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Ambient temperature predicts sex ratios and male longevity

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Curiosity about the effect of ambient temperature on human well being has not only endured (1) but, because of concern over climate change, grown to unprecedented levels (2). No research, however, appears to have focused on how temperature affects population health through natural selection in utero. This finding remains true despite three widely disseminated epidemiologic findings that together suggest such a connection. First, only 30–50% of conceptions yield live births, making gestation as much an opportunity for natural selection as for maturation (3, 4). Second, population stressors increase fetal deaths, particularly among males (5). Third, extreme ambient temperature demonstrably stresses human populations (6).

Natural selection has conserved mechanisms by which women subjected to environmental stressors abort frail fetuses least likely to yield grandchildren (7). These mechanisms purportedly cull males because sons more likely die before reproductive age than do daughters despite receiving greater maternal investment (8, 9). A woman without such mechanisms would have fewer grandchildren because environmental stressors would weaken both her and her son, thereby reducing his already low, relative to a daughter’s, odds of survival and her capacity to invest in him. A stressed woman with these mechanisms would, conversely, abort a frail male, making her available to bear a daughter or more robust son.

Environmental stressors reported to affect the gender of birth cohorts include cold ambient temperature (10). Cold temperature induces the stress response in those not sheltered against it (11). In addition, low temperature can indirectly stress populations by, for example, disrupting the economies that support them (12). Research in Scandinavia, moreover, reports that stressors of all sorts may be more virulent when unusually cold summer weather constrains restorative behaviors (13). Any of these direct or indirect mechanisms could cause gravid women to lower their tolerance for frail male fetuses. Epidemiologic research reports, for example, that preterm delivery, an outcome of gestation that affects more male than female fetuses, appears elevated among cohorts whose second and/or third trimester in utero coincides approximately with cold winter months (14).

The above arguments imply that males from cold-stressed cohorts, which have been “culled” in utero of their least-fit members (15), should, on average, live longer than males from other cohorts. Because of the importance of this implication for evolutionary theory, climate studies, and public health, we test the hypotheses that temperature moves positively with the secondary sex ratio (ratio of male to female live births) but inversely with the life span of men, controlling for life span of women, surviving to age 1 year. We test our hypotheses among annual cohorts born in Denmark, Finland, Norway, and Sweden between 1878 (the earliest year with complete life tables) and 1914 (last birth cohort for which male life span can be estimated). We conclude that ambient temperature affects the characteristics of human populations by influencing who survives gestation, a heretofore unrecognized effect of climate on humanity.
in the opposite direction of high or low values appeared 5 years later.

Given the relatively short time series available for our test, we assessed whether our result could have been induced either by outliers in the sex ratio or variability in its variation over time. We used the methods devised by Chang et al. (20) to detect and adjust outliers; none was detected. We then transformed the sex ratio to its natural logarithms and estimated our final equation again to assess any effect of variability in variation. The results of the test, with the obvious exception of the metric of the coefficients, remained the same.

The temperature coefficients (Table 1) suggest that a 1°C increase in annual temperature predicts one more male than expected for every 1,000 females born in a year. The median annual number of female births over the test period was 167,046. A rise of 1°C would, therefore, imply preservation of 167 males in the median year.

As evident in Fig. 3, life span for both men and women rose significantly during our test period, requiring us to use the first differences of both variables in our tests. Like the sex ratio, the differenced life expectancy variable exhibited autocorrelation in that echoes of high or low values appeared 5 years later.

Consistent with the culled cohort argument, the cohort life span of Scandinavian males declined with warmer, and increased with colder, ambient temperatures during their gestation ($P = 0.02$; see Table 1). This association survived controlling for variance shared between male and female cohort life span. As with the sex ratio test, we repeated our life span test, controlling for outliers and, separately, with the dependent variable transformed to natural logarithms. The results remained the same as from the original test.

The trends inherent in longevity required us to take the first differences of the life span series to arrive at their expected values. We, therefore, also differenced the temperature variable to ensure that our tests detected associations that persisted into subsequent years. To determine the sensitivity of our test to differencing of the temperature variable, we reestimated the life span equation with the temperature variable in its original rather than differenced metric. The resulting coefficient [i.e., $-0.0324 \pm 0.0113$ (SE)] changed very little from the original estimation [i.e., $-0.0377 \pm 0.0155$ (SE)].
The temperature coefficient, shown in Table 1, implies that an increase of 1°C from one year to the next predicts a decrease in male life span of, on average, 14 days among those who survived to age 1. Combining the sex ratio and life span results suggests that in a year with the median number of live female births (i.e., \(167,000\)), a 1°C rise in annual temperature from the previous year would preserve \(167\) male gestations that would otherwise have ended without live births. The unexpectedly early deaths of these males, however, would reduce the average life span of males who survived to age 1 year in their birth cohort by 2 weeks.

We combined the northern and southern temperature measurements, but population in the region has historically been greater in the south. We estimated our final equations for both outcomes separately with only the northern and then only the southern temperature series. Results did not differ significantly from those yielded by the average of the two temperature series. The point estimates for the southern series, however, were larger, although not statistically different from, those of the northern series.

Very warm temperature may also induce maternal stress through direct and indirect mechanisms. Temperatures in our study area unlikely reached levels that would induce stress in humans, but we repeated both of our tests with the square of the temperature variable added to the test equations. This addition tests whether the “dose–response” of our dependent variables to temperature resembled hyperbola more than straight lines. Neither squared term yielded significant associations.

### Discussion

Data from Denmark, Finland, Norway, and Sweden suggest that at least one ubiquitous stressor, unexpectedly cold ambient temperature, influences the characteristics of populations by affecting selection in utero. Mean temperature varies positively with the sex ratio but inversely with male cohort life span at age 1 year. Low temperatures, therefore, may dull males in utero and leave a more robust cohort compared with males born in years with warmer mean temperature.

Our findings may not describe other regions, particularly those with warmer climates. In addition, changes in interrelated climate parameters, particularly temperature and humidity, may mask or amplify associations between temperature and human adaptation and do so differently in different regions. Cold might stress pregnant women by several mechanisms, including direct thermal impact, lower nutrition because of poorer crop yields, changes in cloudiness/sunlight, and more exposure to indoor pollutants. Additional work must disentangle these effects and test for dose–response differences by latitude before we can make more global inferences regarding climate change, selection in utero, and life span.

Although these northern European datasets provide an opportunity to gauge the association of population health with cold temperature, they do not allow a symmetrically satisfying test for heat. Such a test awaits the discovery of life table and temperature data from warmer regions.

Our findings do not directly contribute to estimates of the health effects of long-term global climate change because we studied annual variations from long-term trends in longevity. The results, however, suggest a hitherto unrecognized impact of variation in global climate. Changes in ambient temperature affect the characteristics of human populations by influencing who survives gestation.

### Methods

#### Variables and Data

We acquired annual birth counts of males and females as well as birth cohort life span for Sweden, Norway, Finland, and Denmark from the Human Mortality Database (HMD) (www.mortality.org). Birth registry data for all four countries allowed calculating a sex ratio time series dating to 1865. We computed the secondary sex ratio by summing all male births across the four countries in each year and dividing this value by the sum of all female births.

We calculated cohort life span at age 1 year through the following steps. We retrieved, from the HMD cohort life tables, the standardized number of individuals surviving to age 1 year (i.e., \(L_1\)) and the standardized total person-years remaining for individuals that survived to age 1 (i.e., \(T_1\)). We also retrieved the HMD estimates of annual counts of individuals who survived to age 1 year. We calculated the total person-years remaining for individuals that survived to age 1 by applying the standardized values to the annual population counts. We then summed these person-years across the four countries and divided this value by the sum, also across four countries, of the population counts of individuals aged 1.

Growing concern over climate change has led to the validation and publishing of historic climate data. Much of this work has focused on Scandinavia, where scientists maintained continuous instrument-based measurements of surface temperature from as early as the mid-18th century. We used two criteria in selecting among several available temperature series for our tests. First, we wanted series that climate scientists had validated through well described procedures and made widely available to researchers like us and those who might replicate our work. Second, we wanted series that gauged temperature in northern as well as southern latitudes. As noted above, we chose a series based on instruments in the Torneåleden region of Sweden (18) (i.e., \(-68^\circ\) north) and another derived from instruments near Stockholm (19) (i.e., \(-59^\circ\) north).

#### Statistical Analyses

Our correlational tests turn on whether the observed sex ratios and male cohort life span vary, in the direction predicted by theory, from their statistically expected values in the same years that temperature varies from its expected values. Such tests typically use the mean of a dependent variable as its expected value. Cohort sex ratios and life span, however, often exhibit autocorrelation, including trends, cycles, and the tendency to remain elevated or depressed after high or low values. Autocorrelation complicates...
correlational tests because the expected value of an autocorrelated series is rarely its mean.

Researchers typically respond to this problem by identifying autocorrelation and expressing it as an effect of earlier values of the dependent variable itself. The residuals from these equations exhibit no autocorrelation. The analyst can, therefore, add the independent variables to the equation to determine whether their coefficients differ from zero in the hypothesized direction. Removing autocorrelation from the independent variable has the added benefit of precluding type I errors that could otherwise result from third variables that exhibit trends, seasonality, or other patterns.

Our test of the hypothesized relationship between temperature and the sex ratio proceeded through the following steps.

1. We used strategies attributed to Box and Jenkins (21) to identify and model autocorrelation in the sex ratio. The strategy, autoregressive, integrated, moving average (i.e., ARIMA) modeling, draws from a very large family of models to empirically specify autocorrelation in time series. Autoregressive parameters typically express long-term memory in a series such that high or low values persist, although diminish, over at least several time periods. Moving average parameters gauge short-term memory of outliers. Integration induces secular trends and strong cycles that must be removed by differencing before modeling autoregressive and moving average behavior.

2. We specified the test equation by adding the annual temperature variable to the model resulting from Step 1. We specified the weather variable such that we could detect an association between temperature in year $t$ and cohorts born in that year as well as those born in year $t+1$ because fetuses in gestation during year $t$ could have been born early in the next year. The effect of cold temperature on gestation in a given year can, in other words, persist into the next, and our tests capture such persistence.

3. We estimated the equation resulting from Step 2 and inspected the error terms for autocorrelation. When needed, we included additional ARIMA parameters and estimated the resulting equation,

$$\nabla^c Y_t = c + \frac{\omega \nabla^d X_t}{1 - \delta B} + \frac{(1 - \theta \delta B)^q}{(1 - \phi B)^q} a_t,$$

where $\nabla$ is the difference operator that indicates differencing of a series (i.e., values at subtractions from values at $t+q$); to remove any secular trends or cycles; $Y_t$ is the sex ratio for the cohort born during year $t$; $c$ is the mean, if significantly ($P < 0.05$; two-tailed test) different from 0, of the observations; $X_t$ is the temperature variable, defined above, for year $t$; $\omega$ is the effect parameter for the temperature variable; $\delta$ measures the proportion of $\omega$ that carries into year $t+1$ because a fraction of infants in gestation during year $t$ were born in year $t+1$; $\theta$ is the moving average parameter; $\phi$ is the autoregressive parameter; $B$ is the “backshift operator” that yields the value of the series it conditions at time $t - p$ for the autoregressive parameter or $t - q$ for the moving average parameter; and $a_t$ is the error term for month $t$.

4. We specified a final model by removing any variables with coefficients that failed to reach significance at Step 4. We then estimated the final equation.

Our test of the hypothesized inverse association between temperature and male cohort life span proceeded as above except female cohort life span was included as a predictor in the model. Including female cohort life span controlled for the effect of unmeasured confounders that affected the both males and females over the test period.

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