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Authors

Catalano, Ralph
Bruckner, Tim
Smith, Kirk R.

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Ambient temperature predicts sex ratios and male longevity

Ralph Catalano, Tim Bruckner, and Kirk R. Smith*

School of Public Health, University of California, Berkeley, CA 94720-7360

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The theory that natural selection has conserved mechanisms by which women subjected to environmental stressors abort frail male fetuses implies that climate change may affect sex ratio at birth and male longevity. Using time series methods, we find that cold ambient temperatures during gestation predict lower secondary sex ratios and longer life span of males in annual birth cohorts composed of Danes, Finns, Norwegians, and Swedes born between 1878 (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.

climate change | global warming | natural selection | Scandinavia | time series

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 male 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 Scandinavian life tables) and 1914 (the last birth cohort for which male life span can be estimated) [University of California Berkeley and Max Planck Institute for Demographic Research (2007) Human Mortality Database, www.mortality.org]. We use data from these four countries because they provide a unique combination of high-quality vital statistics as well as continuous instrument-based measurements, kept since the mid-19th century, of surface temperature. Empirical research, moreover, confirms the importance of ambient temperature to the health and well being of populations in this region (16, 17).

We use temperature data that climate scientists have validated (18, 19) through well described procedures and that gauge temperature in northern as well as southern latitudes in our test region. The data, the longest available time series of instrument-based measurements of surface air temperature in the world, come from the Tornedalen region of Sweden (i.e., $\approx 68^\circ$ north) (18) and from instruments near Stockholm (i.e., $\approx 59^\circ$ north) (19). Climate scientists have calculated daily, monthly, and annual average temperatures from these instrument-based data. We use the average of the two annual series as our independent variable.

We specified our temperature 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 in one year could have been born in the next. 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.”

Results

Mean annual temperature ranged from 0.6125°C to 4.8792°C over the years 1865 through 1914 [3.3520 ± 1.0006 (mean \pm SD)] (see Fig. 1). The sex ratio variable ranged from 1.0471 to 1.0617 over the test period (Fig. 2). Cohort life span varied from 54.57 to 63.72 years for the males and 56.59 to 70.73 for the females (Fig. 3).

Consistent with the culled cohort argument, the annual secondary sex ratio in Scandinavia rose with warmer, and declined with colder, ambient temperatures ($P < 0.0001$; see Table 1). The association persisted, although attenuated, into the following year. The sex ratio exhibited autocorrelation in that “echoes”

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*To whom correspondence should be addressed. E-mail: krksmith@berkeley.edu.

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Table 1. Final models of the secondary sex ratio and male cohort life span as a function of temperature in year of birth and of autocorrelation

Variables	Secondary sex ratio	Male cohort life span
Mean	1.0167* (0.0122)	None
Female cohort life span	Not applicable	0.6616* (0.0380)
Change in dependent variable associated with increase of 1°C in ambient temperature	0.0010* (0.0002)	−0.0377* (0.0155)
Proportion of coefficients from above row persisting into subsequent year	0.9168* (0.0406)	None
Parameters needed to express autocorrelation in the dependent variable	Moving average parameter at 5 years 0.5633* (0.1217)	First differencing Autoregressive parameter at 5 years −0.3838* (0.1588)

*, $P < 0.05$; two-tailed test. Standard errors are in parentheses.

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., $\approx 167,000$), 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 heat 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 cull 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 heretofore 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.

Complete cohort life table data in all four countries begins in 1878 and ends in 1914 with the birth of the last cohort in which sufficient deaths have occurred to estimate life span. Consistent with the earlier literature (15), we chose male life span at age 1 year rather than life span at birth as our other dependent variable because culling induced by unexpectedly cold temperature could presumably act on newborn males as well as on male fetuses.

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 in life table labeling conventions) as well as the standardized total person-years remaining for individuals that survived to age one (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 Tornedalen region of Sweden (18) (i.e., $\approx 68^\circ$ north) and another derived from instruments near Stockholm (19) (i.e., $\approx 59^\circ$ 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 dependent 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,

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

where ∇^d is the difference operator that indicates differencing of a series (i.e., values at t subtracted from values at $t + d$) 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 ; ω is the effect parameter for the temperature variable; δ measures the proportion of ω that carries into year $t + 1$ because a fraction of infants in gestation during year t were born in year $t + 1$; θ is the moving average parameter; ϕ 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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