Sea were also inhabited at this time, although the number and density of people seems not to have been very high. Evidence for these networks comes from the female statuettes of that time. Given the striking similarities between, for example, the specimens from Willendorf and Gagarino (e.g. Djindjian *et al.*

1999: fig. 12.6), located some 1900km apart, communication can be the only convincing explanation, as the probability of equifinality is vanishingly low.

A loss of cultural complexity?

Many studies have pointed out a strong connection between the demographic and cultural evolution of a population (e.g. Shennan 2001; Riede 2009; Vaesen 2012; for an opinion to the contrary, see Collard et al. 2016). Typological and technological impoverishments have been described for populations that became cut off from their original population, or became otherwise less numerous (e.g. Henrich 2004; Richerson et al. 2009; Roebroeks et al. 2011; but see also Collard et al. 2016). They have also been modelled for a metapopulation with frequent extinction of local sub-populations (Premo & Kuhn 2010). For the Gravettian, an apparently substantial decline in population during P2 coincided with an impoverishment of the typological and technological spectrum. The evidence for high technological standards almost entirely relates to sites dated to P1. In Central Europe, the spectrum of artisanal craftwork seems to become less complex (Svoboda 2007: 207), and in Western Europe, there is a trend from easily identifiable typological facies (e.g. Fontirobertian and Noaillian) to apparently typologically simpler assemblages (Laugerian and Protomagdalenian). These observations might indicate a general loss of knowledge and complexity due to population decrease. To the best of our knowledge, there are no quantitative estimates for the complexity of different tools and skills, making it difficult to quantify any associated loss or increase of knowledge over time between phases such as P1 and P2 more meaningfully.

Conclusion

The early Gravettian was a period of cultural and technological prosperity, whereas the late Gravettian seems to have been a period of pronounced crises. The population shrank by about 60 per cent, and a simplification in the material culture that affected typology, technology and artisanal craftwork indicates a broader loss of knowledge. When faced with environmental deterioration, Gravettian hunter-gatherers did not respond by migration. Instead, we observe several breakdowns of regional populations, particularly in the more northerly latitudes. Perhaps as an adaptation to the altered resource bases, people dispersed themselves more widely during the later phase, and exhibited stronger residential mobility, at least in Central Europe. While the later Gravettian seems to have been the lowest point for Upper Palaeolithic demographic development, the LGM was a period of population consolidation and renewed growth. Many aspects of this could only be touched on briefly in this article. It is our hope that future research will allow us to further investigate issues relating to demographic changes during this period: for instance, whether the Heinrich 3 event was the principal trigger for population breakdown, or rather one factor among many others in the process of long-term climatic cooling and population decline; or to find ways to quantify gains and losses in cultural complexity.

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Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.15184/aqy. 2017.37

References

- Bicho, N., J. Marreiros, J. Cascalheira, T. Pereira & J. Haws. 2015. Bayesian modeling and the chronology of the Portuguese Gravettian. *Quaternary International* 359–60: 499–509. https://doi.org/10.1016/j.quaint.2014.04.040
- BINFORD, L.R. 2001. Constructing frames of reference: an analytical method for archaeological theory building using hunter-gatherer and environmental data sets.

 Berkeley: University of California Press.
- BJÖRCK, S., M.J.C. WALKER, L.C. CWYNAR, S. JOHNSEN, K.-L. KNUDSEN, J.J. LOWE, B. WOHLFAHRT & INTIMATE Members. 1998. An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. *Journal of Quaternary Science* 13: 283–92. https://doi.org/10.1002/(SICI)1099-1417(199807/08)13:4<283::AID-JQS386>3.0.CO;2-A
- BOCQUET-APPEL, J.-P. & P.-Y. DEMARS. 2000. Population kinetics in the Upper Palaeolithic in Western Europe. *Journal of Archaeological Science* 27: 551–70. https://doi.org/10.1006/jasc.1999.0471
- BOCQUET-APPEL, J.-P., P.-Y. DEMARS, L. NOIRET & D. DOBROWSKY. 2005. Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data. *Journal of Archaeological Science* 32: 1656–68. https://doi.org/10.1016/j.jas.2005.05.006
- Bosselin, B. & F. Djindjian. 1994. La chronologie du Gravettien français. *Préhistoire Européenne* 6: 77–115.
- CLARK, P.U., A.S. DYKE, J.D. SHAKUN, A.E. CARLSON, J. CLARK, B. WOHLFARTH, J.X. MITROVICA, S.W. HOSTETLER & A.M. McCabe. 2009. The Last Glacial Maximum. *Science* 325: 710–14. https://doi.org/10.1126/science.1172873

- COLLARD, M., K. VAESEN, R. COSGROVE & W. ROEBROEKS. 2016. The empirical case against the 'demographic turn' in Palaeolithic archaeology. *Philosophical Transactions of the Royal Society B* 371: article no. 20150242. https://doi.org/10.1098/rstb.2015.0242
- DJINDJIAN, F., J. KOZŁOWSKI & M. OTTE. 1999. *Le Paléolithique supérieur en Europe*. Paris: Armand Colin
- FAGAN, W.F. & E.E. HOLMES. 2006. Quantifying the extinction vortex. *Ecology Letters* 9: 51–60.
- Fišáková, M.N. 2013. Seasonality of Gravettian sites in the Middle Danube Region and adjoining areas of Central Europe. *Quaternary International* 294: 120–34. https://doi.org/10.1016/j.quaint.2011.08.017
- French, J.C. & C. Collins. 2015. Upper Palaeolithic population histories of southwestern France: a comparison of the demographic signature of ¹⁴C date distributions and archaeological site counts. *Journal of Archaeological Science* 55: 122–34. https://doi.org/10.1016/j.jas.2015.01.001
- GILPIN, M.E. & M.E. SOULÉ. 1986. Minimum viable populations: processes of extinction, in M.E. Soulé (ed.) Conservation biology: the science of scarcity and diversity: 19–34. Sunderland: Sinauer Associates.
- HAESAERTS, P. & N. TEYSSANDIER. 2003. The Early Upper Palaeolithic occupations of Willendorf II (Lower Austria): a contribution to the chronostratigraphic and cultural context of the beginning of the Upper Palaeolithic in Central Europe, in J. Zilhão & F. d'Errico (ed.) The chronology of the Aurignacian and of the transitional technocomplexes: dating, stratigraphies, cultural implications. Proceedings of Symposium 6.1 of the XIV Congress of the UISPP (University of Liège, Belgium, September 2–8, 2001) (Trabalhos de Arqueologia 33): 133–51. Lisbon: Instituto Português de Arqueologia.

- Henrich, J. 2004. Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *American Antiquity* 69: 197–214. https://doi.org/10.2307/4128416
- Hey, J. 2005. On the number of new world founders: a population genetic portrait of the peopling of the Americas. *PLoS Biology* 3: 965–75. https://doi.org/10.1371/journal.pbio.0030193
- JACOBI, R.M., T.F.G. HIGHAM, P. HAESAERTS, I. JADIN & L.S. BASELL. 2010. Radiocarbon chronology for the Early Gravettian of northern Europe: new AMS determinations for Maisières-Canal, Belgium. Antiquity 84: 26–40. https://doi.org/10.1017/S0003598X00099749
- JAUBERT, J. 2008. L'«art» pariétal gravettien en France: éléments pour un bilan chronologique. *Paleo* 20: 439–74.
- JÖRIS, O. & B. WENINGER. 2004. Coping with the cold: on the climatic context of the Moravian Mid Upper Palaeolithic, in J. Svoboda & L. Sedláčková (ed.) The Gravettian along the Danube (Dolní Věstonice Studies 11): 57–70. Brno: Academy of Science of the Czech Republic.
- KLARIC, L. 2008. Anciennes et nouvelles hypothèses d'interprétation du gravettien moyen en France: la question de la place des industries à burins du Raysse au sein de la mosaïque gravettienne. *Paleo* 20: 23–42.
- KOZŁOWSKI, J.K. 2015. The origin of the Gravettian. Quaternary International 359–60: 3–18. https://doi.org/10.1016/j.quaint.2014.03.025
- Kretschmer, I., A. Maier & I. Schmidt. 2016. Probleme und mögliche Lösungen bei der Schätzung von Bevölkerungsdichten im Paläolithikum, in T. Kerig, K. Nowak & G. Roth (ed.) Alles was zählt ... Festschrift für Andreas Zimmermann (Universitätsforschungen zur prähistorischen Archäologie 285): 47–58. Bonn: Habelt
- MAIER, A. & A. ZIMMERMANN. 2016. CRC806-E1 Gravettian-sites database V-20160219. CRC806-database. https://doi.org/10.5880/SFB806.18
- MAIER, A., F. LEHMKUHL, P. LUDWIG, M. MELLES, I. SCHMIDT, Y. SHAO, CH. ZEEDEN & A. ZIMMERMANN. 2016. Demographic estimates of hunter-gatherers during the Last Glacial Maximum in Europe against the background of palaeoenvironmental data. *Quaternary International* 425: 49–61. https://doi.org/10.1016/j.quaint.2016.04.009
- MIX, A.C., E. BARD & R. SCHNEIDER. 2001. Environmental processes of the ice age: land, oceans, glaciers (EPILOG). *Quaternary Science Reviews* 20: 627–57. https://doi.org/10.1016/S0277-3791(00)00145-1

- Mussi, M., J. Cinq-Mars & P. Bolduc. 2000. Echoes from the mammoth steppe: the case of the Balzi Rossi, in W. Roebroeks, M. Mussi, J. Svoboda & K. Fennema (ed.) *Hunters of the golden age. The Mid Upper Palaeolithic of Eurasia 30,000–20,000 BP*: 105–24. Leiden: University of Leiden.
- Noiret, P. 2004. Le Paléolithique supérieur de la Moldavie. *L'Anthropologie* 108: 425–70. https://doi.org/10.1016/j.anthro.2004.10.003
- 2009. Le Paléolithique supérieur de Moldavie (ERAUL 121). Liège: Université de Liège.
- Nuzhnyi, D.Y. 2009. The industrial variability of the eastern Gravettian assemblages of Ukraine. *Quartär* 56: 159–74.
- OTTE, M. & P. Noiret. 2007. Le Gravettien du nord-ouest de l'Europe. *Paleo* 19: 243–55.
- Pettitt, P. & M. White. 2012. The British Palaeolithic: human societies at the edge of the Pleistocene world. London & New York: Routledge.
- Posth, C., G. Renaud, A. Mittnik, D.G. Drucker, H. Rougier, Ch. Cupillard, F. Valentin, C. Thevenet, A. Furtwängler, Ch. Wissing, M. Francken, M. Malina, M. Bolus, M. Lari, E. Gogli, G. Capecchi, I. Crevecoeur, C. Beauval, D. Flas, M. Germonpré, R. Cottiaux, B. Gély, A. Ronchitelle, K. Wehrberger, D. Grigorescu, J. Svoboda, P. Semal, D. Caramelli, H. Bocherens, K. Harvati, N. Conard, W. Haak, A. Powell & J. Krause. 2016. Pleistocene mitochondrial genomes suggest a single major dispersal of non-Africans and a Late Glacial population turnover in Europe. Current Biology 26: 1–7. https://doi.org/10.1016/j.cub.2016.01.037
- Premo, L.S. & S.L. Kuhn. 2010. Modeling effects of local extinctions on culture change and diversity in the Paleolithic. *PLoS ONE* 5: e15582. https://doi.org/10.1371/journal.pone.0015582
- Rasmussen, S.O., K.K. Andersen, A.M. Svensson, J.P. Steffensen, B.M. Vinther, H.B. Clausen, M.-L. Siggard-Andersen, S.J. Johnsen, L.B. Larsen, D. Dahl-Jensen, M. Bigler, R. Röthlisberger, H. Fischer, K. Goto-Azuma, M.E. Hansson & U. Ruth. 2006. A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research* 111: 1–16. https://doi.org/10.1029/2005JD006079
- RICHERSON, P.J., R. BOYD & R.L. BETTINGER. 2009. Cultural innovations and demographic change. *Human Biology* 81: 211–35. https://doi.org/10.3378/027.081.0306
- RIEDE, F. 2009. The loss and re-introduction of bow-and-arrow technology: a case study from the Northern European Late Paleolithic. *Lithic Technology* 34: 27–45. https://doi.org/10.1080/01977261.2009.11721072

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- RIGAUD, J.-P. 2008. Les industries lithiques du Gravettien du nord de l'Aquitaine dans leur cadre chronologique. *Paleo* 20: 149–66.
- ROEBROEKS, W., J. HUBLIN & K. McDonald. 2011.
 Continuities and discontinuities in Neandertal presence: a closer look at northwestern Europe, in N. Ashton, S.G. Lewis & C. Stringer (ed.) *The ancient human occupation of Britain*: 113–23.
 Amsterdam: Elsevier. https://doi.org/10.1016/B978-0-444-53597-9.00008-X
- SHENNAN, S. 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal* 11: 5–16. https://doi.org/10.1017/S0959774301000014
- SMITH, C.M. 2014. Estimation of a genetically viable population for multigenerational interstellar voyaging: review and data for project Hyperion. *Acta Astronautica* 97: 16–29. https://doi.org/10.1016/j.actaastro.2013.12.013
- SOFFER, O. 2000. Gravettian technologies in social contexts, in W. Roebroeks, M. Mussi, J. Svoboda & K. Fennema (ed.) *Hunters of the golden age: the Mid Upper Palaeolithic of Eurasia 30,000–20,000 BP*: 59–75. Leiden: University of Leiden.
- SOFFER, O. & J.M. ADOVASIO. 2004. Textiles and Upper Paleolithic lives: a focus on the perishable and the invisible, in J. Svoboda & L. Sedláčková (ed.) *The Gravettian along the Danube* (Dolní Věstonice Studies 11): 270–82. Brno: Academy of Science of the Czech Republic.

- STRAUS, L.G. 2000. The 1991–1993 excavations by the University of New Mexico and Liège, in L.G. Straus, M. Otte & P. Haesaerts (ed.) *La station de l'Hermitage à Huccorgne* (ERAUL 94): 69–95. Liège: Université de Liège.
- Surovell, T.A. & P.J. Brantingham. 2007. A note on the use of temporal frequency distributions in studies of prehistoric demography. *Journal of Archaeological Science* 34: 1868–77. https://doi.org/10.1016/j.jas.2007.01.003
- SVOBODA, J. 2007. The Gravettian on the Middle Danube. *Paleo* 19: 203–20.
- Traill, L.W., B.W. Brook, R.R. Frankham & C.J.A. Bradshaw. 2010. Pragmatic population visibility targets in a rapidly changing world. Biologist Conservation 143: 28–34. https://doi.org/10.1016/j.biocon.2009.09.001
- VAESEN, K. 2012. Cumulative cultural evolution and demography. PLoS ONE 7: e40989. https://doi.org/10.1371/journal.pone.0040989
- Valde-Nowak, P., A. Nadachowski & M. Wolsan. 1987. Upper Palaeolithic boomerang made of a mammoth tusk in south Poland. *Nature* 329: 436–38. https://doi.org/10.1038/329436a0
- Weninger, B., O. Jöris & U. Danzeglocke. 2012. CalPal-2007. Cologne radiocarbon calibration and palaeoclimate research package. Available at: http://www.calpal.de/ (accessed 9 November 2016).

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