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Reproduction in the Baka pygmies and drop in their fertility with the arrival of alcohol.

Short title: Fertility and effects of alcohol among the Baka pygmies

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Key words: Baka pygmies, hunter-gatherers, fertility pattern, mortality, cheap alcohol

Abstract

To understand the diversity of human growth and development from an evolutionary point of view, there is an urgent need to characterize the life history variables of vanishing forager societies. The small body size of the Baka pygmies is the outcome of a low growth rate during infancy. While sexual maturity, menarche and first delivery occur at similar ages to other populations, fertility aspects are unknown. In the Le Bosquet district in Cameroon, thanks to systematic birth records kept from 1980 onwards, we were able to assign ages to individuals with certainty. In this study, based on chronological records and on data collected from 2007 to 2017, we present life history variables related to fertility and mortality among the Baka pygmies: total fertility rate, age-specific fertility rate, completed family size, reproductive span, age at menopause, infant and juvenile mortality. The Baka present a low infant and juvenile mortality and their fertility pattern differs from that of other forager societies in the higher age-specific fertility rates found in the two lower age classes. Future studies will need to assess whether this particular pattern and the short interbirth interval are related to a high cooperative childrearing which in the Baka is associated with slow growth. The fertility rate has fallen drastically since 2011 and this matches the arrival of cheap alcohol in the community. Our data provides a first-hand record of the impact of alcohol on fertility in a hunter-gatherer society which appears to be seriously compromising the survival of the Baka.

Significance

Humans are a polymorphic species with a broad geographical distribution. Diversity in growth and development plays an important role in biological adaptation and can be addressed through studies of life history variation across different populations, particularly in hunter-gatherer societies. We present here, based on the study of individuals of known age, the results from our study on fertility and mortality in the Baka pygmies. The Baka are characterized by low mortality, slow growth and high fertility at an early age. However, the arrival of cheap alcohol has drastically reduced fertility early on in life, which seriously compromises this population's survival. We provide the first empirical evidence of the effects of alcohol consumption on the fertility rate of a hunter-gatherer society.

\body

Homo sapiens is the most polymorphic species of primate and is distinct from all others in the wide range of contrasting environmental conditions it inhabits. Although culture in the broad sense is largely responsible for the broad geographical distribution of our species, biological plasticity has certainly played a fundamental role in our adaptation (1). Biological adaptation to environmental conditions depends on the allocation of an organism's energy to growth, maintenance, reproduction (including raising offspring to independence), and avoiding death. The timing of key developmental events that determine the pace at which these factors play out within the lives of humans is called "life history" and is described by a suite of life history variables (LHVs) that include age at first reproduction, number of offspring, interbirth interval, age at menopause, infant mortality and survival to maturity (2).

LHVs are well known for several modern human groups (3) and their variability through time can be tracked over several decades. But a broad knowledge of the variability of life history in our species requires studies of LHVs in many human societies. Along this line of reasoning, as argued by Hill & Hurtado (4), the adaptive functional significance of human life history can be understood better by studying forager societies (5). Although variation in life history has been studied across several forager societies, these studies have shown that significant differences exist between societies living under dissimilar environmental conditions (4, 6, 7, 8). This has led to the suggestion that no single society can be taken as representative of all hunter-gatherers (4), and more importantly, that we need broad-ranging studies of LHVs in more societies to understand the variation we observe across hunter-gatherer societies.

Particular attention has been paid to populations with a small adult body size (6, 7). From an evolutionary developmental perspective, adult size is the final product of growth. Energy acquired throughout life must be allocated to growth, on the one hand, and reproduction on the other (9). A small adult body size therefore implies a specific growth pattern with low energy allocated to it, but enough to ensure an adult size capable of producing the necessary energy for reproduction. Migliano et al. (10) have suggested that small body size in the Aeta results from precocious reproduction due to a high mortality rate; in other words, small body size might be a by-product of growth ceasing at an early age to divert energy away from growth and towards reproductive activity. However, this observation cannot be extrapolated to all forager societies with a small body size. For instance, among the Baka pygmies in Cameroon (*SI Appendix*, Text S1), a low rate of growth from birth to 2.5 years of age accounts for the pygmy phenotype, and this process is not followed by any change in the

timing of sexual maturation (i.e. age at menarche, age at first reproduction) (11). But it is not known whether fertility parameters such as the total fertility rate, age-specific fertility rate or age at menopause are affected by the particular growth pattern that produces a small adult size. Knowledge of these parameters is fundamental to understand life history variations since a small adult body size produces less energy to be allocated to reproduction by lowering the fertility rate or by advancing the age at menopause. The aim of this study is thus to characterize fertility in the Baka.

The relationship between fertility and mortality is often used to build models for demographic transitions and is essential to understand population dynamics (12). Any change in fertility is associated with change in mortality. At population level, a reduction in the fertility rate is expected after a drop in the infant mortality rate; conversely, a rise in fertility can be observed after high mortality due to natural disasters (13). At the family level, the average birth interval following an infant death is substantially shorter than when an infant survives (14). Mortality in infants and mothers is complementary to data on fertility aspects.

During our 10-year study, we witnessed the arrival of cheap alcohol which became widely available to the community. We observed that changes in human fertility occurred at that point. The relationship between these two phenomena is discussed.

Overview: Moange le Bosquet

Most studies on life history variation as an aspect of the demographics of forager societies have been hampered by the lack of chronological data for individuals. This is a fundamental problem because our understanding of population dynamics and evolution revolves around processes that occur at known chronological stages. Except for Early & Headland's work (7) on the Agta, in which the ages of 271 out of 857 individuals (31.6%) were known - 117 individuals to within a year, 80 to within a month, and 74 exactly to the day (their Table 4.1: 65) - authors have had to develop various methods to estimate the missing chronological information (15). From data provided by many scholars, Weiss (16) built model life tables to infer, from a limited number of variables, many demographic/life history parameters, such as life expectancy or the age-specific fertility rate for each 5-year age cohort. Until recently, these tables were widely used to characterize all forager societies. The lack of chronological data available to benchmark his models means his data should be viewed as preliminary and used cautiously.

Because we were aware of the limitations imposed by the lack of chronological dates, we carried out field studies at Moange Le Bosquet, a Baka pygmy village in south-eastern Cameroon where birth records were kept for many years. Le Bosquet was founded in 1973 by Sister Marie-Albéric of the Congregation of Holy Spirit. Given the complex socioeconomic relationships that the Baka have with their Bantu-speaking farming neighbours (17), Sister Marie-Albéric invited those Baka living in camps attached to nearby Bantu villages to move to a new locality in order to found a village where, for the first time, the chief would be a Baka. One of the first buildings erected by the Catholic mission was a medical centre run by nuns with medical training, who provided health care for the community, kept birth records and carried out regular censuses in order to integrate the Baka into the organizational structure of the civilian community in Cameroon (e.g. helping to obtain identity cards and land titles). By the end of 1973, about 700 Baka were living at the village of Le Bosquet.

Le Bosquet comprises an aggregate of Baka camps. As people come in from different camps attached to nearby Bantu villages, they form different neighbourhoods, each keeping the name of the original village, possessing its own meeting hut and organized socially around a family chief. Le Bosquet extends over ~5 km from east to west along the road from Lomié to Messok. The neighbourhoods near the Catholic mission are very close to one another while others are separated by large tracts of forest and look like the camps attached to Bantu villages.

Although the Baka are ‘inhabitants’ of Le Bosquet, their way of life has remained semi-nomadic. Many individuals and family groups arrive or leave from one year to the next with no particular pattern: some families leave and return a few years later while other families leave after staying at Le Bosquet for a time and never return. During each field season, we met some Baka who would spend several months of the year away from the village, moving to camps in the middle of the forest where they feel ‘at home’. Hunting and gathering are the main activities in the forest camps. When at Le Bosquet, the main activity for women is gathering, on top of other chores including housekeeping, childcare, and fishing; the men’s activities include agricultural work for farmer neighbours, carrying logs cut by clandestine timber companies, hunting and sometimes gathering (18). Many Baka also cultivate their own banana and/or manioc crops. According to several censuses carried out by the nuns and to their own records kept over eleven years, the number of Baka individuals at Le Bosquet has remained more or less constant at around 800 individuals.

Birth records with both parents mentioned are available from 1980 to 1983 and from December 1987 until the present (*SI Appendix*, Table S1). Demographic records had previously been kept in the 1960s and 1970s by Father Dhellemmes (19), who lived and travelled in the region. Dhellemmes built up an enormous database from individual index cards identifying people by family and clan links, including a large number of Baka living in the wider area of south-eastern Cameroon. The nuns used these index cards to provide identity cards for the first inhabitants at Le Bosquet, a strategy that allowed us to determine exact ages for a subset of people ~50+ years of age.

Ages are not known for all of the people living at Le Bosquet. The nuns constantly encourage the Baka to declare births. Because of the fluid residential pattern mentioned above, many families live at Le Bosquet for only a short period, while others may have lived at a forest camp at the time of birth and forgotten to formally declare the baby later on as part of the census exercise. To further complicate census efforts, if a new-born dies during the first year of life and another baby follows within a short time (< 2 years), the new baby is considered as the same baby who has ‘left for a while and returned a little later’, so that the parents believe it is enough to declare the first birth. A consequence of this cultural belief is that the number of deliveries, both live and dead, is not the same as the total number of offspring for a couple during their entire reproductive period. Births may also not be declared because of the wishes of one or both parents: for instance, one father stopped declaring births after his fourth girl and opted in the future only to declare a new birth if it was a boy.

With around 800 Baka inhabitants, Le Bosquet is not a Baka settlement, as these are made up of only 45 people on average (20, 21, 22). We are aware that the social and economic situation at Le Bosquet is probably not the same as that described for the camps; however, it should be remembered that the main characteristic of Baka society is the heterogeneity of its camp environments and its patterns of economic and social organization (23). While the social and economic aspects of Baka society have been investigated many times (24, 25, 26), variations in key reproductive aspects of their life history have never been explored. Thanks to the birth records available at Le Bosquet, we were able to describe growth and life history variables based on an absolute chronology, for the first time for any hunter-gatherer society. Although our analysis centres on the subpopulation at Le Bosquet (only individuals with a known date of birth), we believe the results presented here are representative of the entire population at Le Bosquet, that they reflect a transition to a period increasingly affected by

external influences and that they provide a basis for studies of other pygmy groups that are genetically close to the Baka (e.g. the Aka from Central-Africa Republic).

Results

Timing of reproduction and family size

Conjugal relationships do not occur immediately after menarche: there is a gap while young adult Baka enjoy different kinds of friendly relationships. In the past, the choice of partner could have been directed by clan membership (same clan to be avoided) but almost all clans in and around Le Bosquet have abandoned this practice. Some constraints do exist in the case of widowhood, since widows and widowers have to choose a new partner among members of the family; the widow or widower can only make her/his own choice if the deceased partner's family refuses to provide a new partner. There are no cultural factors regulating delayed or precocious conception: the first birth therefore reflects fecundity. In the Baka at Le Bosquet, the earliest first births occurred at 16 years of age, and the average age at first birth was at 18 years. The age at latest birth varies widely (from 25 to 51 yrs) and averages 39.9 years. The average age at menopause is estimated at around 42.

The average completed family size for post-menopausal women (n=15, *SI Appendix*, Table S2) in this sample is 7.3 living offspring, varying from 4 to 10 children per woman. Nine out of 16 women declared they had lost one baby in its infancy (at or before one year of age) while three women had each lost two infants. Four women said they had experienced a miscarriage. The difference between average ages at first and last birth suggests a reproductive span of 22 years, although the average reproductive period for the 15 women is 20.2 years. An average family size of 7.3 people therefore generates an average interbirth interval (IBI) of 3 years or 2.77 years, respectively, the latter figure being very close to the modal value of 2.5 and 2.75 years obtained in a previous study on the Baka (11). Comparisons with other hunter-gatherer societies (4, 6, 7, 27-36) shows that results for the Baka are similar to those suggested for the Aché, the Agta and the Yanomamo, although the Baka have the shortest IBI (Table 1).

Total fertility rate (TFR) and Age-specific fertility rate (ASFR)

The total fertility rate (TFR) by year is shown in Table 2 and Figure 1. The average TFR is very close to the average completed family size of 7.3 individuals. Clearly, two periods can be distinguished, one from 2007 to 2010, when the TFR values are high (> 7), and another from 2011 to 2015 when the TFR decreases markedly ($p = 0.008$). The TFR values are not associated with any variation in the number of women or in the number of births ($p > 0.05$). The TFR for the Baka during the first period (2007-2010), which varies from 7.71 to 11.03 ($\bar{x} = 8.8$), is close to that for the Aché (for forest and reserve populations, $\bar{x} = 8.08$ and 8.53, respectively) and Yanomamo ($\bar{x} = 8.1$) but a little higher than for the Agta ($\bar{x} = 7.04$) (Table 3). During the second period (2011-2015), the TFR for the Baka is much lower ($\bar{x} = 5.53$), higher than for the Ju/'hoansi ($\bar{x} = 4.69$) but much lower than for all other hunter-gatherer populations reported here.

The Baka present the same pattern in the age specific fertility rate (ASFR) in all years (2007-2015), with the highest value occurring in the second age class (20-24 years). In general, the highest values occur in the first two age classes, declining throughout a woman's reproductive life (Table 4, Figure 2) (*SI Appendix*, Text S2). Longitudinal ASFR data reinforce the identification of two different periods, as suggested by the TFR data. During the first period (2007-2010), births were recorded for mothers of 45-49 years of age, but not during the second period (2011-2015). Furthermore, ASFR values in the two younger age classes are much higher in the first period than in the second ($p < 0.05$). The proportion of births per woman declines during the second period, but only in the two youngest age classes ($\bar{x} = 0.55$, and 0.45 for the first period; $\bar{x} = 0.21$ and 0.26 for the second period).

When compared with other hunter-gatherer societies reported here, the Baka have the highest ASFR values in the first two age classes; the values for the second period come closer to those reported for other populations (Table 3, Figure 3). For the third age class the low values for the Baka are close to those observed for the Ju/'hoansi. In other hunter-gatherer societies, the ASFR increases from the first years of reproductive activity and reaches the highest values in the third age class (25-29 years) in the Yanomamo and the Aché living in the reserve, and in the fourth age class (30-34 years) in the Aché living in the forest. Weiss (16) suggested that the highest values in the third or fourth age classes are “virtually universal among human females” (Ref. 16: p.31) and he followed this pattern to establish his models of anthropological fertility rates. However, the Ju/'hoansi, like the Baka, have the highest value in the second age class (20-24 years). The Baka thus have a very characteristic ASFR pattern

that clearly distinguishes them from other hunter-gatherer societies, with a high rate of reproduction from 15 to 29 years of age and a lower rate in the older age classes (Fig. 3).

ASFR enables estimations of the mean annual probability of birth in the last two reproductive age classes (40-49 year age class). In forager societies, this ranges from 0.044 (Ju/'hoansi) to 0.158 (Aché). In the Baka it falls between those two populations, with a probability of 0.081 during the first period (2007-2010) and 0.045 for the second period (2011-2015).

Infant and juvenile mortality

Table 5 shows the number of births, the number of infant deaths during the first year of life, the number of infants who survive the first year of life and the number of infants who moved out from Le Bosquet from 2007 to 2015 (although we don't know if they are alive or not). The infant mortality rate from 2007 to 2015 is extremely low as only six infants died before the first year of life out of 229 births (this number was obtained by subtracting the number of infants reported as 'out' from the total number of births). This corresponds to an infant mortality rate of 2.62 %. It is possible that infants who died within a few days after birth were not declared. In the reproductive history of the 44 women used to obtain parity-specific infant mortality (see below) we observed that four infants who died a few days after birth were not declared, which corresponds to 50% of cases. Even with this correction, the estimated infant mortality rate remains low at 5.24 %. This value is extremely low compared to infant mortality in other hunter-gatherer societies (Table 1). Marlowe (37) reported a mean infant mortality rate of 23.29 for twelve hunter-gatherer groups living in a warm climate. It is worth noting that no infant death is recorded from 2007 to 2010: the first evidence of infant mortality appears in 2011 (Table 5). There is no difference between the two periods in weight during the first two months of life (*SI Appendix*, Table S3).

Among the 44 mothers with a known full reproductive history used to obtain infant mortality per woman by parity (Table 6), 13 miscarriages were recorded. Two mothers had two successive miscarriages. The abortion indicated in Table 6 was produced deliberately because the woman became pregnant when her last child was still 'too small', which for the Baka means less than one and a half years old. Abortions recorded for other women or at other periods and thus not included in this analysis were performed for the same reason. Parity-specific infant mortality per woman obtained for the Pumé (36) shows that Pumé mothers can have 5 children by 25 years of age. None of the Baka mothers of 15 to 25 years of age had 5

infants: only one mother of 25 had 4 infants. This difference with the Pumé can be related to the age at first pregnancy, the average being 15.5 years for the Pumé (36) but 18 years for the Baka (11). Parity-specific infant mortality per woman was obtained in June 2010 and in June 2014. Two main differences can be observed: the number of miscarriages was higher in 2010 than in 2014 while infant mortality in first-time mothers reached 50% in 2014 but was 0% in 2010. In 2010, 9 out of 12 mothers with a first live infant were 19 years of age or less. In 2014, however, the three mothers with one live infant were 21-23 years of age whereas of the mothers with one dead-infant, two were 18 and one 21 years of age. Infant mortality in mothers with more than one infant was much lower than in mothers with only one infant, which probably suggests that high infant mortality is a new phenomenon.

Average IBI for mothers of 15-25 years of age in 2010 was 2.85 years ($n = 19$), but in three cases the IBI may have been affected by particular factors: two high IBI occurred when the mothers suffered miscarriages and the other high IBI happened when the woman was not married for a while. When these particular IBI are excluded, the average IBI for 2010 is 2.36 years. For mothers 15-25 years of age in 2014, the average IBI is 2.77 years ($N = 11$). Only one IBI was very long, most certainly due to two miscarriages. When this is excluded, the average IBI is 2.56 years. When these two IBI are compared, no significant difference is found ($p=0.384$).

Mortality was estimated for Baka children born from 1996 to 2001 and reaching 15 years of age in 2011 and later. The high mobility of the Baka prevented an accurate estimation. As shown in Table 7, 60 children (30 girls and 30 boys) out of 212 births (28%) were no longer living at Le Bosquet and it was not possible to find out whether they had lived to 15 years of age. If these children are considered dead, juvenile mortality in the Baka varies from 29% to 41% with a mean for the six years of 34% (66% probability of survival to maturity). If only alive and dead infants are considered (excluding those classified as 'out'), juvenile mortality drops to 8% (92% probability of survival to maturity). The values are the same for males and females (Table 7). Among the hunter-gatherer groups compared with the Baka, only the Ache present a high probability of survival (68% in female, 79% in male) (Table 1). Walker et al. (29) reported values of around 80% for the Tsimane and Turkana. However, the lower value of 66% for the Baka is certainly an underestimation of the probability of survival in this group because it assumes that all the young adults who left Le Bosquet are dead. A 92% probability of survival to maturity in the Baka is much higher than in any other hunter-gatherer group and has to be considered with caution. Table 5 also provides some information on juvenile

mortality. It is surprising that the number of children died among those who were born in 2011-2015 is as high as in 2007-2010.

Only four cases of death of young Baka mothers were recorded. If a mother dies during the first year of life of the infant, it is abandoned by the family in practice, and dies (*SI Appendix*, Figure S1).

Discussion

The first pregnancy marks an abrupt change in the life of any mammal, since the energy used for growth until this point is allocated from then on to reproduction (9). Given the intersection of ecology and demography in any population, natural selection can presumably act on the timing of this important life history event, resulting in either an earlier or a later age at first reproduction. Any organism will favour growth in order to reach its maximum size, which is closely linked to energy production: a larger size will produce more energy for reproduction and survival. However, each time unit of delay before the onset of reproduction decreases the organism's chances of surviving to reproductive age (38). The average age at first birth thus appears to be the best compromise that a population can achieve between allocating surplus energy to growth or to reproduction.

The hunter-gatherer populations compared in this study have a small average adult size and an average age at first reproduction of 18 to 19 years, which is similar to that of European populations. Thus, the small body size with the limited amount of surplus energy it provides for reproduction does not appear to be related to the age at first delivery in these populations. Results for the Pumé point to the same conclusion. The Pumé are relatively tall compared to other hunter-gatherer populations referred to here (Table 1) and the first birth occurs at a much younger age (15.5 years) (35). This seems to be coupled with rapid juvenile growth, which produces greater gains in stature than in adolescence to achieve a body size close to that of neighbouring populations. As adult stature may not be associated with age at first birth (36), short stature is not necessarily linked with early maturation. Variations in adult size (height and weight) probably play some role in the age at maturation among individuals from the same population (4), but extrapolating this relationship to entire populations seems hazardous.

However Kramer (39), like Migliano et al (10) for the Aeta, sees faster growth as an adaptive response in high mortality environments where early reproduction is advantageous. This links

up with the suggestion made by Walker et al (29) that a high survival rate is associated with slower and later development. The Baka show a very low infant mortality rate and a high, even extremely high, probability of survival to maturity (Table 1). The environmental conditions of the Baka thus do not appear to be challenging in terms of mortality and offer appropriate conditions for a slow growth pattern. This agrees with the pattern of growth described for the Baka, who reach maturity at a similar age (menarche, first reproduction) to non-forager populations (11). The short stature of the Baka is not a consequence of early cessation of growth as has been suggested for the Aeta, but of a slower rate of growth during infancy (11), which has a genetic foundation (40, 41, 42). Therefore, high mortality rates (infant, juvenile or adult) may be influencing the timing of development (39, 43) but do not seem to be linked with adult body size.

Walker et al (29) propose that Pygmies (as well as Negritos and Hiwi) have a faster growth rate and that this is related to high juvenile mortality. Our results suggest, on the contrary, a low infant mortality and a high proportion of survival to maturity which agree with slow growth in the Baka (11). This difference in results certainly comes from the methodology and data samples as these authors recognise (29). Based on cross-sectional data, Walker et al assume a linear growth rate from 3 to 10 years of age, suggesting that this is one of the best measures for comparisons across societies, although the assumption of linear growth in humans is much criticised (44, 45). Furthermore, sample size is limited to a few individuals with considerable uncertainty as to their estimated age, and the 0.78 probability value for survival to maturity for the Eastern Pygmies is disregarded (33). High quality data (longitudinal data based on many individuals whose ages are known from birth to adulthood) is needed for an appropriate assessment of life history variation in human populations.

Low infant and juvenile mortality rates in the Baka contrast with fertility aspects, as shown by the ASFR and the short IBI. The pattern of shifting ASFR shown by the Baka, with high values in the lower age classes and lower values in the higher age classes, suggests that the main reproductive period for Baka women is between 15 and 29 years of age. The age of menopause at around 42 years is close to the ages reported by Goodman et al. (46) (43.9 years; 175) and by Early and Headland (7) for the Agta (early 40s; 95) (Table 1). Therefore, the age of reproductive senescence in the Baka is not a constraint that induces a high rate of reproduction in the lower age classes. Furthermore, the Baka have an average interbirth interval of ~ 33 months (2.77 years), which is shorter than the IBI for the Aché, Batek, Inuit, Ju/'hoansi and Pumé from savannah areas (4, 6, 11, 34, 47, 48) but not the Batak (49), Agta

(7) and the Pumé from the river (34). It is well known that cooperative childrearing benefits mothers by redistributing the energy cost of raising offspring, which allows shorter birth intervals, higher maternal fertility or increased infant survival (50). In the geographically and genetically closely-related Aka pygmies, Meehan (51, 52) has quantified the parental and alloparental assistance a mother receives during the period of bride service (~1 year). Fathers and grandmothers provide the second and third highest frequency of direct care to infants, but unlike the father's presence, which increases the mother's energy expenditure by increasing her work, a grandmother's presence is a substitute for maternal care and allows the mother to invest energy in other activities, including those that increase maternal reproductive success. Another Pygmy group, the Efe from the Ituri forest, have a child-rearing system in which infants receive a remarkably high level of parental and alloparental assistance (53). Child-care is mainly provided by non-reproductive women and characterized primarily by intermittent play and physical contact, whereas mothers invest in more demanding forms of care and economic tasks. Interestingly, mothers are also relieved of competing child-care demands and can engage in subsistence activities from which children and others benefit (53): the help received by mothers seems to translate into infant survival and not into fertility. It is possible that the Baka share a high level of parental and alloparental assistance in childrearing with the Aka and the Efe. The high rate of reproduction in the lower age classes, the short interbirth interval and the low infant mortality rate might be favoured by the help that other adult individuals are able to provide to young mothers with caring for new-borns and infants or sharing resources. But unlike the Aka and the Efe, Baka mothers can probably engage more time and energy in increasing reproductive success which would explain that the Baka have the lowest IBI (Table 1). If parental and alloparental investment in the Baka is confirmed by empirical data, it is worth noting that a such child rearing system would not be exclusively associated with fast growth, as has been suggested for the Pumé (35) and speculated for the Aka and Efe (29).

It is worth noting that if the mother dies when the infant is younger than 1 or 1.5 years of age, nobody replaces the mother in child caring, not even members of the family, including the child's father. Even if a close member of the family is breastfeeding, she does not invest in the survival of the orphaned baby. As a result, this infant died a few months after its mother (*SI Appendix*, Figure S1).

From 2007 to 2010 (Period 1), the ASFR in the lower age classes were higher than those observed in any other hunter-gatherer societies, but they dropped from 2011 to 2015 (Period

2), resulting in a 37% reduction in the TFR. This drop in fertility in the lower age classes during Period 2 is also observed from the results concerning infant mortality per woman by parity (Table 6), because the mothers with one infant in Period 1 were 19 years of age or less, whereas in Period 2 five mothers out of six were at least 21 years of age. Several studies on forager societies made at intervals over a long period have enabled us to observe various changes in life history variables that can be related to new living conditions (4, 7). Hill & Hurtado (4) reported a lower age at menarche and at first reproduction for the Aché when they settled in a reserve, developing a horticulturalist economy and reducing hunting treks in the forest. They also showed that ASFR increased in the lower age classes but decreased later, producing a minimal increase in the TFR in the reserve. Many factors can lead to a change in the fertility rate of a population. Physiological causes can alter fertility as a result of reproductive failure or reduced fecundity. Various social or environmental constraints, such as migration, war, work stress, epidemics and starvation, can reduce access to mating or increase the energy cost of childbearing.

A change in the frequency of miscarriages or in the interbirth interval may lead to a change in the fertility rate. However, even if they are associated with fertility, they do not explain the underlying cause of change in fertility. The number of miscarriages was higher in Period 1 (2007-2010) than in Period 2 (2011-2015) (Table 6). Tables 6 and 7 show that infant mortality was higher in Period 2. Higher infant mortality is associated with a shorter IBI (14). However, in the Baka, neither the IBI nor infant weight in first two months of life differed between the two periods. The number of miscarriages, IBI and weight in early infancy are not associated with the drop in fertility during Period 2. It would be expected that the drop in fertility during Period 2 would be associated with a drop in mortality (12, 14), but infant and juvenile mortality seems, on the contrary, to increase during this period compared to the previous one.

From the foundation of Le Bosquet in 1977 until our first field study in 2007, and during the eleven years of our regular visits to Le Bosquet, there is no record of epidemics, mass mortality or starvation (a word that does not exist in the Baka language). There was no demographic change: the population of Baka at Le Bosquet has remained at around 800 individuals since the 1970s. The Baka have no access to clinics, and vaccination programmes are random. Basic health care and education are provided by the health centre and the school established by the nuns in the 1970s. A drop in fertility is sometimes associated with parental investment in child skills, and investment in education is a particularly favored option in transitional conditions. Records of school attendance in Le Bosquet are scattered over the

years but they show 131 enrolments in 1989-1990, 125 in 2010-2011 and 129 in 2015-2016. Analysis of school attendance has not revealed any change in parental investment from Period 1 to Period 2 (*SI Appendix*, Text S3).

One change in the lives of the Baka relates to logging, both legal and illegal. Both activities obey the same dynamic, advancing along forest tracks to fell only well identified trees and moving on when all of these have been cut. Legal and illegal logging companies employ local villagers, preferably the Baka since they know the forest very well and can penetrate deep into the interior. The villagers do not move on with the employers: they are not welcome in neighbouring villages because they would deprive local people of work. Legal timber felling ended in the Le Bosquet area at the end of 2006 and moved away in 2007, and illegal logging was present at Le Bosquet during 2010 and 2011 with chainsaws that could be dismantled for easy transport. In 2012, illegal logging moved away to the east. The impact of legal and illegal logging has therefore been irregular and limited in time.

One major event occurred in the last month of 2010, when cheap alcohol arrived in the community. Local wine and beer were already consumed by the Baka: a bottle of palm wine cost 500 CFA (€0.75; \$0.87) and beer around 800 CFA (€1.20; \$1.40). Salaried employment is very uncommon among the Baka but when available, the daily wage for working in a plantation is 300 CFA (€0.45; \$0.52). The high cost of these alcoholic beverages thus prevented widespread consumption on a daily basis. In 2010, a bar was set up within the confines of Le Bosquet with cheap alcohol sold in plastic bags as the main commodity, costing 50 or 100 CFA (€0.07 - 0.15; \$0.08 – 0.17) per bag, a lower price than for any other consumer product and corresponding to the lowest value coins in the country. Although very little money circulates among the Baka, occasional work in plantations, for illegal loggers and for nuns or researchers, produces some monetary income for the Baka community, which they mainly use to buy alcohol (54). From the end of 2010, consumption of these newly introduced alcoholic drinks, called '*nofia*' locally and '*whisky*' in general, became wide spread among individuals of all ages: even infants were picking up the bags from the floor, opening them and sucking on them. Although this is anecdotal evidence as we have no data on the frequency of such behaviour, we observed it several times (54, minute 25:22). During each field season, the first comments from our Baka collaborators were always about people who had died in Le Bosquet since our last visit. Never previously mentioned as such, alcohol poisoning has become one of the main causes of death since 2011. The chemical composition of *nofia* has never been studied in detail but it is a mixture of ethanol and methanol whose

main purpose is to make people drunk as quickly as possible. Government authorities have recognized that these drinks are causing major disorders of the nervous system, cancers and death, even when consumed in small quantities. Their production has been banned but traders are still allowed to sell them until current stocks are exhausted (55).

The impacts of alcohol in encounters between different cultures have been widely analyzed (e.g., 56). The effects of drinking alcohol are determined largely by the rate at which it and its main by-products are metabolized after consumption. It is well established that the main metabolic pathway for ethanol involves a variety of enzymes, and that their presence and proportions vary among populations (57). It is also well established that the consumption of alcohol has a direct impact on reproduction by increasing the risk of infertility in women or altering semen quantity or quality (58, 59, 60), even in people with a low level of alcohol intake (e.g., 61). At Le Bosquet, the consumption of cheap alcohol that began in the last month of 2010 has continued until now. It is not a one-off phenomenon whose effects would dissipate over time: its arrival changed the behaviour of people at Le Bosquet because buying alcohol has become one of the main motivations for taking on any kind of work to earn cash. Alcohol has also shifted the centre of activities in Le Bosquet. For years, the Catholic Mission was the main place where people converged to discuss matters concerning the village. Since 2010, the main place has become the bar, where people meet at any time and talk while drinking. It is difficult not to infer a direct link between the arrival and mass consumption of cheap alcohol and the drop in TFR in the Baka.

During a meeting with Baka women, we asked them if they had noticed any change in fertility over time and if so, whether they had any idea about its cause. They said that there probably was a change in fertility due to living close to the road. This implied a need to give more care to children, mainly by giving more attention to clean clothes: having more children implies having more resources, which they do not have, in order to pay for clean clothes for themselves and the children. Asked about how they could control the number of children, they said they could reduce the number of times they have intercourse. We then asked about the alcohol. After a great many exclamations, they said that the arrival of alcohol had affected everybody, even the children who would rush to buy some when they obtained a coin. About the possible link between fertility reduction and alcohol, they said that alcohol was now very cheap and consumption was massive. They said that men coming back from the field spend a few coins on alcohol before going home and arriving there drunk, and that the women refused to have sexual relations when the men are in this condition. This situation persists during the

entire period of wage labour, which can last from a few days to several weeks. The women then added that this situation was mainly affecting young mothers who, even if intercourse is easier now than before, took longer to become pregnant. They thought that young mothers were probably more affected than older ones because they had been drinking alcohol since they were young.

It is very interesting to note that these Baka women have realised that fertility in younger women has become more problematic. The lower age classes are the most important in the reproductive cycle of the Baka and make the largest contribution to total fertility rates. Reproduction in the lower age classes is the most distinctive aspect in the Baka and probably reflects a particular adaptation that we cannot elucidate at the moment. Surprisingly, these are the age classes most affected by the drop in fertility. There is no record of any major and enduring change in Le Bosquet, except for the arrival of cheap alcohol at the end of 2010, which coincides with the drop in fertility in the Baka. Alcohol consumption could thus be the main reason for the drop in fertility in the younger age classes. Our results provide clear, first-hand evidence of the damaging effects on fertility produced by alcohol in a hunter-gatherer society. Downward trends in TFR such as those seen in the Baka will have the long-term impact of reducing the number of Baka individuals.

Materials & Methods

The data presented in this article were obtained over 11 years from 2007 to 2017. At least one field study was conducted each year in May-June, and from 2011 to 2015, a second field study in October was added. Only individuals whose age was known or could be estimated accurately were included in the study. Thanks to Dhellemmes' records, the age of some women more than 25 years old is known to within a year. By combining census and birth records with our questionnaires, we were able to establish the first birth and the total number of infants for each woman very accurately. The modal interbirth interval in the Baka is 2.5 years (11) and we worked on this assumption for children for whom we had no birth record. Similarly, since 18 years is the average age for the first delivery (11), this was the age assumed for the mothers at first birth. For instance, if we knew that the first record of the birth of a sibling was for the third infant, we assumed that the first infant was born 5 years earlier (two interbirth intervals of 2.5 years each) and that the mother was 18 years old. We are aware that this procedure introduces some bias but when it was applied to mothers and infants whose

real chronology was known, the differences were never greater than 2 years. The bias therefore has a minimal impact, if any, on the distribution into 5-year age classes. Many analyses were performed in this study and the sample size varies from one to another (*SI Appendix*, Table S2).

Timing of reproduction and family size

In order to obtain these variables, only 16 women whose birth records were available were included in the analysis. These were women born between 1952 and 1970. The majority had already begun their reproductive life when systematic record-keeping started at Le Bosquet in 1988, except for two whose first baby was born during the earlier period when records had been kept. The birth dates were recorded and full personal histories detailing the number of live births, still-births and miscarriages were established by questionnaires. Among the women whose reproductive history is fully recorded (N=16), one woman had only one child, which is very rare among the Baka: she was not included in the calculation of the average completed family size. The reproductive period was obtained by subtracting the age at the first birth from the age at the last birth. For these women, the last birth had occurred several years previously, which implied that their reproductive life was over. An estimated age at menopause is suggested, which we obtained by averaging the ages at last birth of the 15 women. The full family history is also known for many other women but it was not certain that their reproductive life was already over.

Total fertility rate and age specific fertility rate

The total fertility rate (TFR) and age-specific fertility rate (ASFR) were obtained every year from 2007 to 2015. For each year, the number of births was taken from the records in the medical centre and we used questionnaires to establish the number of women present at Le Bosquet (Table 2).

It is important to emphasise that the ASFR does not mean the same thing to all authors (*SI Appendix*, Text S4). In our study, as in Hill & Hurtado (4) and Howell (6), the ASFR is the number of women in a five-year age group who gave birth during a given year, divided by the total number of women in that age group; the TFR corresponds to the sum of all ASFR multiplied by 5.

Since two periods can be distinguished, one from 2007 to 2010, and the other from 2011 to 2015, the ASFR and the TFR were compared with the Mann-Whitney U test (SPSS) in order to establish the significance of any changes. The same test was used to observe whether the TFR values are related to changes in the number of women or in the number of births.

The ASFR and TFR for the Baka were compared with those for other hunter-gatherer populations with a low average adult stature, the Agta, Yanomamo, Ju/'hoansi and Aché. The ASFR values for the Yanomamo are those reported by Melancon (28) and used by Hill & Hurtado (4); for TFR we used Neel and Weiss' (27) results which we multiplied by 2.05. Hill & Hurtado (:255) provided the basis for choosing Melancon's study for the ASFR by pointing out problems in previous studies. They do not reject a variation in ASFR among Yanomamo populations (see variation in the Baka), but none has been accurately observed to date.

Infant and juvenile mortality

The infant mortality rate (percentage of children who die within the first year of life) and the juvenile (or child) mortality rate (percentage of children who die within the first 15 years of life) were obtained for the Baka. Their seminomadic lifestyle makes it difficult to measure mortality: families move at any time of the year and whether an infant or child has died or not can only be established when the family is found again at a later date. In order to estimate the infant mortality rate, we recorded, for each year from 2007 to 2015, the number of births, the number of infant deaths during the first year of life, the number of infants who survived beyond the first year of life (we know this because we met them) and the number of infants who moved away from Le Bosquet and who we never met again.

Deliveries take place in private at home so it was not possible to obtain birth weights, but many mothers go to the health centre a few days later to declare the birth and have the baby weighed. Infant weight is monitored by the nuns for several months. We used these measurements to compare weight during the two first months of life for infants born between 2008 and 2010 and between 2012 and 2014 in order to observe any differences in birth weight between Period 1 (2007-2010) and Period 2 (2011-2015). The Mann-Whitney U test (SPSS) was used to compare the significance of results.

To estimate infant mortality per woman by parity (34), we used the individual reproductive histories of 44 mothers between 15 and 25 years of age whose age at birth was recorded or well established because their deliveries were recorded. Some children were not declared at

birth but we were able to place them thanks to siblings whose age was known. Since fertility seems to change from 2011, suggesting the probability of two distinct periods, infant mortality per woman by parity was obtained in May 2010 for mothers born between June 1985 and May 1995 (n=32), and in May 2014 for mothers born between June 1989 and May 1999 (n=24). Mothers 15-21 years of age in 2010 are those who were 19-25 years of age in 2014. Miscarriages and abortions were also recorded. Interbirth intervals were obtained for both periods when exact chronological data were available for successive deliveries.

We estimated juvenile mortality for children who were born from 1996 to 2001 and had reached 15 years of age. Again, mobility prevented from obtaining exact values because several families had moved away and we did not know if their children were alive or not. When we never met the children and could not find out whether they were alive or not they are referred to as 'out'.

Deaths of young mothers can affect infant survival. We report here what happens with infants when the mother dies, but the number of such cases is very small among the Baka at Le Bosquet.

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Figure Legends

Figure 1: Total fertility rate in the Baka from 2007 to 2015. High values during the first years of the study are followed by a drop in the TFR. The year 2011 marks a significant change in the TFR in the Baka.

Figure 2: Age-specific fertility rate over nine years among the Baka. From 2007 to 2010 (Period 1), the lower age classes have much higher values than the next classes; these values dropped from 2011 to 2015 (Period 2) suggesting a major change in the reproduction capacities of young adults.

Figure 3: Pattern of the ASFR in the Baka compared to other hunter-gatherer societies. In contrast to ASFR variations in other forager societies, for which the curve is bell-shaped, the highest values for the Baka are found in the lower age classes, which produces a particular pattern of reproduction. Fr: forest, Rs: reserve.

Table 1: Reproductive aspects in hunter-gatherer societies

	H F	H M	CFS	Ibi	First Birth	Last Birth	RS	IM	PS F	PS M
Ache Forest ^(4, 30)	149*	158*	8.15	3.1	19.5	42.1	22.6	11	68* (61)	79* (70)
Hiwi ^(30, 31)	145	154	5.13	3.76	20.5	37.8			45	51
Ju/'hoansi ⁽⁶⁾	150	161	4.7	4.12	18.8	34.4	15.6	20,2	60	56
Yanomano ⁽²⁷⁻²⁹⁾	142	152	7.8	3.3	18.4	37.9	19.5	19	70 (48n)	70 (48n)
Agta ⁽⁷⁾	143	153	7.6	2.82-2.85	19.5	early '40s	24	29	42	42
Aka ^(29, 51)	145	153		3.5					55	55
Efe ^(29, 32, 33)	136	144	2.7	3.1					78	
Pumé savanna ⁽³⁴⁻³⁶⁾	151.5	163,2'		3.1	15.5					
Pumé river ⁽³⁴⁾				2.87						
Hadza ^(29, 30)	150	160			19				54 (58)	54 (58)
Baka	147	154	7.3	2.77	18	39.9	22	5,2	66-92	66-92

* from Reserve (3)

H: height, F: female, M: male, CFS: completed family size, IBI: average interbirth interval, IM: infant mortality, RS: reproductive span, PS: proportion of survival to maturity. All in years.

RS corresponds to the difference between ages of last and first births. For the Baka, this was also obtained from the full reproductive history of 15 women as 20.2 years.

Table 2: Total fertility rate in the Baka

year	Total Fertility Rate		N° women	N° births
	TFR	log		
2007	8.21	0.9143	95	17
2008	11.03	1.0426	113	37
2009	8.23	0.9156	163	40
2010	7.71	0.8873	167	37
2011	5.26	0.7213	157	26
2012	5.82	0.7648	180	33
2013	4.62	0.6651	155	21
2014	6.25	0.7959	189	35
2015	5.83	0.7658	177	30
average	7	0.8303		

Table 3: Comparison of TFR and ASFR between the Baka and other hunter-gatherer societies

Age	Baka		Aché ⁽⁴⁾		Ju/'hoansi	Agta	Yanomamo
	Period 1	Period 2	Forest	Reserve	(6)	(7)	(28)
15 - 19	0.550	0.212	0.151	0.253	0.135	0.126	0.295
20 - 24	0.448	0.259	0.275	0.333	0.242	0.299	0.267
25 - 29	0.233	0.220	0.298	0.341	0.203	0.344	0.361
30 - 34	0.200	0.210	0.318	0.333	0.152	0.282	0.364
35 - 39	0.168	0.109	0.279	0.265	0.119	0.213	0.205
40 - 44	0.088	0.090	0.219	0.157	0.071	0.144	0.063
45 - 49	0.073	0,000	0.069	0.019	0.016	0	0.063
> 50	0,000	0.012	0,000	0,000	0	0	
TFR	8.797	5.558	8.081	8.529	4.69	7.04	8.098

Table 4: Age-Specific Fertility Rate by year

Age	2007	2008	2009	2010	2011	2012	2013	2014	2015	X 1°P	X 2°P
15 - 19	1.00 4/4	0.53 8/15	0.39 7/18	0.28 8/29	0.12 3/26	0.24 9/37	0.19 5/26	0.21 6/28	0.30 8/27	0.55	0.21
20 - 24	0.26 6/23	0.65 11/17	0.47 15/32	0.42 10/24	0.30 7/23	0.26 7/27	0.22 4/18	0.27 8/30	0.24 7/29	0.45	0.26
25 - 29	0.23 5/22	0.32 7/22	0.17 6/35	0.22 8/37	0.22 8/36	0.25 8/32	0.18 5/28	0.29 9/31	0.16 5/31	0.23	0.22
30 - 34	0.08 1/13	0.25 5/20	0.30 6/20	0.17 4/23	0.29 6/21	0.22 6/27	0.12 3/26	0.23 7/30	0.19 5/26	0.20	0.21
35 - 39	0.00 0/11	0.27 4/15	0.18 4/22	0.22 4/18	0.06 1/16	0.07 1/14	0.11 2/19	0.20 4/20	0.11 2/19	0.17	0.11
40 - 44	0.00 0/8	0.10 1/10	0.08 1/12	0.17 2/12	0.06 1/16	0.12 2/17	0.11 2/18	0.05 1/22	0.11 2/18	0.09	0.09
45 - 49	0.08 1/13	0.09 1/11	0.05 1/19	0.07 1/14	0.00 0/8	0.00 0/12	0.00 0/10	0.00 0/8	0.00 0/10	0.07	0.00
> 50	0.00 0/1	0.00 0/3	0.00 0/5	0.00 0/10	0.00 0/11	0.00 0/14	0.00 0/10	0.00 0/20	0.06 1/17	0.00	0.01

i/j: i: number of birth, j: number of women

X 1°P: average for the first period; X 2°P: average for the second period.

Table 5: Mortality in Le Bosquet

	2007	2008	2009	2010	2011	2012	2013	2014	2015
Birth	17	38	38	37	25	33	22	35	30
InM					1	2		3	
JuM		1		2			3	2	1
out	3	10	6	6	4	3	5	3	6

InM: number of infant death, JuM: number of children death. out: number of individuals never met again and we don't know if they are alive or not.

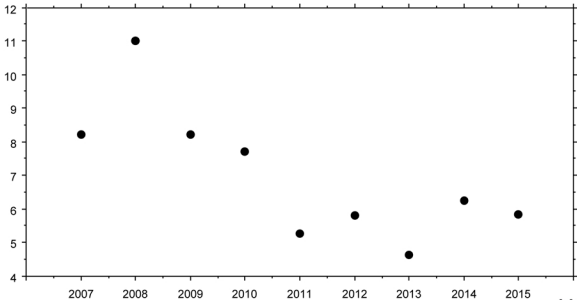
Table 6: Infant mortality per woman by parity

Infants deaths	Parity			
	1	2	3	4
	2010 (n = 32)			
0	12 (100%)	8 (80%)	7 (78%)	1
1		2 (20%)	2 (22%)	
2+				
Miscarriage	3	3	4	
Abortion				
	2014 (n = 24)			
0	3 (50%)	12 (92%)	4 (80%)	
1	3 (50%)	1 (8%)	1 (20%)	
2+				
Miscarriage		3		
Abortion		1		

Table 7: Juvenile mortality in the Baka

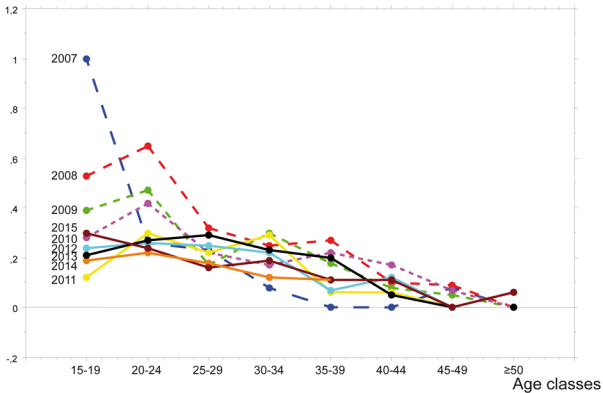
	Year	N° birth recorded	N° reaching 15 yrs age	Dead	Out	% reaching 15 yrs age minimum maximum	
Males	1996	15	9	2	4	60	82
	1997	8	7		1	88	100
	1998	17	9		8	53	100
	1999	19	14		5	74	100
	2000	19	10	2	7	53	83
	2001	28	21	2	5	75	91
			106	70	6	30	66
Females	1996	26	17	1	8	65	94
	1997	17	10	1	6	59	91
	1998	10	7		3	70	100
	1999	20	12	3	5	60	80
	2000	20	16	1	3	80	94
	2001	13	8		5	62	100
			106	70	6	30	66
Total		212	140	12	60	66	92

TFR



Year

ASFR



SI Appendix

Supporting Information for

Text

SI. What does the term Pygmy mean?

The term ‘pygmy’ was first used by Purchas (1) and later by du Chaillu (2) to refer to populations with a small adult height living in African Equatorial rain forests (3). These authors used the word ‘pygmy’ with reference to the term used by Herodotus and Aristotle in ancient times for populations with this phenotype living close to the source of the Nile. From the 20th century until now, the term ‘pygmy’ was extrapolated to any population with a small adult body size. Cavalli-Sforza (4) suggested that the term should describe populations whose average adult stature is less than 155 cm. This distinction is completely arbitrary and does not have any biological foundation.

The term ‘pygmy’ was, and is, largely used to refer to populations living in African Equatorial rain forests whose economy is based on hunting and gathering. These groups have a complex socioeconomic relationship with their farming neighbours. Moreover, pygmy peoples are systematically identified by their culture and behavior as pygmies by farming neighbours, who in turn identify themselves as non-pygmies and are recognized as non-pygmies by pygmies, as well as by other non-pygmies (5, 6). African pygmies can be grouped into two clusters. One is in East Africa (Ruanda, Uganda and Eastern DRC) and comprises the Aka, Sua and Efe groups (also frequently called ‘Mbuti’) and the Batwa. The other cluster, in West Africa (Cameroon, Central Africa Republic, Congo, Gabon and Western DRC), includes the Kola, Bongo, Koya, Aka, Baka and Twa. Studies on population genetics (7) have shown that African pygmies share a common ancestor and split from Bantu-speaking populations at around 60,000 years BP. Patin et al. (7) suggested that the eastern and western clusters split later, at around 20,000 years BP.

Therefore, the term ‘pygmy’ should be restricted to African populations as in its original usage to cover several populations who share not only a phenotype and an economy based on hunting and gathering but also a common ancestor and an evolutionary history not shared by any other African group.

S2. Year 2007

2007 is the year showing the all-time lowest number of births among the Baka at Le Bosquet – but it is interesting to note (*SI Appendix*, Table S1) that the all-time highest number of births (n=55) in the history of Le Bosquet was recorded two years previously (2005). The low number of births in 2007 probably results from the fact that many mothers had infants less than two years of age. The number of mothers at Le Bosquet was also low in 2007 (Table 2), which seems to be the year when it had the smallest number of inhabitants. This isolated instance of migration concerns only that year and although the reason for it is unknown, it was probably due to the lack of particular resource at that time in Le Bosquet. It is possible that only first-time mothers who had just given birth or were close to doing so remained in Le Bosquet when other young women moved out, which would explain the high value of the ASFR observed for the 15-19 age class in that year.

S3. Living condition in Le Bosquet

The Baka living in Le Bosquet have kept to a semi-nomadic life, leaving the village for forest camps during specific periods of the year to gather various products (fish, mangoes) and sometimes for hunting or gathering expeditions at any time of the year. The Baka diet at Le Bosquet did not change during the entire period of study. It is based on manioc, plantain and bananas from crop plantations, vegetables (leaves, nuts, roots, fruits) and mushrooms and bushmeat from the forest. Fish is more common during the dry season (February), moabi oil and mango are available for a few months from the short dry season (June) and different kinds of honey are mainly available from the rainy season (October). Hunter-gatherer activities are complemented by work in their own or Bantu fields. When they earn wages as farm labourers (Bantu neighbour's field, clandestine mill, researchers), the Baka buy groundnuts and macabo. There is no record of any major change in these activities since the foundation of Le Bosquet, except for the arrival of cheap alcohol at the end of 2010 (see Discussion).

The work done by the Baka from Le Bosquet differs according to sex as in any other Baka community. No increase in Baka women's working activity at Le Bosquet was observed. Only the men are involved in extra activities other than those specific to the Baka, such as farm labour and working for logging companies. Farm labour is confined to fields close to the

locality and does not require the men to be absent for days at a time. It is usual for the Baka to go to work and back every day. This situation has not changed over the years.

Cameroon has undertaken major economic projects in the last ten years (e.g. deep water port in Kribi, iron mine in Mbalam) and has been involved directly or indirectly in armed conflicts (in Nigeria [Boko Haram] and the Central African Republic). However, neither project nor armed conflicts have brought changes to the Le Bosquet area. In 2009, a project for a cobalt mine which has been launched some years before seemed set to bring major changes to the area. Large areas of forest were cleared close to the Congo locality (~30 km from Le Bosquet). The mining company, Geovic, launched various kinds of projects to mitigate mining impacts in the region. When the 2008 crisis caused a fall in cobalt prices on the international market in 2010, the project was abandoned. The road linking Le Bosquet to Congo was closed in 2013 because of forest encroachment. Le Bosquet is a long way from the frontier zone with the Central African Republic, where mass migration has been reported due to the war in that country. Probably the most important effect of political activities in Cameroon on Le Bosquet was the placing of boundary markers around the forest community of Le Bosquet in 2009. It seems that Le Bosquet has become the only forest community in Cameroon attributed to a group of Baka pygmies, thanks to the work of the nuns who dealt with all the administrative procedures. However, this means that all other Baka communities who have not claimed the same land titles rights within the prescribed time could be deprived of their land if one day the central government decides to take possession of them.

S4. Total Fertility Rate and Age Specific Fertility Rate

Weiss (8), in his model tables (MT), proposed an ASFR and TFR based on data for female births only: ASFR is the ‘chance of person x years old giving birth to offspring of same sex’ (Table 0, page 2) and TFR is ‘the average size of the family (in daughters) after the mother has reached menopause’ (Ref. 8, p. 7). To other authors, the TFR corresponds to the Completed Family Size in the Weiss tables. When both sexes are considered, Weiss calls this the Mean Family Size. Howell, however, in her study on the Dobe !Kung (Ju/hoansi) (9), used the ‘number of children’ (boys and girls) to estimate ASFR and TFR (Table 6.1, page 124) and indicated that ‘we tabulate the estimated age of the mother at the birth of each of her children to construct ASFR’ (Ref. 9, P. 123). Hill & Hurtado (10) state ‘ASFR for Aché women who probably reported all live births in the forest are shown in Table 8.1 and Figure 8.3’ (pages 253, 261 and 265) and define it as ‘the number of women who gave birth at age x

divided by the total number (of women) who complete that age interval' (Ref. 10, p. 253). At no time do they mention that *only* female births are included in the analysis. ASFR for the Aché were compared with Howell's data without any kind of correction for the sex ratio, which reinforces the idea that Hill & Hurtado calculated ASFR and TFR using the total number of births and not exclusively female births as suggested by Weiss (8). In their work on the Yanomamo, Neel & Weiss (11) obtained ASFR after several corrections using the total number of births, but in Table 2 they give an ASFR in which 'daughters only are born by assuming a sex ratio at birth of 1.05 males per females' (Ref 11, p. 33). It is obvious that comparisons of data from different sources have to consider the different ways in which the data were obtained and make the necessary corrections.

Kramer & Greaves' work (12) deserves a special comment. They mention that TFR can be obtained by 'cohort rate', which means following 'a group of women in the same birth or marriage cohort as they pass through their reproductive careers, documenting births and deaths as they occur' (Ref 12, p. 718). In other words it is equivalent to monitoring women during their entire reproductive life, which is 'impractical', as the authors state. For this reason, Kramer & Greaves, like the majority of authors, obtain a TFR based on what they call 'period rates', which 'are constructed cross-sectionally from the numbers of births that have occurred over some period of time, usually within a calendar year, to women in different age groups' (Ref 12, p. 719): these are the ASFR. Since the number of births is divided by the total number of women, the specific fertility rates varies from 0 (no births) to 1 (same number of births as women, in other words all women give birth). It is confusing that the values for specific fertility rates for the four younger age classes of the Pumé are higher than 1.

We used data from 2012 to obtain ASFR, crude birth rate (CBR) and TFR (Weiss' Completed Family Size, CFS) in a similar way to Weiss (8); TFR was obtained from female births only. As in previous studies (4, 11), the few data available (ASFR, CBR and CFS) were entered into a Weiss table in order to find the values for other variables predicted by the model. We obtained a CFS of 2.317, which is close to that presented in MT 33.0-55.0. This MT suggests a mean family size of 3.64, which is much smaller than our value of 7.3. Another difference concerns the ASFR, since in the MT the higher value corresponds to ages 20 – 29 (0.117) whereas for the Baka it falls into the 15-19 age class (0.158). CBR for the Baka in 2012 is 0.021, which is lower than predicted in MT (0.0346). Thus, the data from the Baka do not fit into any of the Weiss model tables.

Cavalli-Sforza's study (4) on the Aka pygmies in the Central African Republic used only one variable, the average age of the population, to suggest the Weiss model table (MT: 22.5-40) as

probably representing this population. This table was used by Migliano and colleagues (13) to attribute several life history variables to the Aka pygmies. Our study of the Baka suggests that many variables have to be used to assess whether a model table fits the population under study. The use of tables inferred from only one variable can lead to an inaccurate description of the life history variables of a population.

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Figure S1

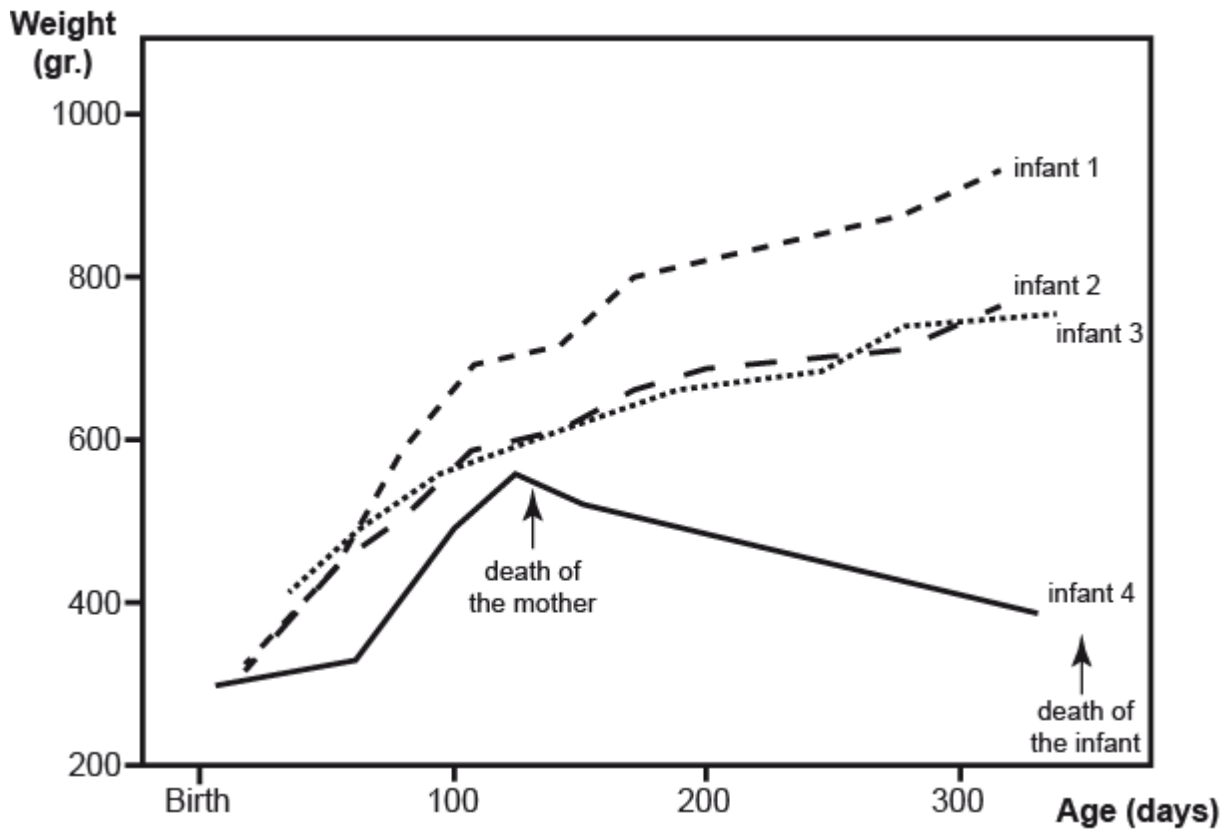


Figure S1: Loss of weight and death of an infant whose mother died. All infants shown in the graph were born around the same date: infants 1, 2 and 3 illustrate the normal increase in weight during the first year of life. Infants 1 and 2 are twins and their father is a half-brother of infant 4's father. Infant 4 was born in June 2011. After the death of his mother in November 2011, his father and other members of the family neglected him. They did not provide any care for him and never brought him back to the medical centre to be weighed; the last measure of his weight was taken by us one month before his death in June 2012. We recorded four cases like this one, which seem to illustrate the usual behaviour when a mother has died. The case presented here occurred in the family of our closest collaborators.

Table S1: Number of births recorded by year in Le Bosquet

Year	Births recorded	Year	Births recorded
1988	24	2002	36
1989	30	2003	30
1990	35	2004	39
1991	38	2005	55
1992	36	2006	25
1993	36	2007	17
1994	32	2008	37
1995	31	2009	40
1996	41	2010	37
1997	25	2011	26
1998	27	2012	33
1999	39	2013	21
2000	39	2014	35
2001	41	2015	30

Table S2: Sample size for each analysis

Analysis	N
Known reproductive history	16*
Average completed family size	15*
Reproductive period	15*
Age at menopause	15*
TFR & ASFR 2007	95 (17)
TFR & ASFR 2008	113 (37)
TFR & ASFR 2009	163 (40)
TFR & ASFR 2010	167 (37)
TFR & ASFR 2011	157 (26)
TFR & ASFR 2012	180 (33)
TFR & ASFR 2013	155 (21)
TFR & ASFR 2014	189 (35)
TFR & ASFR 2015	177 (30)
Infant mortality by parity	44
Children mortality	212
Weight first two months	90

*: same individuals

TFR & ASFR: total fertility rate and age specific fertility rate – number of reproductive women (number of births)

Table S3: Weight of infants in the two first month of life

	Month	2008-2010	2012-2014	<i>p</i>
Female	1°	3,6 (13)	3,7 (14)	0.709
	2°	4,3 (11)	4,4 (10)	0.614
Male	1°	4 (11)	3,5 (12)	0.243
	2°	4,8 (9)	4,9 (10)	0.808

The average and the sample size (in brackets) is given for each period.