Original Research Article

Climatic Variability and the Population Dynamics of Historical Hunter–Gatherers: The Case of Sami of Northern Finland

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ABSTRACT   Our current knowledge on climate-mediated effects on human population dynamics is based on preindustrial agrarian societies where climate-induced crop failures had a major impact on fertility and mortality rates. However, because most of the human evolutionary history has been shaped by hunter–gatherer lifestyle relying on diverse plant and animal food sources, it is also important to understand how climate affected the population dynamics of hunter–gatherers. We thus studied whether climate, measured as a reconstructed annual mean temperature, had concurrent or delayed effects on the key components of population dynamics, annual births and deaths, in three historical (1722–1850) Sami populations of Northern Finland that depended mainly on fishing, hunting, and reindeer herding for their livelihood. We found only weak concurrent effects of mean temperature on annual births and deaths, although in general warm years correlated with increased birth and reduced mortality rates. Likewise, temperature-mediated delayed effects were mainly absent: in one population only, a warm previous year tended to reduce the number of births. By contrast, annual numbers of births and deaths were more closely associated, as indicated by negative correlations between births and deaths up to three previous years. To summarize, in contrast to historical agrarian societies, the population dynamics of historical Sami seemed to be only weakly associated with annual mean temperature, which may indicate that these populations, probably due to their dietary breadth, were rather unaffected by climatic variation. Am. J. Hum. Biol. 19:844–853, 2007.   © 2007 Wiley-Liss, Inc.

Births, deaths, and migration determine the size and growth rate of open populations (Turchin, 2003; Yaukey and Anderton, 2001) and prevailing environmental conditions can have profound effects on all of these factors. For example, food shortage because of abiotic hazards can increase mortality, reduce fertility, and induce migration (Ottersen et al., 2001; Scott and Duncan, 2002; Scott et al., 1998; Stenseth et al., 2002). Hence, environmental conditions play an essential role in population dynamics. Together with intrinsic biological processes, i.e., direct and delayed density-dependence, extrinsic factors can produce large temporal and spatial variation in population abundance (Turchin, 2003).

Abiotic environment can influence demographic parameters directly and indirectly (Galloway, 1986; Lee, 1987; Richards, 1983). Adverse environmental conditions, such as heat and cold shocks, UV-radiation from the sun, and diverse extreme weather events, can directly increase mortality and reduce reproduction (McMichael et al., 2006; Patz et al., 2005). The indirect environmental effects instead include, for example, effects on the prevalence and species richness of infectious diseases and on diverse food sources, like cultivation, animal husbandry, and water supply, that affect mortality and fertility (Guernier et al., 2004; Koelle et al., 2005; McMichael et al., 2006; Patz et al., 2005).

The magnitude of such effects may depend on the characteristics of populations, as some populations may be better buffered against adverse and unpredictable environmental hazards. For example, less developed societies depending mainly on one climate-sensitive subsistence are likely to be the most vulnerable to fluctuations in environmental conditions. This

definition may apply particularly to historical preindustrial populations that experienced natural fertility and mortality because of the lack of effective birth-control methods and advancements of modern medical care.

Associations between climatic factors and demography in preindustrial humans have been addressed before by Bengtsson et al. (1984), Eckstein et al. (1985), Galloway (1985, 1986, 1994), Hammel (1985), Lee (1981, 1987), Richards (1983), and Scott et al. (1998). These studies suggest stronger indirect, measured as agricultural yields and crop prices, than direct effects of climate (e.g. temperature) on birth and death rates. In general, cold years, particularly cold winters, and high crop prices, indicating food shortage, seemed to increase mortality and reduce fertility in pre-industrial humans. Hot summers tended to have similar effects.

All the afore mentioned studies have however examined agrarian societies, in which climate-mediated crop failures causing famines had paramount effects on demography (Scott and Duncan, 2002). Much less is currently known how climatic factors affected the dynamics of populations that depended on fishing, hunting, and gathering instead of agriculture (Lee, 1987), which has been the main livelihood for the most human societies only for the last 10,000–12,000 years (Scott and Duncan, 2002). Differences in dietary breadth and lifestyle between hunter–gatherers (Cordain et al., 2000 for a review of world-wide hunter–gatherer diets) and agricultural populations are believed to have had important bearings on how climate affected the demography of populations through the quality of nutrition, individual health, and disease load (Armelagos et al., 2005; Larsen, 2005). It could be argued that the demography of hunter–gatherers that depend not merely on one source of food might be less affected by climatic factors compared to agricultural populations relying solely on crop yields. On the other hand, because basically all plant and animal populations are directly and indirectly under climatic forcing (Mysterud et al., 2003; Straile et al., 2003), their population fluctuations could bear at least some influence on humans depending on them. These points make it rather hard to predict how hunter–gatherer populations might respond to climatic variability. Because human evolutionary history has been mainly shaped among hunter–gatherers (Scott and Duncan, 2002), these kinds of studies may also help to shed more light into those ecological factors responsible for natural selection on human life history.

We investigated how temporal climatic variability affected the two key components of population dynamics, annual births and deaths, in three historical Sami populations that lived in Northern Finland during the 18–19th centuries. Similarly to other hunter–gatherers living in Northern areas (Cordain et al., 2000), these populations depended mainly on animal food sources, by practicing hunting, fishing, and reindeer herding, and, to a lesser extent, on gathered plants. It is practically impossible to obtain multiannual data on the variation of these main livelihoods. We cannot thus directly contrast the direct and indirect effects (through nutrition) of climate on the demography of the populations studied. However, one potential way to evaluate these effects is to look at the timing (or delays) of climatic effects on demographic parameters. One could reason that direct effects (e.g., temperature extremes) act nearly simultaneously, i.e., with no particular delay. Instead, indirect effects, mediated through various sources of food supply and disease susceptibility, might operate with the lags of even several years. In other words, given annual data on vital rates, it could be expected that the direct effects of climate on birth and death rates should be visible immediately at the same year (or on the next year in the case of annual births), whereas the climatic conditions acting indirectly may be seen with a delay of couple of years or more. Naturally, it is likely that most environmental conditions act through both direct and indirect effects. The potential path how climatic variability may directly and indirectly affect birth and death rates is illustrated in Figure 1.

MATERIALS AND METHODS
Demographic data

Data on annual baptisms and burials, i.e., the estimates of respective numbers of annual births and deaths, in three populations of Northern Finland (Enontekiö, Utsjoki, and Inari) were extracted from computerized parish records (http://www.hiski.fi/hiski/b36d17?en+A19), collected by the Lutheran church since the 16th century. These populations occupied large, partly overlapping geographical areas; Inari being the largest population (15,400 km^2), followed by Enontekiö (8,150 km^2) and Utsjoki (5,200 km^2) (Itkonen, 1948). When measured as the number of inhabitants
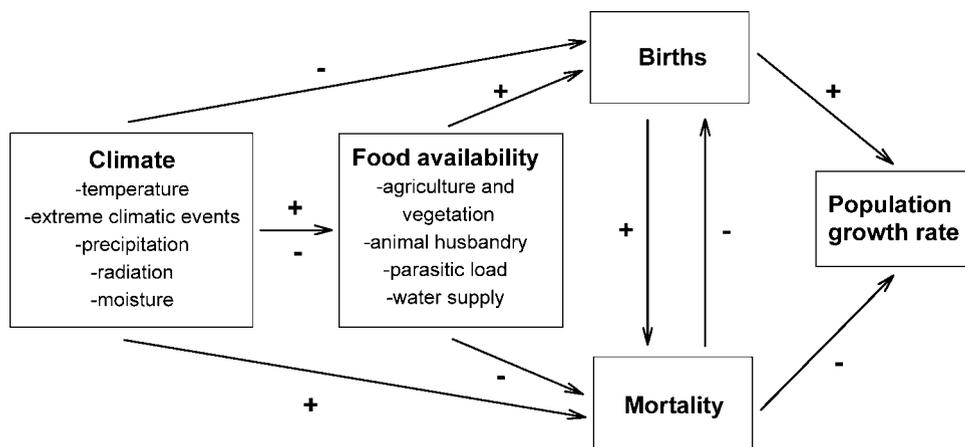
Fig. 1. A simplified model how climate may affect population size through births and deaths (e.g. Galloway, 1986, 1994 and Scott and Duncan, 2002 for a more detailed illustration). Arrows and accompanying signs represent the predicted direction of associations. Potential feedback loops from population size to climate, the effects of climate on migration, and the autocorrelation of births and deaths are omitted for simplicity. Climate has most likely both direct and indirect effects on births and deaths. Direct effects are mediated through the effects of climatic conditions acting simultaneously on vital rates, whereas indirect effects are mediated through the delayed effects of climate on the main livelihoods of populations.

during the study period, Enontekiö was the largest population (Itkonen, 1948). The annual number of inhabitants is not available for these populations, making it hard to evaluate population densities (i.e., inhabitants per area; Yaukey and Anderton, 2001). The inhabitants of Utsjoki and Inari were Sami, whereas Enontekiö consisted of both Sami and Finns. The ethnic identity of the births and deaths in Enontekiö cannot be determined from the data used here. However, in the beginning of the study period, most of the inhabitants were Sami, but towards the end of the 19th century they were mostly of Finnish origin and only about 10% of them were Sami (Itkonen, 1948). In Enontekiö, marriages between Sami and Finns were nevertheless rare (Itkonen, 1948).

These populations can be considered to have experienced natural mortality and fertility because of the lack of any advanced medical care or birth-control methods. Environmental conditions were harsh. For example, average annual mean temperature was roughly 2°C below zero (temperature ranged, for example, from −47 to +32°C in Inari during the years 1900–1930), growth season lasted 110 days only, and lakes were frozen more than 230 days in a year (Itkonen, 1948). Mean annual precipitation was 454, 393, and 300 mm in Inari, Utsjoki, and Enontekiö, respectively (Itkonen, 1948). Until the middle of the 18th century, the Sami practiced hunting (mostly deer and elk), fishing (mostly white fish, vendace, grayling, and salmon), gathering plants, and reindeer herding, but thereafter increasing number of families began to practice nomadic or seminomadic reindeer herding for their main livelihood (Itkonen, 1948). These populations also differed in their chief source of livelihood. The Utsjoki Sami were mainly seminomadic reindeer herders, practicing also fishing (Itkonen, 1948). In Inari, the Sami lived mainly on fishing and hunting all year around, whereas the Sami of Enontekiö practiced nomadic reindeer herding (Itkonen, 1948). Accordingly, the Sami of Inari and Utsjoki lived mainly in permanent dwellings, whereas the Enontekiö Sami lived in temporary tents and followed the seasonal migrations of their reindeer herds (Itkonen, 1948). Contrary to Sami, the Enontekiö Finns were mainly agriculturalists (Itkonen, 1948). These between-population differences in lifestyle were reflected into the life histories of these people, as, for example, mean family size and lifespan differed between populations (Helle et al., 2002). Mean (±1 SD) and the coefficient of variation (CV) for annual baptisms and burials in the populations studied are given in Table 1.

Reconstructing historical climate from proxy records

Relationships between the population dynamics of historical humans and climate could

TABLE 1. Summary statistics of baptisms, burials, and mean temperature in the populations studied

Population	Study period	Baptisms (mean ± SD)	Burials (mean ± SD)	Baptisms (CV)	Burials (CV)	Temperature (CV)
Enontekiö	1722–1850	21.6 ± 8.7	10.6 ± 7.9	40.5	75.0	−39.0
Inari	1730–1814	9.3 ± 3.2	4.9 ± 3.4	34.5	68.0	−40.9
Utsjoki	1749–1813	8.0 ± 3.6	4.3 ± 2.7	45.2	60.6	−42.7

be ideally examined using the direct measurements of local climate. However, most of the Finnish meteorological records started during the 20th century (Heino, 1994), and thus do not overlap with the data used here. Therefore, we must rely on the proxy records of historical climate.

Perhaps the most frequently used proxy records for climatic series are tree-rings (Fritts, 1976). A tree-ring chronology is a mean of sample series of tree-ring measurements from individual trees. It is a regional average of a given population of trees of the same species, and expected to reflect climatic variability much more reliably than single trees or local chronologies that may contain micro-ecological information unique to that location (Fritts, 1976). Two types of tree-ring chronologies from Scots pine (*Pinus sylvestris* L.) were used here: tree-ring width (TRW) and maximum density (MXD). The former was constructed by Helama et al. (2005) and the latter was the chronology of Briffa et al. (1990). In Northern Finland, the annual growth of trees is controlled by summer temperatures, and hence, past summer temperatures can be reconstructed by using the TRW and MXD chronologies from living and sub fossil Scots pines (Briffa et al., 1990; Helama et al., 2002). In Finland, tree-rings of Scots pine have previously been used as proxies for temperature (Helama, 2004; Helama et al., 2002), precipitation (Helama, 2004; Helama and Lindholm, 2003) and large-scale atmospheric indices, such as North Atlantic Oscillation, NAO (Lindholm et al., 2001). Detailed description of the methodology and chronology construction has been given in Helama et al. (2005).

Natural climatic variability over North-West Europe is often described using the index of North Atlantic Oscillation (NAO) (Wanner et al., 2002). This variability is characterized by an oscillation of atmospheric mass (i.e., sea level pressure) between the Arctic (Reykjavik, Iceland) and the subtropical Atlantic (Ponta Delgada, Azores), which produces large changes in the mean wind speed and direction over the North Atlantic. NAO thus regulates the heat and moisture transport between the Atlantic and surrounding continents, markedly dictating the climate in North-West Europe (Hurrell et al., 2001). The relationship between NAO and terrestrial climate, and hence biotic systems, is especially strong during the cold season (Dec-Mar) of the year, and this holds also for Fennoscandia (Hurrell, 1995). Hurrell (1995) calculated monthly and annual NAO indices since 1868, but Luterbacher et al. (2002), based on historical weather diaries, reconstructed the variability of NAO indices since 1659. The study of Luterbacher et al. (2002) was adopted for the purposes of present study.

These two tree-ring chronologies for summer month temperatures and the NAO-index of Luterbacher et al. (2002) for December to March temperatures were used to retrodict the climatic conditions during the 17–19th centuries in Northern Finland. The climatic variable that was reconstructed was annual mean temperature. All three datasets, the NAO-index of Luterbacher et al. (2002) and the tree-ring indices of Helama et al. (2002) and Briffa et al. (1990) were integrated into one palaeoclimatic model using a linear regression. In this regression model, annual mean temperature of the concurrent year was reconstructed using the annual NAO-index of a concurrent year and the TRW and MXD chronologies of concurrent and two forthcoming years. The rationale of using the TRW and MXD values of two forthcoming years was the significant autocorrelation of the tree-ring time-series. This is due to the physiology of trees and needs to be modified according to the structure of climatic autocorrelation (Helama and Timonen, 2004). Reconstructed annual mean temperature is in good agreement with the observed annual temperature variability in Karasjok weather station in Northern Norway between the years 1890 and 1978 ($r_{\mathrm{pearson}} = 0.722$, $P < 0.0001$), indicating high reliability of the reconstruction (Fig. 2).
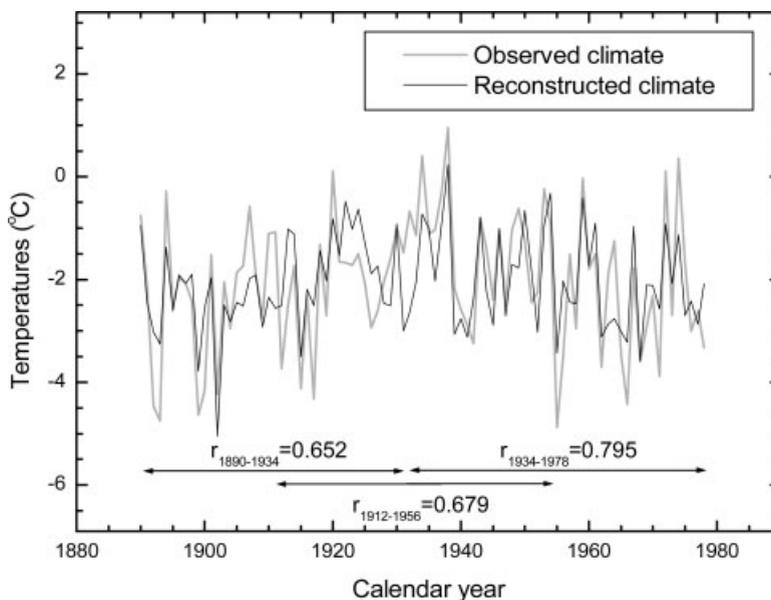
Fig. 2.   Comparison of observed and reconstructed annual mean temperature in the study region over the calibration period. Time-dependent Pearson correlation coefficients (*r*) between reconstructed and observed temperatures do not show notable variations over the three subperiods given.

Statistical analysis relating climate and demography

We started by comparing the population means of annual baptisms and burials to examine differences in the demography of populations. Because the assumptions of parametric analyses were not satisfied, we used Kruskal-Wallis test for comparing means. If statistically significant differences were found, Mann-Whitney test for multiple comparisons between populations was applied.

Relationships between annual mean temperature and the annual numbers of baptisms and burials were examined by linear transfer function (dynamic regression) models (Brocklebank and Dickey, 2003; Pankratz, 1991; Yaffee and McGee, 2000). Using this approach, one can simultaneously relate annual variation in baptisms and burials to current and past values of annual mean temperature. The possibility to model delayed effects is important here, since climate likely has both direct and indirect effects on vital rates (Fig. 1), and the indirect effects may act with a lag of several years. In addition to annual mean temperature, we included the annual number of burials to explain the annual number of baptisms and vice versa, since popula-

tion dynamics are also likely affected by such endogenous factors. For example, high mortality may reduce the number of fertile and pregnant women, and thus births at the same or a subsequent year. Likewise, high birth rate may correlate with higher mortality at the same or subsequent years due to increased maternal and infant mortality (Fig. 1; see also Richards, 1983).

Prior to fitting the global models, potential delayed effects were estimated by separate cross-correlation analyses between explanatory and response variables. The interpretation of cross-correlation analysis is however meaningful only after the both series analyzed are prewhitened with the same filter (Brocklebank and Dickey, 2003; Yaffee and McGee, 2000). That is, the potential autocorrelation structure of annual mean temperature was also removed from the baptisms and burial series, by estimating first a proper ARIMA-model (Autoregressive Integrated Moving Average) for mean temperature and then filtering the baptisms and burial series with this model. Similar procedure was applied when estimating the potential delayed effects of burials on baptisms and vice versa. Cross-correlation coefficients exceeding the 95% confidence intervals were included into the global model
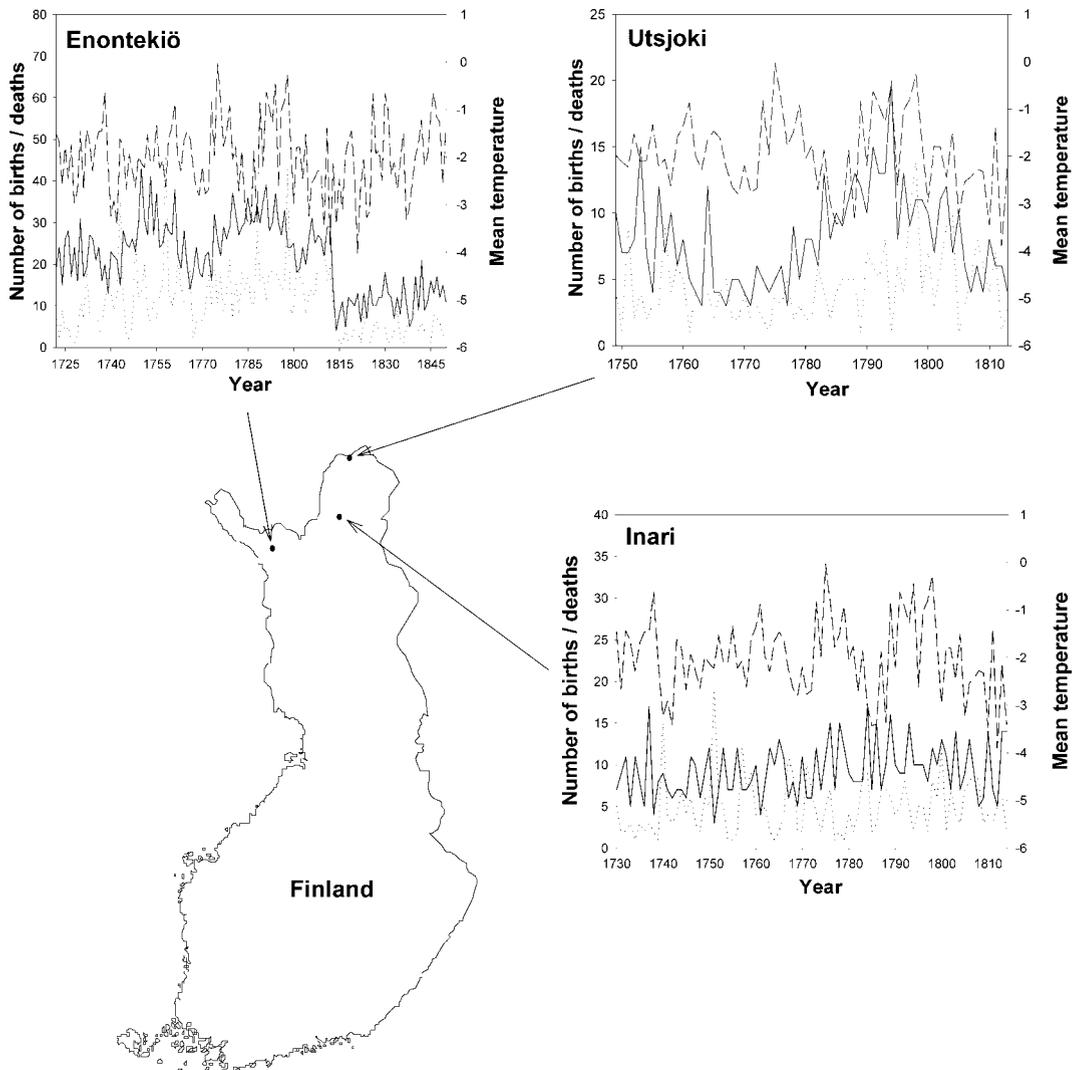
Fig. 3. Annual variation of the number of baptisms (solid line) and burials (dotted line) and reconstructed mean temperature (short dash line) among the populations studied.

to represent the potential delayed effects of explanatory variables. Backward selection procedure was used to select the minimal models including only statistically significant delayed effects. Before accepting these models, the coefficients of delayed effects and model residuals were confirmed to be uncorrelated, because cross-correlation between these two would have indicated an improper identification of lagged effects (Brocklebank and Dickey, 2003; Yaffee and McGee, 2000). Prior to analy-

ses, linear trends were removed from the log transformed response series and all series were centered to their mean, and thus the intercept was omitted from the models (Brocklebank and Dickey, 2003; Yaffee and McGee, 2000). Among independent variables, the largest inflation factor was 1.03 and the smallest tolerance value was 0.97, suggesting no bias in the standard errors of estimated regression coefficients because of multicollinearity. Analyses were performed with SAS

TABLE 2. *Effects of annual mean temperature and burials on annual baptisms*

Population	Mean temperature			Burials			Autocorrelation		
	lag	β ($\pm$SE)	P	lag	β ($\pm$SE)	P	lag	β ($\pm$SE)	P
Enontekiö	0	0.051 (0.036)	0.15	0	0.061 (0.041)	0.14	1	0.213 (0.091)	0.02
	1	−0.068 (0.036)	0.057	2	−0.168 (0.038)	<0.0001	2	0.285 (0.092)	0.002
Inari	0	0.010 (0.037)	0.79	0	−0.072 (0.042)	0.09	1	−0.204 (0.098)	0.038
							3	0.272 (0.105)	0.01
							10	0.310 (0.106)	0.004
Utsjoki	0	0.014 (0.055)	0.81	0	−0.028 (0.061)	0.65	2	0.406 (0.111)	0.0002
				1	−0.204 (0.061)	0.0008	3	0.334 (0.112)	0.003

TABLE 3. *Effects of annual mean temperature and baptisms on annual burials*

Population	Mean temperature			Baptisms			Autocorrelation		
	lag	β ($\pm$SE)	P	lag	β ($\pm$SE)	P	lag	β ($\pm$SE)	P
Enontekiö	0	−0.028 (0.077)	0.72	0	0.283 (0.181)	0.12	1	0.254 (0.088)	0.004
				1	−0.600 (0.171)	0.0004			
				2	−0.619 (0.180)	0.0006			
Inari	0	−0.213 (0.084)	0.011	0	−0.322 (0.207)	0.12	8	0.251 (0.114)	0.029
				3	−0.635 (0.215)	0.003			
Utsjoki	0	0.088 (0.093)	0.35	0	0.058 (0.185)	0.75	5	0.277 (0.128)	0.03

statistical package version 9.1 (SAS Institute Ins, Cary, NC, USA, 2002–2003).

RESULTS

Between-population comparison of annual baptisms and burials

Temporal variation of annual baptisms, burials, and reconstructed mean temperature in the populations studied is shown in Figure 3. We found between-population differences in annual birth (Kruskal-Wallis test, $\chi^2_2 = 140.82$, $P < 0.0001$) and mortality rates ($\chi^2_2 = 54.85$, $P < 0.0001$; Table 1). In Enontekiö, annual birth rate was higher than in Inari (Mann-Whitney test adjusting for multiple comparisons by Bonferonni ($k = 3$), $Z = -9.83$, DF $= 1$, $P < 0.0001$) and Utsjoki ($Z = -9.59$, DF $= 1$, $P < 0.0001$), and more offspring were born annually in Inari than in Utsjoki ($Z = -2.53$, DF $= 1$, $P = 0.034$). Likewise, in Enontekiö more deaths took place annually than in Inari ($Z = -6.02$, DF $= 1$, $P < 0.0001$) and Utsjoki ($Z = -6.18$, DF $= 1$, $P < 0.0001$), but not in Inari compared to Utsjoki ($Z = -0.73$, DF $= 1$, $P =$ ns).

Utsjoki showed the highest variation of annual births, followed by Enontekiö and Inari. By contrast, the highest variation of annual deaths was observed in Enontekiö, followed by Inari and Utsjoki. During our study periods, reconstructed annual mean temperature showed the highest temporal variation in Utsjoki, followed by Inari and Enontekiö (Table 1).

Effects of mean temperature on annual births and deaths

In all populations, warm years weakly correlated with increased annual birth rate (Table 2). In Enontekiö only; however, we found a marginally significant correlation between annual births and mean temperature, but with a lag of 1 year (Table 2). In contrast to concurrent effects, a warm previous year tended to instead reduce annual births. Annual birth rate seemed to be more closely related to annual mortality. Depending on a population, high mortality during up to previous 2 years was associated with the decline in annual births (Table 2). Furthermore, mainly positive autocorrelations among annual births up to previous 3 years were found (Table 2).

In Enontekiö and Inari, warm years were associated with reduced mortality, although this correlation reached statistical significance only in Inari (Table 3). No delayed effects of mean temperature on annual deaths were found. Moreover, depending on a population, decreased annual mortality was related to increased birth rate in preceding 1–3 years (Table 3). The autocorrelation structure of the annual deaths seemed rather inconsistent, showing a positive autocorrelation with a lag

of 1, 5, and 8 years in Enontekiö, Utsjoki, and Inari, respectively (Table 3).

DISCUSSION

We found only a weak evidence for the concurrent or delayed effects of annual mean temperature on annual births and deaths among historical Sami populations. In general, mean temperature tended to weakly positively correlate with birth rate, whereas in one population a warm previous year was instead associated with a reduction in annual births. Likewise, in one population only, mean temperature had a negative concurrent effect on annual mortality. No delayed effects of mean temperature on mortality were found. By contrast, we found more indication to suggest that among Sami mortality and birth rates were coupled with a lag of 1–3 years. Moreover, particularly annual births were positively autocorrelated with a lag of up to 3 years.

Our finding that in general cold years seemed to be associated with reduced births and increased mortality are somewhat compatible with the results from preindustrial agrarian populations. Similar associations have previously been reported in preindustrial Europe (Eckstein et al., 1985; Galloway, 1985, 1994; Lee, 1981, 1987; Scott et al., 1998), although in these studies cold winters and hot summers in particular increased annual mortality and, to a lesser extent, reduced annual births. One should note, however, that in contrast to the agrarian populations of preindustrial Europe, the magnitude of the climatic effects found here were much weaker and largely statistically nonsignificant (as also found by Richards (1983) and Hammel (1985) in some agricultural populations), and included likely both direct climatic and indirect nutritional effects on births and deaths. Hence, the overall effect of mean temperature on the population dynamics of Sami was minor. Furthermore, the observation that among the populations studied high mortality during the up to previous 3 years reduced the annual number of births, and vice versa, is compatible with previous studies on preindustrial England and France (Lee, 1981; Richards, 1983). This suggests that also intrinsic factors influenced the population dynamics of historical humans.

The inconsistency of the results further suggests that temperature-mediated effects on annual births and deaths were only of a minor general importance among these populations.

For example, in Enontekiö only, reduced annual birth rate was weakly associated with a warm previous year, whereas in Inari and Utsjoki annual birth rate was unrelated to mean temperature at the same or previous years. One explanation for why such an effect was seen in Enontekiö only might be that in contrast to Inari and Utsjoki the inhabitants of Enontekiö consisted mainly of Finns depending on climate-sensitive agriculture towards the end of our study period. Hunter–gatherer and semi-nomadic lifestyles of the Sami of Inari and Utsjoki might explain why these populations seemed to be rather well buffered against climatic fluctuations. The association found in Enontekiö may thus represent an indirect effect of mean temperature on annual births, because a delay of 1 year may hint a decrease in nutritional conditions related to, for example, drought, leading to reduced female fecundity (Nepomnaschy et al., 2006) and lower birth rate at the next year. It is, however, unclear why in Enontekiö mean temperature, if related to crop yields, did not affect mortality. It might be that female fecundity is more sensitive to nutritional and climatic stress than, for example, their immune defenses, which may explain this pattern.

The following potential reasons that may explain our findings and point out some shortcomings of previous studies deserve mentioning. First, climate-mediated effects on mortality might be age-dependent. That is, extreme temperatures, weather conditions, and nutritional stress may promote mortality mainly among the old and young individuals (Galloway, 1985; Scott et al., 1998). This may have masked the relationship between temperature and mortality among Sami, as we used age-independent total annual deaths only. Second, the mortality of men and women in response to environmental and nutritional hazards may differ. In general, male mortality exceeds female mortality (Kruger and Nesse, 2006), for example, because of higher susceptibility to infectious diseases in men. On the other hand, women may be more vulnerable to heat and cold stress than men (McMichael et al., 2006). It would thus be preferred to investigate climate-mediated effects on mortality separately in men and women. Third, similarly to mortality, investigating the effects of climate on the number of total births only may not fully describe the potential climate-mediated effects on human fertility. Faster-growing male fetuses are more vulnerable to environmental stress than female fetuses, result-

ing in a male-biased abortion rate during maternal malnutrition (Stinson, 1985). Furthermore, temperature variability has been speculated to directly bias offspring sex ratio in humans, as more males are suggested to born during warm years (Crech et al., 2000; Lerchl, 1999; McLachlan and Storey, 2003). Therefore, we might learn more by comparing how environmental factors, including temperature, affect the numbers of male and female births separately. Availability of these kinds of data may explain the scarcity, particularly in terms of gender-specific mortality, of studies investigating these issues in historical settings. Fourth, yet another factor that may play a role how populations are affected by climate is population density. For example, large and denser populations, often accompanied by sedentarism, domestication of animals, and dietary deficiencies, are more vulnerable to disease epidemics, leading to higher mortality and lower fertility (Armelagos et al., 2005). Finally, climate-induced nutritional stress among mothers may have far reaching effects on many aspects of offspring fertility, health, and survival that become manifested decades after an individual is born (Gluckman and Hanson, 2004; Lummaa and Clutton-Brock, 2002). These kinds of "fetal programming"-effects may introduce an important factor in the long-term dynamics of human populations that is not yet well understood.

Likewise, uncertainties could be attached to the climatic record used. It is possible that relationships between demographic parameters and external forcing by climate could be better described using some other climatic variable(s) than mean temperature. Moreover, albeit the resolvability of the climatic and demographic time-series was the same (annual), this does not necessarily mean that it was optimal. For example, if deaths and births show strong seasonal dependence (Becker and Weng, 1998; Lam and Miron, 1991), then it might be more appropriate to compare, for example, monthly records of climate and demography. In the populations studied here, seasonality of births and deaths has not been studied. It is thus hard to evaluate whether this issue introduced bias in our analyses. In general; however, strong seasonal patterns of births and deaths are linked particularly to agricultural lifestyle (Scott and Duncan, 2002), and thus may not be expected in the Sami populations studied. Yet, the influence of climate on births and deaths may be more related to extreme but rather rare climatic phenomena not captured by annual mean temperature.

CONCLUSIONS

Annual mean temperature seemed to have only minor effects on annual births and deaths among historical hunter–gatherer Sami populations that, in contrast to historical agricultural European and Finnish populations (Pitkänen, 1993), were largely unexposed to famines caused by climate-driven crop failures. Warm years tended to reduce mortality and increase births at the same year, although in one population, a warm previous year was instead related to reduced annual births. By contrast, endogenous demographic factors seemed to be more important in influencing the population dynamics of Sami. That is, high mortality during the previous 3 years indicated a decline in annual births. Also, autoregressive factors, particularly in annual births, were important. This suggests that these populations, most likely due to their dietary breadth, were rather well buffered against climatic forcing. An inability to incorporate age- and gender-specific mortality and birth rates may have however resulted in a loss of power to detect climate-driven effects on the demography of the populations studied. It is also possible that among Sami population fluctuations might have been better explained by some other external variable(s) than mean temperature.

ACKNOWLEDGMENTS

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