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Polygenic Scores Mediate the Jewish Phenotypic Advantage in Educational Attainment and Cognitive Ability Compared With Catholics and Lutherans

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A newly released multivariate polygenic score for educational attainment, cognitive ability, and self-rated mathematical ability in the Wisconsin Longitudinal Study was examined as a mediator of the group difference between Jews ($n = 53$) and 2 Christian denominations, Catholics ($n = 2{,}603$) and Lutherans ($n = 2{,}027$), with respect to educational attainment, IQ, and performance on a similarities measure. It was found that the Jewish performance advantage over both Catholics and Lutherans with respect to all 3 measures was partially and significantly mediated by group differences in the polygenic score. This result is consistent with the prediction that the high average cognitive ability of Jews may have been shaped, in part, by polygenic selection acting on this population over the course of several millennia.

Public Significance Statement
Ashkenazi Jews exhibit high levels of general intelligence. The hypothesis that differences in general intelligence between Jews and Catholics and Lutherans is partially mediated by polygenic scores for educational attainment was tested. The results support the hypothesized partial mediation.

Keywords: general intelligence, polygenic scores, religious groups

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This research uses data from the Wisconsin Longitudinal Study (WLS) of the University of Wisconsin–Madison. Since 1991, the WLS has been supported principally by the National Institute on Aging (AG-9775, AG-21079, AG-033285, and AG-041868), with additional support from the Vilas Estate Trust, the National Science Foundation, the Spencer Foundation, and the Graduate School of the University of Wisconsin–Madison. Since 1992, data have been collected by the University of Wisconsin Survey Center. A public use file of data from the Wisconsin Longitudinal Study is available from the Wisconsin Longitudinal Study, University of Wisconsin–Madison, 1180 Observatory Drive, Madison, Wisconsin 53706, and at http://www.ssc.wisc.edu/wlsresearch/data/. The opinions expressed herein are those of the authors.

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Jews, and Ashkenazi Jews in particular, exhibit possibly the highest group mean for IQ of any population. Systematic reviews of the Jewish IQ average indicate that it falls between 109 and 115 (Lynn, 2011), with the difference between Jewish and non-Jewish populations being greatest on the more highly *g*-saturated measures—indicating that the advantage is primarily on the underlying general cognitive ability (GCA) factor (Dunkel, 2014; te Nijenhuis, David, Metzen, & Armstrong., 2014). Jews also exhibit a strong tilt toward verbal and quantitative reasoning and away from visuospatial ability (Lynn, 2011; Nisbett, 2009). These psychometric advantages are likely a major factor associated with their high representation in elite professions, such as media, academia and among those winning Nobel Prizes (Cofnas, 2018; Lynn, 2011; Murray, 2007).

Two major theories have been proposed to account for the Jewish IQ advantage. The first is based on the observation that their capabilities and even affinities for various economic niches may have been shaped by selective pressures acting on these populations over hundreds of years, and thus, their advantage might be genetic (MacDonald, 1994). Cochran, Hardy, and Harpending (2006) proposed that in the Middle Ages, Jews in Europe were essentially pigeonholed into certain social and economic niches by virtue of religious and social pressure. This in turn led to culture-gene coevolution shaping the Jewish ability structure. Cochran et al. (2006) posited that the primary genetic locus of this selection might have been rare variants associated with sphignolipid (lipid storage) disorders, common among Jews, such as Tay-Sachs disease. This theory has not been tested directly; however, there are hints in the data that those who are heterozygous for the Tay-Sachs allele in particular appear to have higher levels of educational attainment, when compared with heterozygotes for other diseases (Kohn, Manowitz, Miller, & Kling, 1988). This finding is at least in line with predictions from the theory.

The second major theory is that the Talmudic tradition among Jews incubates high ability via the construction of a culture that emphasizes learning and abstract reasoning and that is transmitted from generation to generation vertically as an environmental cause (Botticini & Eckstein, 2012; Ferguson, 2007). This model purports to be able to account for the Jewish advantage in ability and educational achievement without recourse to genetic selection (Ferguson, 2007). This model should be considered speculative because shared environment and in particular vertical transfer effects are generally small or zero for GCA and are not generally found in adulthood (Bouchard, 2013; Hatemi et al., 2010; Eaves et al., 1999; Odenstad et al., 2008).

An additional possibility, apparently thus far not considered at length, is that polygenic selection acting over the course of several thousand years and on multiple genetic variants, which cumulatively account for variance in GCA, may also have contributed to the group difference in ability between Jews and non-Jews. This could have been engendered by factors such as cultural group selection favoring higher group-level GCA as an adaptation to heightened intergroup competition, as envisaged by MacDonald (1994). Culture-gene coevolution involving niche provisioning and specialization of a sort envisaged by Cochran et al. (2006) may also have been a source of this polygenic selection. Indeed, the endogenous cultural forces identified by proponents of culture-only theories (such as the development and vertical transmission of scholarship and rule-based systems of social organization, e.g., Ferguson, 2007) might themselves have been sources of selective pressure acting on these populations over time, with fitness payoffs having accrued to those most capable of learning and using such innovations. Consistent with this, MacDonald (1994) has noted that the Talmud contains injunctions against marriage involving those who exhibit signs of low social status (specifically the *'am-ha-ares*, or the ritually unclean). The precise nature of the selective pressures that might have shaped (in particular) Ashkenazi Jewish GCA are not known with any certainty at present. A necessary criterion for invoking these in the first place is the demonstration of systematic differences between Jews and non-Jews with respect to salient genetic variants.

Selection acting on polygenic scores (PGS)[1] can substantially shift the population means of traits in relatively short amounts of time. For

[1] Polygenic scores are constructed using results from a GWAS of the trait of interest. Essentially, they are the sum of the alleles multiplied by their beta on the trait from the regressions.

example, in the population of Iceland, polygenic selection against variants predictive of educational attainment may have reduced the IQ of the population by 0.3 points per decade, or 2.1 points over 70 years (Kong et al., 2017). Indeed, this may even be an excessively conservative estimate (for alternative calculations see Woodley of Menie, Figueredo et al., 2017). When comparing ancient Bronze and Early Iron Age genomes, sourced from Eurasia, with those from ancestrally matched modern European populations, significant differences in the frequencies of positively predictive alleles for educational attainment and GCA have also been found, favoring the modern populations. This is consistent with a long-term Holocene selective sweep in these populations, favoring higher GCA (Woodley of Menie, Younuskunju, Balan, & Piffer, 2017). Even among a subsample of the ancient genomes for which radiocarbon dates were available, significant associations between sample age and positive allele frequency were noted across a span of 3250 years (Woodley of Menie, Younuskunju et al., 2017).

Given the recent availability of high-quality PGS on educational attainment and related cognitive phenotypes from large samples (Lee et al., 2018), some of which contain Jews, it should be possible to carry out a genetically informed study on the etiology of the group difference in GCA and educational attainment between Jews and non-Jewish Caucasians of other religious denominations (Catholic and Protestant). The comparison of these two groups is desirable because of the following: (a) evolutionary theories of high Jewish ability have emphasized a role for intergroup competition and niche provisioning between these two groups in particular (Cochran et al., 2006; MacDonald, 1994, 1998); and (b) population differences studies using PGS are potentially sensitive to linkage decay, which results from recombination randomizing the associations between alleles on chromosomes over time (Bush & Moore, 2012). This is problematic when the single-nucleotide polymorphisms are noncausal variants that are flagged by the genome-wide association study (GWAS) procedure because they happen to be in consistent linkage phase with the causal variants (Zanetti & Weale, 2016). This problem reduces the utility of PGS when used for populations relatively distant to the training sample (Li & Keating, 2014; cf. Piffer, 2015). Ashkenazi Jews and non-Jewish Caucasians have been found exhibit relatively low levels of genetic differentiation. Tian et al. (2008) found that Ashkenazi Jews exhibited F_{ST} values ranging from .0040 when compared with Italians to .0144 when compared with Basque (across eight Caucasian populations, the unweighted F_{ST} average is .009). This means that Ashkenazi Jews exhibit little genetic differentiation, relative to non-Jewish Caucasians (F_{ST} values ranging from 0 to .05 correspond to little genetic differentiation; Hartl & Clark, 1989). Values this low also correspond to negligible amounts of prospective linkage decay because this parameter has been found to scale quite strongly with F_{ST} (Scutari, Mackay, & Balding, 2016).

To test the polygenic selection theory, a large sample of predominantly Caucasian individuals of European descent from the United States, which also contains Jews will be utilized in a mediation analysis. We first examine the group difference between Jews and non-Jews belonging to two large Christian denominations on PGS and indices of GCA and, second, test examines the degree to which a PGS capturing phenotypic variance in educational attainment, IQ, and self-reported mathematical aptitude ($\text{POLY}_{\text{MTAG}}$), mediates the group difference. Full mediation is not expected for two reasons. First, the PGS used does not account for all of the variance in the phenotypes of interest (5–10%; Lee et al., 2018) and is thus a rather noisy estimate of the genetic potential. Second, there may also be contributions stemming from cultural (i.e., environment) causes and additional nonadditive genetic causes not captured by the PGS (which captures additive effects only), such as the heterozygote advantage for certain carriers of sphingolipid disorders posited by Cochran et al. (2006). Some indication of polygenic mediation is nevertheless what would be expected if polygenic selection has played a role in shaping the group differences with respect to measures of cognitive ability.

Method

Sample and Religious Orientation

Data were sourced from the Wisconsin Longitudinal Study (WLS). The WLS is a longitudinal study of randomly sampled Wisconsin high school students beginning in 1957; the last wave of data collection was in 2011. The 1957 sample included 10,317 Wisconsin high school seniors. The sample is overwhelmingly of European descent (Herd, Carr, & Roan, 2014; Sewell, Hauser, Springer, & Hauser, 2004), reflecting mid-20th century state demographics.

In the 1975 wave of data collection, participants were asked, "What was the main religious preference of your family in 1957?" A total of 76 options were coded, but for the public release data set, the codes were collapsed into 17 categories. For the current analyses, three of the 17 categories were used (Catholic, Lutheran, and Jewish). Catholic and Lutheran were chosen because they are different religious orientations yet were also most strongly represented in the original sample, $n = 3690$ for Catholic (29.8% of the WLS sample) and $n = 2619$ for Lutheran (21.2% of the WLS sample). No other identifiable single orientation or denomination accounted for more than 5% of the WLS sample. Beginning in 1977, a subsample of the original participants' siblings was also enrolled in the study with iterations of sibling enrollment occurring in the subsequent waves. Among the original participants and siblings, we first selected only those who had undergone genotyping. If both an original participant and a sibling had undergone genotyping, we then randomly selected from among the pair for inclusion in the analyses. After these selection criteria, the sample included 2,603 Catholics (51.2% female), 2,027 Lutherans (50.5% female), and 53 Jews (58.5% female).

Genotyping

A total of 9,012 WLS study participants were genotyped on the Illumina HumanOmniExpress array as part of the recent GWAS for IQ, educational attainment, and self-reported mathematical ability (Lee et al., 2018). The genetic samples came from saliva collected first in 2007–2008 and then during the course of home interviews conducted initially in March 2010. For full information on sampling and genotyping procedures, see https://www.ssc.wisc.edu/wlsresearch/documentation/GWAS/Herd_QC_report.pdf. In the present study, the educational attainment polygenic score was used. The educational attainment phenotype was defined based on the International Standard Classification of Education 1997 United Nations Educational, Scientific and Cultural Organization classification, which is associated with seven, internationally comparable categories of educational attainment, rescaled as U.S. years-of-schooling equivalents (Lee et al., 2018). The polygenic score for educational attainment used in this analysis (PGS_EA3_MTAG) was computed using multivariate analysis of educational attainment along with data on cognitive performance (evaluated using a single measure IQ test from U.K. BioBank along with various neuropsychological functioning tests and IQ subscales from Cognitive Genomics Consortium) in addition to self-reported mathematical ability and highest mathematics class successfully completed. This multivariate PGS was selected because it likely captures the largest degree of shared (i.e., GCA-like) genetic variance common to these cognitive phenotypes. The PGS were standardized (transformed to z-scores) to aid interpretation.

Measures of Cognitive Ability in WLS

Henmon-Nelson Test of Mental Ability. The Henmon-Nelson Test of Mental Ability is a 30-min test consisting of 90 items of increasing difficulty in spatial, verbal, and mathematical ability. Test administration was standardized across the state of Wisconsin during the first wave of data collection in 1957. The reliability of the test is estimated to be high ($\alpha \approx .95$; e.g., Ganzach, 2016; Hansen, 1968; Harley, 1977) and scores on the Henmon-Nelson test exhibit a strong association ($r \approx .80$ - $.85$) with full IQ test scores (e.g., Wechsler Adult Intelligence Scale [WAIS]) scores (Klett, Watson, & Hoffman, 1986; Kling, Davis, & Knost, 1978). The WLS data file includes a variable labeled as preferred measure of IQ based on the participant's Henmon-Nelson test score, and this variable was the one used in the current analyses. It was found that siblings had a slightly higher score than the original participants. Therefore, the scores for each group were standardized (transformed into z-scores) prior to merging. Once the scores were merged, the scores were transformed again so that the scores represent IQ values.

Educational level. Education level was measured in 1975 when participants were in their mid-30's. Participants reported their level of education using a 9-point scale anchored at *high school graduate or less*, *less than one year of college*, and *PhD, MD, other doctorates not previously included, and post doctorate education*.

Similarities. During the 1992–1993 wave of data collection when participants were in their early 50's, they were interviewed over the telephone. The interview included a brief cognitive assessment. Eight items from the WAIS similarities subtest were also used as the assessment tool (sample item: In what way are air and water alike?). A total score based on the eight items was used in the analyses. The total was standardized by transforming the values into *z*-scores.

Results

The correlation matrix for the study variables for the full study sample can be seen in Table 1. As seen in Table 1, all the variables were significantly and positively correlated; most notably this includes the correlations between the PGS and the three measures/proxies of GCA.

The descriptive statistics for the PGS and the measures of cognitive ability for the three religious groups can be seen in Table 2. Additionally, four one-way analysis of variance models were run with religious orientation (Jewish, Catholic, Lutheran) as the independent variable with the dependent variables being the PGS and the three measures of cognitive ability. As seen in Table 2, all of the analyses of variance were significant, with Tukey's-b post hoc tests showing that the Jewish group differed from the Catholic and Lutheran groups on each variable, whereas the Catholic and Lutheran groups did not differ from each other on any variable. Note that the difference between Jews and the Catholic and Lutheran groups is larger (as measured by standard deviation units) for educational attainment. This could be due to the measurement error in measures of GCA or the heightened effect of differences between groups in genetic composition and cultural importance placed on education.

Furthermore, after creating groups of equivalent size, we conducted a random sampling analysis by taking a subsample of Christians the same size as the Jewish sample and then ran *t* tests looking at the group differences in PGS. This was done 1,000 times. Each time the *p* value of the *t* test was recorded. The plot of the log10 (*p* values) can be seen in the online supplemental material. The mean *p* value for equivalent groups is $p < .000000001$. Thus, it is reasonably concluded that the effect is reliable. To illustrate the differences between the Jewish and two Christian groups, we combined the two Christian groups and computed Cohen's *d* for PGS and IQ. For PGS Cohen's $d = 1.33$, which is a very large effect size. For IQ, Cohen's $d = .57$, which is a medium effect size. These group differences are portrayed in Figure 1.

Next, we tested for the possibility that the PGS mediates the association between religious orientation and cognitive ability. The mediation model and the associated components can be seen in Figure 2. The PROCESS macro for SPSS (Hayes, 2012) was utilized for testing for mediation, and following the recommendations of Zhao, Lynch, and Chen (2010), the output from the bootstrap test for the indirect effect was used as an indicator of mediation. Prior to analyses, two dummy coded religious orientation variables were created; one variable (Catholic = 1 and Jewish = 2) and the other (Lutheran = 1 and Jewish = 2). Thus, for each GCA index, two analyses were performed: first with the Jewish-Catholic dummy variable and second with the Jewish-Lutheran dummy variable. The dummy coded religious orientation variable was entered as the X variable, the PGS was entered as the mediator, and the GCA index was entered as the Y variable. In PROCESS the number of bootstrap samples was kept at the default of 5,000, the confidence intervals were kept at 95%, and the mediation model was set to the specified model (i.e., Model 4).

Zhao et al. (2010) recommend reporting the mean value of the indirect path ($a \times b$) and the associated 95% confidence interval from the bootstrap method. As seen in Table 3, the confidence intervals for the indirect path for each

Table 1
Bivariate Correlations Between Study Variables

Variables	PGS	IQ	Years of education	Similarities
PGS	—			
IQ	.31	—		
Educational level	.28	.44	—	
Similarities	.21	.46	.36	—

Note. PGS = polygenic scores. All correlations are significant at $p < .001$, $N = 5513–6256$.

Table 2
Descriptive Statistics and ANOVA Results by Religious Orientation

Variables	Religious Orientation			ANOVA
	Jewish	Catholic	Lutheran	
PGS	1.37 (1.07)	.01 (.99)	−.04 (.98)	$F(2, 4680) = 52.88, p < .001$
IQ	109.72 (14.36)	101.48 (14.43)	101.36 (14.66)	$F(2, 4554) = 8.41, p < .001$
Educational level	5.62 (2.12)	2.45 (2.17)	2.39 (2.13)	$F(2, 4183) = 51.57, p < .001$
Similarities	.42 (.94)	.06 (.98)	.02 (.96)	$F(2, 4438) = 4.34, p < .05$

Note. PGS = polygenic scores. Standard deviations are in parentheses.

analysis did not include zero, indicating significant mediation. Zhao et al. (2010) also recommend reporting the unstandardized regression coefficients to enhance the interpretation of the results. For example, it was consistently found, across analyses, that moving from Lutheran or Catholic to the Jewish religious category (path *a* in Table 3) resulted in a .21- or .22-unit increase in PGS. An additional analysis, included in the online supplemental material, showed that results remained when controlling for family socioeconomic status.

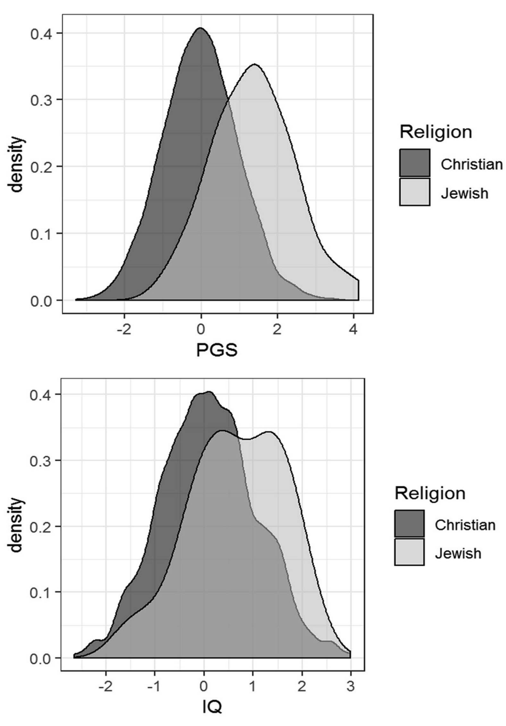

Figure 1. Distribution of Jewish and Christian IQ and PGS.

Discussion

In the present study, we found that Jews in a large cohort had higher GCA, educational attainment, and similarities scores than non-Jews and that this group difference was partially mediated by a PGS constructed from a recent GWAS for GCA-related traits. There are a number of limitations to the present analysis. First, the number of Jews was relatively small at $n = 53$ and may therefore be unrepresentative, although it appears that contemporaneous Wisconsin Jews are fairly representative of the U.S. Jewish population in terms of socioeconomic characteristics (see Appendix for analysis). Second, the PGS used was only a poor estimate of the genetic potential, which would by definition be equal to the additivity value of IQ in terms of trait-variance explained. Depending on which part of the variance of the genetic potential this proxy captures, it might affect the results in unknown ways. Third, we relied on religious denomination as a proxy for Jewish ancestry. If the ubiquitous negative relationship between IQ and religiosity that has been noted in Western populations (e.g., Kanazawa, 2010; Zuckerman, Silberman, & Hall, 2013) extends to the Jewish population, then it might be the case that by excluding nonreligious Jews (who will simply not self-identify as such for the purposes of listing religious affiliation), we lowered the mean IQ for the Jewish sample. We believe this to be a minor problem because relatively few people, Jews included, were nonreligious in 1975 when the survey item was asked. Furthermore, the Christian comparison group has the same problem, which means both Group IQs are biased in the same direction and the relative difference is thus not likely to be strongly

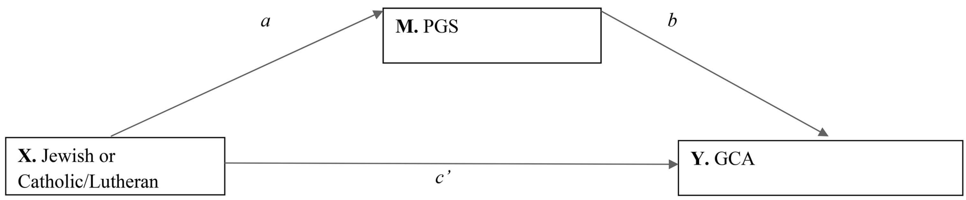

Figure 2. Generalized mediation model.

affected (Kanazawa, 2010). Fourth, the PGS was derived from a GWAS that consisted mostly of European descent peoples, with probably only a minor contribution from Jews. To the degree in which the Jewish population differs genetically from the training sample, this may reduce the validity of the derived PGS. However, as was discussed in the introductory text, Ashkenazi Jews (a recently admixed population) are very closely related to the training sample used in the GWAS (Tian et al., 2008), and any reduction in PGS validity is thus quite minimal, given that F_{st} is strongly and positively associated with linkage decay (Scutari et al., 2016). Given the above limitations, we consider the present results to be tentative and in need of replication with better PGS data and larger samples of the Jewish population. Our findings nonetheless yield an initial positive indication of the polygenic selection model and critically indicate that in the case of the Jewish versus non-Jewish Caucasian comparison, the same source of genetic variance that gives rise to of individual differences in GCA also contributes substantially to the group difference. This militates against a substantive role for Factor Xs (i.e., factors that create differences between groups but do not influence individual-level variation) in the etiology of this particular group difference (for discussion of this, see Jensen, 1998, p. 446).

Table 3
Mediation Analyses

Variables	$a \times b$	95% CI	a	b	C
IQ					
Jewish-Catholic	5.75	[4.31, 7.33]	.21	26.90	2.61
Jewish-Lutheran	5.95	[4.52, 7.48]	.21	29.00	2.28
Educational level					
Jewish-Catholic	.74	[.55, .95]	.21	3.48	2.24
Jewish-Lutheran	.73	[.53, .95]	.22	3.29	2.28
Similarities					
Jewish-Catholic	.27	[.19, .35]	.21	1.26	.09
Jewish-Lutheran	.26	[.18, .34]	.22	1.19	.14

Note. CI = confidence interval.

It finally needs to be stressed that these findings do not militate against the other models considered in the introductory text. Rare variants associated with lipid storage disorders may indeed confer a heterozygote advantage, which may have augmented the Jewish Group GCA above that which would be predicted by differences in the level of PGS alone, perhaps accounting for the relatively higher frequencies of these disorders in this population. Direct tests of this model still need to be carried out, however.

Whereas purely cultural vertical transmission models involving the passing down across the generations of the Talmudic Tradition are unlikely to be causative of the Jewish advantage in GCA, it is possible that the Jewish cultural practice of scholarship coevolved with, and indeed influenced, via culture-gene coevolution, Jewish group-level characteristics, including their high average GCA (MacDonald, 1994). It is important to also stress the potential role played by social epistasis (the moderating effect of a group's average PGS on the expressivity of an individual's PGS on a trait of interest, as captured by the correlation between the PGS and that trait) in maintaining traits within a group. Social epistasis effects have been found to influence educational attainment in human populations (Domingue et al., 2018); the patterns and rules governing these genetic interactions might therefore constitute a source of genetic nurture and may potentially be an important component of the Jewish cultural inheritance system that could be profitably researched in future work.

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(*Appendix follows*)

Appendix

Supplemental analysis 1: The representativeness of Wisconsin Jews

It is possible, although unlikely, that the Jewish population in Wisconsin is an outlier in terms of socioeconomic status among Jewish populations in the US. This possibility is difficult to investigate since there are no large studies of Jewish educational attainment by state. Instead, to get an approximate estimate, we look at the income of federal employees in 2017 and compare the income of Jews to the income of non-Jews in different states. The assumption is that if the Jewish population in Wisconsin in previous generations was an outlier compared to other states, we would also see a higher average income among the Jewish population in Wisconsin in 2017. We acquired 446,603 federal salaries of people living in the largest cities in the US from the Federal DataCenter, including 14,828 salaries of people with Jewish ancestry as determined by surname. For every person we calculate the relative salary, which is the salary of that person divided by the mean salary in the location at which the person works. Finally, we look at whether the relative salaries of Jews in Wisconsin cities is higher than the relative salaries in other US states. We find that the mean relative salary of Jews compared to non-Jews is the same in Wisconsin as the US average. This finding holds when using log transformed salaries. The boxplots for the relative log transformed salaries are shown in Figure A1.

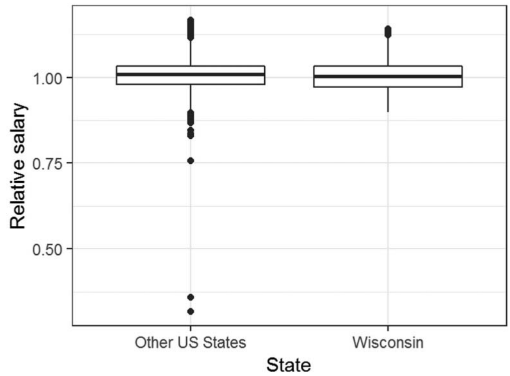

Figure A1. The relative (log-transformed) salaries of Jews compared to non-Jews in Wisconsin vs other US states.

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