CHAPTER 7

The Social Epistasis Amplification Model: A Diachronic Test and Expansion of Theoretical Foundations

Introduction

Assuming that deleterious mutations have been accumulating in Western populations following industrialization, it remains to be established whether this is a serious problem. The eminent geneticist James Crow (1997) did not seem to think it is: "[Deleterious mutation accumulation] is a problem with a long time scale; the characteristic time is some 50–100 generations, which cautions us against advocating any precipitate action. We can take time to learn more. Meanwhile, we have more immediate problems: global warming, loss of habitat, water depletion, food shortages, war, terrorism, and especially increase of the world population" (p. 8385). As we have seen, other geneticists do not agree: "[T]he recurrent load of mutations imposed on the human population [may drag] fitness down by … 1% per generation"; "A fitness decline of a few percent on the timescale of a century is on the order of the rate of global warming, and that is part of the problem" (Lynch, 2016, pp. 872, 874). In any event, both the optimists *and* pessimists in this debate may be vastly underestimating the extent of the problem.

Virtually all attempts to model the fitness costs of deleterious mutation accumulation assume that the harmful effects of mutations are limited to the organisms that carry them. Therefore, it would be expected from these models that in a population accumulating deleterious mutations, fitness losses are merely a function of the proportion of the population carrying these mutations and the mutational burdens of the carriers. But Sarraf and

M. A. Sarraf et al., *Modernity and Cultural Decline*,
https://doi.org/10.1007/978-3-030-32984-6_7

Woodley of Menie (2017) and Woodley of Menie, Sarraf, Pestow, and Fernandes (2017) observe that this is not necessarily the case. Large experimental literatures document a phenomenon known as *social epistasis*, or genomic transactions that occur between or among organisms, such that the genome of one organism, or the genomes of two or more organisms, influences the gene expression of another organism or other organisms (see, e.g., Domingue & Belsky, 2017; Linksvayer, 2007). It has been experimentally demonstrated that social-epistatic transactions regulate the expression of genetic variants underlying fitness-salient traits in at least some social species (e.g. Baud et al., 2017; Teseo, Châline, Jaisson, & Kronauer, 2014). The optimum expression of genes associated with a given trait in members of at least some social species is contingent upon social exposure to individuals within the population exhibiting different levels of expression of the same or other genetic variants (Linksvayer, 2007 gives the example from an experiment involving three ant species of "adult worker size [being] determined by an interaction between the genotypes of developing brood and care-giving workers" [p. 1]. Such social-epistatic effects can arise via *coevolution* of "socially interacting genes" (Linksvayer, 2007, p. 1), which may give rise to correlations between the frequencies and/or expression levels of genetic variants among individuals within a population.

Social-epistatic effects can bias heritability estimates for at least some traits in certain social species, where the genetic effects on trait development or expression are partly due to *indirect genetic influences* arising from the *social genome* (Domingue & Belsky, 2017). Experimental evidence involving mice reveals that social genetic variation may account for up to 29% of the variance in particular phenotypes, such as anxiety and immune function; moreover, effects of social genetic variation were found to associate with changes in mouse gene expression, consistent with the presence of social-epistatic effects (Baud et al., 2017). In human populations, recent research indicates the presence of social-epistatic effects on educational attainment, though this research did not involve direct testing for molecular intermediaries causing changes in gene expression, which is necessary to confirm the presence of social-epistatic effects (Domingue et al., 2018).

An apparently little-appreciated consequence of social-epistatic effects is that they present deleterious mutations with a potentially very large fitness target—one that reaches beyond the individual organism and into the *extended phenotype* (Dawkins, 1982) of that organism's population (in humans, we can safely say that culture makes up at least part of a population's extended phenotype). The potential for mutations present in one organism to affect patterns of gene expression, and thus phenotypic traits, in (multiple) other organisms has something of a parallel in the fact that mutations have *pleiotropic effects* within organisms. As mentioned in the last chapter, a gene exhibits pleiotropy if it influences more than one phenotypic trait. This has been posited as an explanation for the existence of the *f* factor of general fitness, discussed in the previous chapter (Houle, 2000; Miller, 2000).

The extension of the *f* factor to the multiple domains of group functioning that characterize the human population-level extended phenotype suggests that the costs of deleterious mutation accumulation may be far more severe than ordinarily thought. Woodley of Menie, Sarraf, et al. (2017) termed mutations with negative fitness effects on both carriers and, through social epistasis, other organisms, "spiteful mutations," as such variants are globally costly to fitness. Their *social epistasis amplification model* (SEAM) posits that social-epistatic amplification of spiteful mutations' effects has the potential to rapidly and profoundly reduce the fitness of entire populations. Indeed, the SEAM was originally proposed as a partial explanation of the demographic transition,[1] a process that has reduced proxies of group-level fitness far more precipitously than standard mutation-accumulation models would predict: "Total fertility rates in the USA for example fell from 3.7 between 1955 and 1959 to 1.8 between 1975 and 1979"[2] (Woodley of Menie, Sarraf, et al., 2017, p. 183). Moreover, it was argued that the SEAM predicts that certain non- and anti-normative ideologies (in traditional perspective) that negatively associate with fitness, especially for those of high intelligence, such as atheism and certain contemporary Western manifestations of individualizing moral psychologies (see Faria, 2017; Meisenberg, 2019), potentially have their ultimate origin in spiteful mutations, and

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[1] The demographic transition (DT) is a consequence of industrialization, and refers to the movement of populations from high fertility and mortality rates to low fertility and mortality rates. In pre-DT populations, mortality is concentrated in infancy and childhood, and is mostly caused by infectious disease. In post-DT populations, mortality is concentrated in the elderly and is mostly caused by chronic and degenerative diseases (Caldwell, Caldwell, Caldwell, McDonald, & Schindlmayr, 2006).

[2] Hopcroft (2019) objects to certain claims to the effect that low fertility following the DT is maladaptive, but not to claims of the sort that we make in this context: "while below-replacement fertility *is clearly maladaptive for the group*, it is not necessarily maladaptive for individuals" (2019, p. 158; emphasis added).

that the spread of these ideologies may be facilitated through negative social epistasis. Consistent with the predictions of the SEAM, experimental evidence indicates that there are “tipping points” in social convention, such that only ~25% of a group must be committed to some convention to very quickly bring the majority of that group’s non-adopters to take on that same convention (Centola, Becker, & Baronchelli, 2018). While this result needs replication, especially since it is based on analysis of a relatively small sample, it evidences the potentially very rapid rate of cultural change, which suggests a pathway for the effects of deleterious mutations to influence groups in surprisingly little time once such mutations have reached a certain critical frequency in a population.

Thus far, there have only been two attempts to empirically test the SEAM in humans. The first, by Dutton, Madison, and Dunkel (2018), tested the SEAM’s prediction that irreligiosity positively associates with indications of increased mutation load as reflected in markers of developmental instability. Utilizing one such marker (left-handedness; Markow, 1992), these researchers found positive associations with irreligiosity, in line with the predictions of the theory. A second test of the SEAM from Woodley of Menie, Kanazawa, Pallesen, and Sarraf (in preparation) tried to determine if a behavioral correlate of irreligion (operationalized as the opposite of church attendance, or “church absenteeism”) is positively associated with burdens of deleterious mutations using another method. Specifically, it examined two large data sets, each sampled from a different US cohort, for paternal age effects on “church absenteeism” after statistically controlling for a large number of covariates. Paternal age was positively associated with this behavioral correlate of irreligion in the more recent of the two cohorts (born in the 1970s and 1980s) but not the older one (born in the 1930s and 1940s). These findings were interpreted as potentially consistent with the SEAM, since in older cohorts (exhibiting a presumably lower mutation load overall), fitness-enhancing (positive) patterns of social epistasis may have enforced adaptive behaviors even among those born to older parents, who exhibit relatively higher burdens of deleterious mutations. Conversely, in more recent cohorts with higher aggregate loads of harmful mutations and resultantly degraded (and thus negative) patterns of social epistasis, spiteful mutations may be freer to express in the form of maladaptive behavior. Dunne et al. (1997) found a similar effect related to sexual behavior, specifically that the heritability of age at sexual debut rose in the wake of the sexual revolution, that is, the relaxation of traditional norms governing sociosexuality, typically thought to have started in the West around the 1960s–1970s (Inglehart, 1977). Again, this finding may reflect the expression of genetic predispositions toward non-normative behavior upon release from cultural or social-epistatic controls, or the epigenetic activation of such predispositions through negative social epistasis. Nonetheless, with regard to the SEAM, this potential cohort effect should be treated as a prediction, which requires further investigation.

So while preliminary tests of the SEAM in human populations offer some support for the model, they are small in number and have only concerned one of its predictions. More substantial work relevant to the SEAM has been conducted on mice, with results that strongly support its predictions. For example, Crews, Fuller, Mirasol, Pfaff, and Ogawa (2004) found that the distribution of genotypes in the social environment of mice "influence[d] the development of sociosexual behaviors" in the mice (p. 935). The subsequent research of Crews, Rushworth, Gonzalez-Lima, and Ogawa (2009) offers evidence that mouse litter composition has long-term developmental effects on the expression of "aggressive behaviors" in adult mice. More recently, Kalbassi, Bachmann, Cross, Roberton, and Baudouin (2017) found that mice with a mutation related to autistic-like behaviors (deletion of the gene *Nlgn3*) modify the behavior of mice without this mutation, such that the latter act in autistic-like ways. Strikingly, housings of male mice containing carriers of the *Nlgn3* deletion mutation were unable to form normal social hierarchies and exhibited depressed levels of testosterone compared to housings without these carriers; even more interestingly, the behavior of non-carrier mice exposed to carriers normalized after the carrier mice re-expressed *Nlgn3* in relevant brain cells. Sarraf and Woodley of Menie (2017) maintain that these findings are best explained by the SEAM. Furthermore, and as noted in Woodley of Menie, Sarraf, et al. (2017), effects such as these might account for the dynamics that Calhoun (1973) noted in one of his *mouse utopia* experiments (known as "Universe 25"). This experiment involved housing mice in cornucopian conditions to induce substantial population growth and overcrowding, which had the (unintended[3]) effect of minimizing the opportunity for selection to act, necessarily minimizing the opportunity for negative selection specifically. Consistent with the SEAM, complete collapse of the colony, that is, complete loss of group fitness, was preceded by the rise of abnormal mouse phenotypes, which Calhoun termed "the beautiful ones," or

> [a]utistic-like creatures, capable only of the most simple behaviors compatible with physiological survival, emerge out of this process. Their spirit has died ("the first death"). They are no longer capable of executing the more complex behaviors compatible with species survival. The species in such settings dies.[4] (p. 86)

Subsequent experimental work on mice, explicitly informed by the SEAM, has elucidated the specific vector by which carriers of the *Nlgn3* deletion impair the behavior of healthy mice: Mice carrying this mutation secrete a major urinary protein pheromone called Darcin, which induces in non-carriers a socially avoidant phenotype characterized by lack of interest in socially salient olfactory cues and diminished social learning ability (non-carrier mice exposed to carrier mice became far less efficient in marking

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[3] Calhoun's experiments were not informed by evolutionary genetics. Moreover, Calhoun (1973) denied any role for mutations in the social/behavioral disturbances observed in the Universe 25 experiment.

[4] It appears that Calhoun, and other experimenters, had difficulty replicating the colony collapse finding (see Hammock, 1971; Kessler, 1966, while failing to fully replicate Calhoun's Universe 25 findings, documents deviant mouse behavior potentially consistent with negative social-epistatic effects). Calhoun only noticed behavioral abnormalities in mice in his Universe 25 experiment. Similarly, Hammock (1971) found effects consistent with Calhoun's Universe 25 results in a pilot study, but failed to replicate those results in his more involved further experimental work. We surmise that the lack of sophisticated genetic controls in these experiments might have made them insufficiently sensitive to differences in initial conditions—for example, there may have been different levels of homozygosity (inbreeding) and different mouse strains across experiments—which may vary the time needed for spiteful mutations to arise in populations. This could explain the "hit-and-miss" quality of attempts to replicate Calhoun's findings, as well as Calhoun's own trouble achieving the effect.

In experiments that realized or partly realized the "collapse phase" conditions of Calhoun's Universe 25 study, high rates of mortality were noted (Hammock, 1971). One might expect that high levels of mortality would have had the effect of removing deleterious mutations from mouse colonies, allowing them to recover. But if the high mortality was due to spiteful mutational meltdown, as we posit, such mortality, owing to its likely selectively indiscriminate nature, would not enable a recovery (Woodley of Menie, Sarraf, et al., 2017).

territory to facilitate navigation of it) (Bachmann et al., 2018). Even more recently, Cross (2019) presented data indicating that changes in RNA expression in the brain cells of mice seem to result from exposure to mice carrying the *Nlgn3* deletion mutation. This finding offers quite direct evidence of a social-epistatic effect. If Calhoun's "autistic-like creatures" also carried the *Nlgn3* deletion, and this involved negative effects on fitness (as the findings of Kalbassi et al., 2017, indicate it would, given the adverse effects on mouse behavior and physiology that they observed), then this could in part explain the basis of the colony collapse that he observed (Sarraf & Woodley of Menie, 2017; Woodley of Menie, Sarraf, et al., 2017).

In the following, we aim to improve the state of the literature concerning the SEAM applied to humans and to determine if intuitions about Western decline have a substantial and unitary empirical basis. Using temporal data sourced from the US population indicating opportunity for negative selection (through mortality), developmental instability, negative social epistasis, and population fitness, we will test predictions derived from the SEAM. We anticipate that reduction of the opportunity for selection through mortality positively predicts levels of developmental instability (a proxy for mutation load), which in turn positively predict indicators of negative social epistasis, which ultimately negatively predict indicators of the global fitness of the US population. Importantly, we expect that the negative effect of developmental instability on global fitness should be mediated by social-epistatically salient indicators, in that the fitness-depressing effects of deleterious mutations should primarily occur *through* negative social epistasis. Consistent with the broader thesis of this monograph, mental illness and irreligiosity (the latter of which significantly associates with rates of subjective existential nihilism at the national level; Oishi & Diener, 2014) are used as indicators of negative social epistasis. If these predictions are successful, then we would have evidence that the SEAM offers a unified explanation of the major aspects of the apparent crisis of the Western world, from its existential malaise to its anemic fertility rates.

Methods

Analysis

In order to test the SEAM in human populations, we examine the diachronic associations between various indicators that are expected to sequentially predict declining fitness. Four latent chronometric factors will be modeled in this analysis. These include (1) a (proxy) measure of the opportunity for selection through mortality, (2) a measure of phenotypic trends that are hypothesized to at least partly capture the effects of mutation accumulation on developmental stability, (3) a measure of psychobehavioral trends that are hypothesized to at least partly result from negative social epistasis, and (4) a measure hypothesized to at least partly capture changes in the global fitness of the United States population. Data for each of these four categories is used to construct four chronometric factors; each of the four factors involves data from three manifest indicators in order to ensure that the level of aggregation is equivalent across the four factors (see Brunswik, 1952). The composition of these factors will be described in more detail in the succeeding sections.

The factors are computed using unit-weighted factor analysis, which allows for the recovery of highly generalizable factors when either case or variable numbers are low (Gorsuch, 1983). Unit-weighted factors (UWFs) are computed by standardizing the indicator scores and then averaging across the scores, the average becoming the UWF score. UWF loadings are computed by simply correlating the indicator score with the UWF score. Averaging across the standardized scores for each set of time-points furthermore allows for missing data to be multivariately imputed (the average of the non-missing values can be used to impute the missing score in the UWF; Figueredo, McKnight, McKnight, & Sidani, 2000). A form of exploratory path modeling known as Sequential Canonical Analysis (SEQCA; Figueredo & Gorsuch, 2007) is used to examine the sequencing among the predictors, and alternative sequences that can be used to test alternative plausible models. This technique also allows each step of the SEQCA to be statistically controlled for the effects of the natural logarithm of time—thus temporal autocorrelation can be directly controlled and the unique (time-independent) effects among the variables can be examined directly in these models.

Two alternative hypotheses are tested. The preferred hypothesis is that the opportunity for mortality selection chronometric factor (lagged by 25 years, or one "standard" generation) predicts the increase in developmental instability, which predicts the increase in negative social-epistatic psychobehavioral changes, which in turn predicts the decline in global fitness. We furthermore predict direct effects of reduced opportunity for mortality selection on the social epistasis factor (which should reflect the direct contribution of the accumulation of deleterious mutations on these psychobehavioral changes) and also direct effects of the reduced opportunity for mortality selection on decreasing global fitness—this path corresponds to predicted effects of the "rational tradeoff" models favored by certain economists as explanations for the demographic transition.[5] Demonstrating that the sequence opportunity for mortality selection → developmental instability → social epistasis → global fitness is independent of the path from opportunity for mortality selection to global fitness will yield evidence that accumulating mutations, and negative social epistasis in particular, independently contribute to the fertility decline of the demographic transition, as predicted by Woodley of Menie, Sarraf, et al. (2017).

A second potentially plausible causal sequence will also be tested. In this model the ordering of the developmental instability and social epistasis chronometric factors will be reversed, such that the latter goes before the former in the sequence. The rationale for this is that relaxed negative selection (which the opportunity for mortality selection factor should reflect) may be indirectly promoting decreased developmental stability through a condition-dependent, social-epistatic pathway, which might in turn be directly, rather than indirectly, reducing global fitness. The main criterion used to judge model goodness-of-fit in SEQCA is model parsimony—with the model exhibiting the fewest significant paths having higher parsimony (this assumes that the number of paths in all models compared is the same). All analyses are conducted using UniMult 2.

Data

Prior Negative Selection Factor (Opportunity for Selection Through Mortality)

Three variables were selected on the basis that they had broad mortality coverage from the US population. To that end we selected infant (i.e. <5 years old), child (between 5 and 14 years old), and maternal mortality. Infant and child mortality in particular were extremely severe for historical Western populations (around 25% and 50%, respectively, in some coun-

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[5] The idea underlying these models is that as mortality rates decline, the need to have large numbers of children to hedge against the likelihood that some will die young is obviated (Galor, 2012). These models could be extended to predict certain epigenetic responses to reduced environmental harshness, perhaps occasioning life history speed changes, that would, for instance, lead to reduced allocation of bioenergetic resources to mating effort (to which some might predict sperm production is related; this is relevant given that, as will be mentioned in the main text, sperm concentration is included in the global fitness factor of the model; we doubt that this particular life history model of the demographic transition is correct, however—see Barbaro et al., 2019).

tries during the Early Modern Era; Volk & Atkinson, 2013). While these measures only approximate the opportunity for selection through mortality, they should track this factor quite closely; as argued in the previous chapter, the work of Maciej Henneberg and his collaborators has provided evidence that changes in the opportunity for selection through mortality tend to track changes in the strength of negative selection.

These data were sourced from Roser (2018a; infant) and the Center for Disease Control (2009; child; data on all-cause mortality for all races and both sexes were used), and Roser (2018b; maternal) and were collected at yearly intervals from 1913 to 1975, with each indicator available for every year (so $N = 63$ years in each case). The loadings of each indicator onto the UW prior negative selection chronomeric factor (PNS; the values having been lagged by 25 years, or one standard generation relative to the predictors so that, for example, the 1940 PNS value predicts the 1965 values of the subsequent predictors in the cascade; the rationale for this lagging is the same as that for the lagging in the analysis of the prior chapter) are of large magnitude (Cohen, 1988) and are statistically significant in all cases. UWF loading (λ) values were as follows: for infant mortality $\lambda = 0.995$ ($N = 63$, $p < 0.05$), for child mortality $\lambda = 0.977$ ($N = 63$, $p < 0.05$), and for maternal mortality $\lambda = 0.965$ ($N = 63$, $p < 0.05$).

Developmental Instability Factor

Three variables were selected in order to capture temporal trends that could reflect the effects of accumulating deleterious mutations on physical condition, sourced from the United States. The first of these is sinistrality (left-handedness) (sourced from McManus, Moore, Freegard, & Rawles, 2010, obtained from fig. 2; data representative of general US population; data extracted using *WebPlotDigitizer*; Rohatgi, 2017), which is associated with a variety of other developmental instability indicators (Dutton et al., 2018; Ntolka & Papadatou-Pastou, 2018; Woodley of Menie, Fernandes, Kanazawa, & Dutton, 2018). Second, craniofacial shape and size fluctuating asymmetry (sourced from Kimmerle & Jantz, 2006, figs. 3, 4, 5 and 6, data on size asymmetry reported in Woodley of Menie & Fernandes, 2016; data from black and white samples and males and females—unweighted averages of these were computed) were chosen and combined because they potentially index developmental instability (Graham & Özener, 2016; van Valen, 1962), which also has been linked to indicators of elevated loads of deleterious mutations (Woodley of Menie & Fernandes, 2016).

Third, body mass index (BMI) was chosen, sourced from Komlos & Brabec (2010, fig. 1), which has been found to positively correlate in country-level analyses with I_{bs} net of covariates such as calorie consumption and level of physical activity (Budnik & Henneberg, 2017). The association is hypothesized to stem from relaxed negative selection allowing the accumulation of mutations impairing metabolic function (Budnik & Henneberg, 2017). (Data from Komlos & Brabec, 2010, are from black and white samples of males and females, which were combined as unweighted averages.)

Unlike with the opportunity for mortality selection indicators, the temporal coverage for these variables was in some cases associated with high levels of missingness. The craniofacial fluctuating asymmetry data cover the span of years from 1945 to 1985, with only five measurement occasions in total. The BMI measure covered ten measurement occasions spanning 1940 to 1985. The sinistrality measure was, by contrast, very well sampled across time, with 60 measurement occasions spanning 1938 to 2000, and it consequently forms the "spine" of this chronometric factor. The developmental instability chronometric factor covers 62 measurement occasions in total, spanning 1938 to 2000. The λ values for the indicators range from small to large in magnitude (Cohen, 1988). The value for sinistrality is $\lambda = 0.976$ ($N = 60$, $p < 0.05$), for BMI $\lambda = 0.813$ ($N = 10$, $p < 0.05$), and for craniofacial fluctuating asymmetry $\lambda = 0.128$ ($N = 5$, *ns*). While the loadings are all in the theoretically expected positive direction, only two of the three indicators have statistically significant loadings.

Social Epistasis Factor

Three variables were selected on the basis that they might reflect the effects of negative social epistasis. Temporal trend data in church attendance (which measures the frequency with which people attend church per week) were obtained for the general US population from Gallup (2016). Church attendance has been found to be sensitive to paternal age effects in a recently born cohort in the United States, despite controls for a variety of plausible confounds, such as parental religiosity, birth order, income, and education (Woodley of Menie, Kanazawa, et al., in preparation), suggesting that a weakening of norms enforcing religious observance may have allowed accumulated mutations to increase phenotypic variance with respect to religious behavior over time. The normative shift manifested as secularization may also constitute a mechanism through which irreligious values held by the carriers of spiteful mutations among culturally influential people (i.e. elites) can be phenocopied[6] through biased cultural transmission.

Another indicator is psychopathic deviation, which measures a syndrome characterized by general social maladjustment, among some other abnormalities. The item coverage is quite broad and includes domains pertinent to the hypothesized action of spiteful mutations, such as an aversion to family and, more broadly, authority figures, as well as self and social alienation and a tendency toward boredom. These data were collected from Twenge et al. (2010; data extracted from fig. 3 using *WebPlotDigitizer*; data from males and females, predominantly white), who examined trends in psychopathic deviation and other Minnesota Multiphasic Personality Inventory (MMPI and MMPI-2) scales using a large sample of college and high school students.

Temporal trends in another prospectively social-epistatically salient MMPI scale, specifically depression, are also analyzed. These data also came from Twenge et al.'s (2010) study (data extracted from fig. 2 using the *WebPlotDigitizer*; data from males and females, predominantly white).[7] While Twenge et al.'s most expansive analysis was restricted to college samples, they find convergent trends among high school students also (using MMPI-a), indicating that these trends are not primarily driven by demographic shifts affecting college-age samples. There are some indications of paternal age effects on depression (Laursen, Munk-Olsen, Nordentoft, & Mortensen, 2007), suggesting a direct contribution from *de novo* mutations deriving from advanced paternal age. The moderate heritability of the MMPI depression scale (ranging from 0.31 [MMPI] to 0.39 [MMPI-2]; DiLalla, Carey, Gottesman, & Bouchard Jr., 1996) is consistent with the possibility that the trait it measures has a genetic basis, which may be open to social-epistatic effects (DiLalla et al., 1996 also found h^2 values for the

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[6] "Phenocopying" refers to the expression of a phenotype resembling a phenotype that results from some genotype, but in an organism that lacks that associated genotype.

[7] One might be suspicious of our use of these time trend data, given concerns about possible temporal measurement variance. The reader should keep in mind the point raised in our Chap. 5 footnote about the narcissism epidemic and measurement variance, namely that even if some psychometric instrument fails to exhibit measurement invariance over time, this does not necessarily indicate that trends in that instrument's measure lack substance. But further, as our results and discussion sections make clear, the patterns of temporal covariation among the trends that we analyze are so strongly consistent with our theoretical predictions that it is simply unlikely that nothing is at play here but a simple measurement problem.

psychopathic deviation scale ranging from 0.38 [MMPI-2] to 0.61 [MMPI]; note, though, that social epistasis might only be related to the expression of non-additive genetic variants, but this possibility is not clearly true, and indeed we later speculate that social epistasis might be able to, e.g., suppress the effects of additive variants; on the heritability of MMPI-2 scales, see Gizer, Seaton-Smith, Ehlers, Vieten, & Wilhelmsen, 2010. Importantly, there is evidence that depression can spread through social contagion, and a social-epistatic mechanism for this phenomenon has even been proposed: "Fowler et al. (2011) found that people seek out friends who have the same genetic variants that they do beyond just physical characteristics. They hypothesise '*that a person's genes may lead to selection of friends with certain (social/asocial) genotypes which in turn facilitates or modifies the expression of a person's own genes*'" (Bastiampillai, Allison, & Chan, 2013, p. 302; italics in original). Moreover, depression was identified as a prospective target for spiteful mutations in Woodley of Menie, Sarraf, et al. (2017) on the grounds that it has been hypothesized to be a potential manifestation of pathological altruism (Oakley, 2013), that is, a form of altruism that harms rather than helps the intended targets of the altruism.[8] Pathological altruism more generally has been identified as part of a broader negative social epistasis syndrome in which the breakdown of group-selected cultural controls on the development of behavior gives rise to higher variance in behavior within populations, which may further contribute to group fitness decline.

Thus the social epistasis chronometric factor should track some of the temporal variation in those cultural controls (through changes in religious participation), and some of the temporal variation in hierarchy-resistant phenotypes (through changes in psychopathic deviation). This factor may also partly track the increase in the prevalence of prospectively pathologically altruistic behaviors through the depression measure.[9]

As with the indicators comprising the developmental instability factor, the coverage in time of the social epistasis factor is uneven; but overall coverage is more balanced in the case of the social epistasis compared to developmental instability indicators. For church absenteeism (simply the reverse-scored Gallup data), there is a total of 23 observations spanning

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[8] There has been little success in identifying common polymorphisms associated with depression (see Lo et al., 2017). This is perhaps because rare variants have a substantial and underappreciated role in the genetic etiology of the disorder (Dunn et al., 2015). Given that any disruption of social functioning has the potential to trigger depression, its prospective spiteful mutational target is likely very large.

[9] One aspect of this dynamic may involve the deterioration of leadership qualities among elites, which could engender opposition to authority at other levels of the social hierarchy.

the years 1939 to 1999; for psychopathic deviation, there is a total of 41 measurement occasions spanning the years 1938 to 2000; and finally, for depression, there is a total of 41 measurement occasions spanning the years 1938 to 1999. The UWF encompassed 47 measurement occasions covering 1938 to 2000. The λ values for the factors are all positive in direction, large in magnitude, and statistically significant (church absenteeism $\lambda = 0.859$, $N = 23$, $p < 0.05$; psychopathic deviation $\lambda = 0.923$, $N = 41$, $p < 0.05$; and depression $\lambda = 0.956$, $N = 41$, $p < 0.05$).

Global Fitness Factor

For this factor, three separate temporal trend measures of fitness were chosen, reflecting this property at multiple levels of biological organization. The first of these measures is sperm concentration, sourced from Carlsen, Giwercman, Keiding, and Skakkebaek (1992), with additional data from Swan, Elkin, and Fenster (2000), which tracks changes in a population's reproductive viability (the latter paper mentions nothing about BGA, whereas the former indicates that data were taken overwhelmingly from white males; since there was apparently no effort to select on the basis of BGA in these studies, the data may roughly correspond to the BGA demographics of the US male population). In terms of the SEAM, declining sperm concentration may be especially salient, in as much as it may parallel a trend of declining testosterone in males[10] (Travison, Araujo, Hall, & McKinlay, 2009). As noted above, Kalbassi et al. (2017) determined that exposure of mice carrying the *Nlgn3* mutation to non-carriers reduced the testosterone levels of the non-carriers; this may have been a consequence of the breakdown in hierarchy formation that was noted in mixed housings of carrier and non-carrier mice (for further discussion, see Sarraf & Woodley of Menie, 2017). Declining sperm concentration in Western males (a phenomenon for which a recent and particularly well-done study has provided strong evidence; Levine et al., 2017) could stem at least in part from negative social epistasis. These data were available between 1938 and 1996 for a total of 30 measurement occasions.

The second measure is the total fertility rate (TFR) of the general US population. Data for this measure were sourced from Roser (2018c) for a total of 62 measurement occasions from 1938 to 2000. Changes in this

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[10] See Grantham and Henneberg (2014) on the possibility that relaxed selection is contributing to reduced testosterone and sperm counts.

indicator may track factors such as "rational" fertility choices in response to reduced infant and child mortality, as well as other commonly invoked causes of the demographic transition (Galor, 2012). But given the maladaptive nature of sub-replacement fertility (at the group level), it is expected that negative social epistasis might be potentiating the decline in this indicator (via, e.g., the normalization of anti-natalist values; Woodley of Menie, Sarraf, et al., 2017).

The final measure is the US population proportion of world population minus the US population (this being a measure of group or "corporate fitness"; see Figueredo et al., 2019a, 2019b). Data on the size of the US population were available from the US Census Bureau (2016), and on the size of the global population from Earth Policy Institute (2012) and United Nations (2019). This indicator is a standing measure and captures changes in the group-level fitness of the US population, which may be strongly affected by negative social epistasis (Woodley of Menie, Sarraf, et al., 2017).

The factor is quite well balanced in terms of sampling across indicators. All λ values were high magnitude and statistically significant. Sperm concentration $\lambda = 0.828$ ($N = 30$, $p < 0.05$), TFR $\lambda = 0.933$ ($N = 62$, $p < 0.05$), and corporate fitness $\lambda = 0.939$ ($N = 62$, $p < 0.05$).

RESULTS

Figure 7.1 plots the distribution of each chronometric factor over time.

The temporal correlations among the four chronometric factors and the natural log of time (year) are displayed in Table 7.1.

Figure 7.2 displays the results of the SEQCA for the first (favored) hypothesis.

For the first SEQCA (depicted in Fig. 7.2 LnT → PNS → DI → SE → GF), the model exhibits a good fit (as captured by the Pillai-Bartlett $V = 0.934$, and associated effect size = 0.48, $p < 0.0001$). There are six significant paths in this model.

A second SEQCA was run in order to test the alternative model (with the order of DI and SE reversed). This model (LnT → PNS → SE → DI → GF) fits equally well ($V = 0.934$); but this second model has seven significant paths, making it less parsimonious than the first (as more paths are needed to fully model the interrelations among the variables). Therefore, the first model is preferred by virtue of parsimony. In this model, the effect of DI on GF is entirely mediated by SE, as predicted by

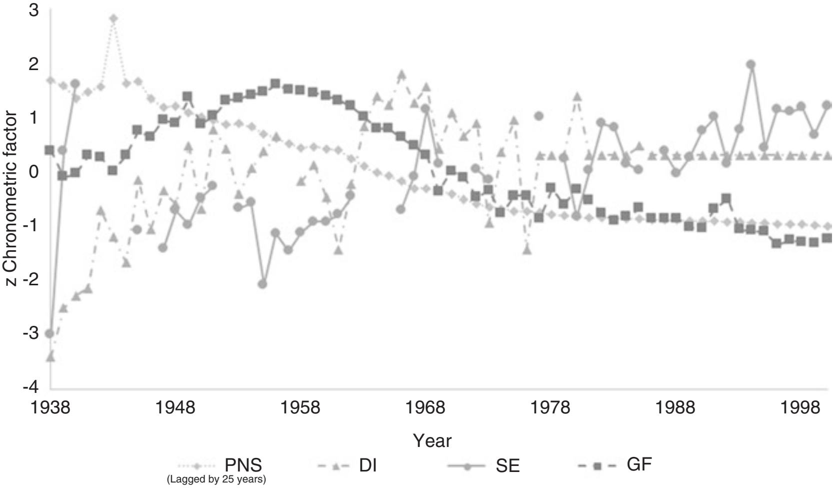

Fig. 7.1 The unit-weighted chronometric factors of prior negative selection (PNS; lagged by 25 years), developmental instability (DI), social epistasis (SE), and global fitness (GF)

Table 7.1 Temporal correlations among the PNS, DI, SE, and GF chronometric factors and Ln Time (Year; LnT)

	LnT	*PNS*	*DI*	*SE*	*GF*
LnT	1				
PNS	−0.941∗	1			
DI	0.509∗	−0.583∗	1		
SE	0.666∗	−0.643∗	0.250∗	1	
GF	−0.787∗	0.695∗	−0.116	−0.757∗	1

All correlations were in the theoretically expected direction

∗$p < 0.05$

the SEAM. There is a direct effect of PNS on GF consistent with economic hypotheses that predict that increased survivorship will decrease fertility. But the direct path from PNS to GF is of much smaller magnitude than the one from SE to GF (0.510 vs. −0.750), which suggests that the SEAM may account for the majority of the variance in the demographic transition (as captured by GF).

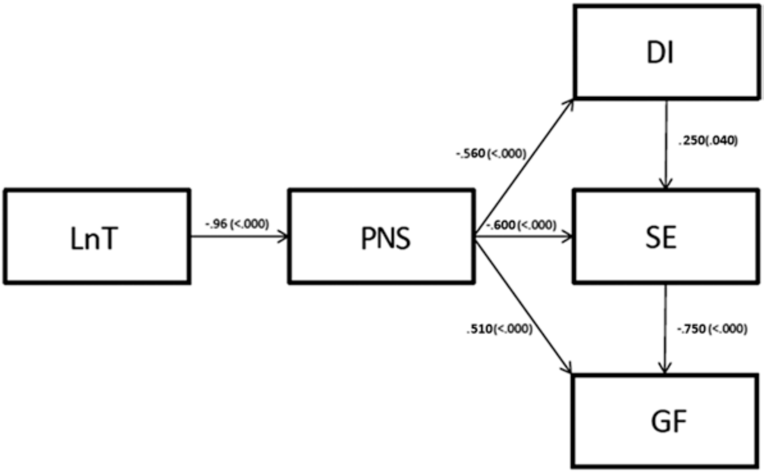

Fig. 7.2 The SEQCA for the first hypothesis, with each step in the cascade controlled for the natural log of time

Discussion

Consistent with predictions, the factor composed of proxies for prior negative selection (PNS) negatively associates with the developmental instability factor (DI) (reduced opportunity for selection through mortality → greater developmental instability). In turn, DI positively predicts a factor of hypothesized measures of negative social epistasis (SE), which negatively predicts a factor tracking the global fitness of the US population (GF). As predicted, SE completely mediates the association between DI and GF; this aligns with the expectation of geneticists that deleterious mutation accumulation *as such* should depress fitness quite gradually, but also with the novel idea that the social-epistatic amplification of spiteful mutations can rapidly depress the fitness of groups at multiple levels of organization (Woodley of Menie, Sarraf, et al., 2017).

Perhaps the most serious limitation of the above analysis is that it was not possible to consistently restrict selection of data to indicators pertaining only to the BGA group of interest, namely European-Americans or whites (since we predict that they have been exposed to relaxed negative selection and its effects to the greatest extent and for the longest amount of time of all BGA groups in the United States); therefore we did not use single-BGA data for any indicator. None of the data sets used exclusively relates to whites or European-Americans, and representativeness of the general US population certainly differs across indicators. Still, the data come from a time period in which European-Americans comprised the overwhelming majority of the US population, so it is reasonable to infer that our data primarily reflect dynamics associated with this BGA group. The indicators perhaps least likely to reflect the demographics of the US population as a whole are the mental health indicators derived from Twenge et al.'s (2010) college samples and the fluctuating asymmetry and BMI indicators (the data for these last two indicators are from blacks and whites, but no other BGA groups). But the mental health indicator data nevertheless are "overwhelmingly white"[11] (Twenge et al., 2010, p. 149), roughly consistent with the racial demographics of the US population in the time period from which data were selected. Indeed, the majority of the data used for each indicator in the analysis is from white Americans. There is likely no substantive confounding with changes in population age over time, in light of the descriptions of the data for the various indicators.

A recent diachronic analysis is congruent with aspects of the above analysis, finding using a longer time series (1800–2005) that the decline in the strength of Western group selection has the entirety of its effect on the year-on-year change in a latent moral foundations factor mediated by the developmental instability factor employed above. It reveals a general decline in binding values and rise in individualizing ones, which is consistent with the prediction of the SEAM that accumulating mutations, a subset of which are likely to have negative social-epistatic effects, should increase the prevalence of individualizing moralities, and decrease that of binding ones. The finding that the developmental instability factor entirely mediates the group selection factor's effect on the individualizing-binding factor is remarkable. This result aligns with the possibility that high levels of group selection might be necessary to mitigate the accumulation of, in particular, spiteful mutations (Woodley of Menie, Figueredo, Jurgensen, Bose, & Sarraf, in preparation).

The SEAM appears to capture pathological aspects of modernity that are missed in standard sociological accounts. In earlier chapters we discussed the work of Ronald Inglehart (2018) and Christian Welzel (2014; see also Inglehart & Welzel, 2005), for whom industrialization and its

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[11] Further, Twenge et al. (2010) state that "[t]he racial composition of college student samples has differed only slightly over this time period" (p. 149).

sequelae have almost exclusively salutary effects, especially in the long run. These processes increase human wealth and eliminate/reduce sources of morbidity and mortality and thereby offer individuals historically unprecedented levels of existential security. When life (or survival) is more secure, "the nature of life [is transformed] from a source of threats into a source of opportunities" (Alexander, Inglehart, & Welzel, 2016, p. 909). Consequently, individuals adopt value systems that enable their acting on these opportunities: "practicing and respecting *universal freedoms* becomes increasingly vital to take advantage of rising life opportunities" (Alexander et al., 2016, p. 909; emphasis added). These predictions, note, are strikingly similar to those of life history theory, which posits that humans who evolve and live under conditions of low uncontrollable and unpredictable morbidity and mortality (those with slow life history, or "high-K" strategies) are more cooperative, pacific, egalitarian, liberal, and happy than those who evolve and live under harsher and more unpredictable conditions (those with fast life history, or "low-K" strategies) (Figueredo et al., 2017). Neither model would predict that the fitness decline of modernized populations has a pathological element, but would instead (in the former case) maintain that falling fertility rates are a rational response to the decreased likelihood that offspring will die prematurely, and to the desire and ability to pursue personal interests and enjoyment, or (in the latter case) assert that low fertility rates are typically a component of slow life history strategies.

In our model, PNS, since it is composed of mortality measures, at least roughly indexes the variables that should contribute to "rational" choices not to have large numbers of offspring and to life history speed variation. But the direct effect of PNS on fitness is of smaller magnitude than that of SE on fitness (0.510 vs. −0.750), indicating that neither modernization theory nor life history theory accounts are sufficient to explain fertility declines and in fact do a poorer job of this than the SEAM. More importantly, it is unclear how life history theory or modernization theory would explain rising developmental instability and its apparent contribution to worsening mental health and increasing irreligiosity (or why variables associated with the last two categories form a well-specified factor). Indeed, modernization theory and life history theory would predict improved physical and mental well-being, given that the former posits that greater freedom through modernization improves happiness and life satisfaction (together, subjective well-being or SWB; Welzel, 2014; note that at the group level, SWB seems to positively predict at least certain dimensions of physical health—see Minkov, 2011) and the latter takes slow life history strategies to predict greater mental and physical health and subjective well-being, as well as religiosity (Figueredo, Vásquez, Brumbach, & Schneider, 2007). Moreover, neither model has a basis on which to explain the fact that the SE factor negatively predicts indicators of global population fitness. Resultantly, life history theory and modernization theory are not alternatives to the SEAM.

It is worthwhile to consider as yet unexplored implications of the SEAM for the fate of Western civilization. We think it is reasonable to hypothesize that general effects from negative social epistasis, characterized by "far-social transfer" of fitness losses from the carriers of spiteful mutations to those in the broader population, are real (such far-reaching effects are to be contrasted with the direct organism-to-organism effects that have been observed in mice; see, e.g., Bachmann et al., 2018). Some evidence for this possibility has already been found in North American red squirrels: it appears that red squirrels that have never encountered one another can have indirect effects on each other's fitness (there is some, albeit weak, evidence that indirect *genetic* effects are involved) (Fisher et al., 2019).

A common complaint about modernized societies is that they lack any strong basis for social cohesion. With the death of nationalism following World War II (Westbrook, 2004), and the much longer-running processes of the decline of religion (Gallup, 2016) and of public ritual (Collins, 2014, p. 331), the "social fabric" of the developed world seems quite weak[12]:

> [S]ince at least AD 800, this thing we call "Europe" has been largely a by-product of Christian civilization. Its more recent love affair with nationalism has offered a substitute value system, but since both religion and nationalism are now deemed retrograde, one can only wonder what value system will unify Europe now. What spirit, aspiration, or ideal might animate European

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[12] In addressing liberal hopes of harmoniously accommodating substantial ideological diversity within societies, Safranek (2015) offers the following observation: "One liberal theorist claims that 'liberalism is a search for principles of political justice that will command rational assent among persons with different conceptions of the good life and different views of the world.' And yet with each passing decade, more rather than fewer public issues are disputed in Western polities. The question of same-sex marriage, which would hardly have arisen but for specifically liberal principles, was hardly an issue in the public square two decades ago. Liberalism has not only failed to provide principles of political justice that command rational assent, but it seems to have stoked the fires of civil strife" (p. xii).

> hearts and provide the connective tissue or civic glue for its peoples? (McNamara, 2017, p. 54)

Empirical evidence for this view comes from a variety of sources. Modernized societies exhibit low trust in major institutions and low social conformism, but are high in out-group trust[13] and social activism (Welzel, 2014, p. 405). Modernization also appears to strongly depress willingness to fight in war for one's country (Inglehart, 2018; Inglehart, Puranen, & Welzel, 2015). Furthermore, as noted in Chap. 2, individualizing moral foundations have been increasing with time, as binding ones have been decreasing (a result replicated in Woodley of Menie, Figueredo, et al., in preparation). Also, to reiterate a point, a number of studies have found indications of declining altruism and groupishness in Western populations[14] (Greenfield, 2013; Kesebir & Kesebir, 2012; Konrath, O'Brien, & Hsing, 2011; Woodley of Menie, Figueredo et al., 2017; Zarins & Konrath, 2017). Perhaps relatedly, there are signs of rising political polarization in at least some Western societies (Steenvoorden & Harteveld, 2018; Twenge, Honeycutt, Prislin, & Sherman, 2016), as well as indications of widespread "societal pessimism," or the belief that "society is changing for the worse"[15] (Houwelingen, 2016; Steenvoorden & van der Meer, 2017). Finally, evidence of increasing intra-group competition in Western populations has been noted: one study found that the rate of cuckoldry, an index of inter-individual sexual competition, rose over a few centuries (Larmuseau, Matthijs, & Wenseleers, 2016), which is consistent with declining group selection (in the most recent period examined by Larmuseau et al., a decline in the cuckoldry rate was noted; but the authors conclude that this was likely a result of the introduction of birth control, not decreased extra-pair copulation). But especially intriguing on this score is a study from Lindfors, Solantaus, and Rimpelä (2012) offering evidence of what might be psychological effects of declining group-selective pressure and increasing intra-group competition—specifically,

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[13] In the United States, however, trust in others fell precipitously from at least the mid-to-late twentieth to early twenty-first centuries (Twenge, Campbell, & Carter, 2014).

[14] Consistent with these trends, there is evidence that at least one aspect of ability-based emotional intelligence has declined over time in English-speaking populations (Pietschnig & Gittler, 2017).

[15] Importantly, attitudes about societies may strongly predict the latter's health and fate, whereas individuals' attitudes about their own lives may not (Eckersley, 2009; Turchin, 2016).

the "fears" that Finnish youth have concerning the future have shifted over time, such as to suggest increasing preoccupation with individual-level as opposed to group-level "risks" (e.g. war vs. loneliness).

The impression these facts offer is that the members of modern Western societies have little commitment to the maintenance of these societies as such, that is, as exclusive communities defined in terms of particular structures, traditions, heritages, religious beliefs, and so on. Rather than orient themselves to the internalization of collective norms and the realization of traditional collective ideals (social conformism), they seek to *change* their societies (social activism), potentially given perceptions of injustice, as reflected in low institutional trust. Similarly, pro-out-group attitudes may motivate efforts to improve societal inclusivity at the cost of traditional norms, values, and demographic conditions. This is consonant with a broader shift of morality in the West, from one that emphasized attainment of objective goods (virtue, fidelity, etc.) to one that prioritizes subjective or mental goods (specifically individual satisfaction and fulfillment) (Manago, Greenfield, Kim, & Ward, 2014; Rubin, 2015), insofar as this shift brings individuals to believe that institutions (especially those of government) should serve their interests, rather than that they (individuals) should serve collective interests (Rubin, 2015). This potentially explains, at a proximate level, the relative lack of willingness to sacrifice for one's nation now common in the developed world, although once the opposite apparently held: "[A]s late as 1914 the flower of both the British and German intelligentsia rushed to die on the killing fields of Flanders" (Young, 2007, p. 465; see also Stromberg, 1982). Everywhere that modernization is long established, prevailing desires seem to be for open, non-competitive (in the sense of explicit and especially violent competition), peaceful, egalitarian, and inclusive societies that cater to individuals' idiosyncrasies and maximize their preference satisfaction (see Meisenberg, 2004; Minkov, 2009). These aspirations seem to co-occur with certain features of societies and general social behavior, such as generous welfare states and consumer/service economies, and readily dissolvable interpersonal ties (also known as relational mobility; see Thomson et al., 2018)—all of which appear to augment individuals' security or range of options in the pursuit of desire satisfaction.

We posit that the ultimate basis for these developments does in fact partially consist of slowing life history speed (as discussed in Chaps. 2 and 3), but more importantly of the synergistic effects of slowing life history speed, individual-level (as opposed to group-level) selection, mutation accumulation, and (resultantly) disturbed patterns of social epistasis.

As noted in Chap. 3, it appears that pre-industrial group-selected human societies of the West exhibited high levels of social cohesion and rigid conformity to received norms of conduct, deviations from which were often harshly punished. Theoretically, one expects that a social order of this kind would have the effect of imposing *centripetal selection*, that is, selection that has the effect of limiting at least certain kinds of genetic variance in a population (Meisenberg, 2007, predicts low levels of genetic variation in pre-industrial societies, but does not frame this as a consequence of group selection). Populations involved in regular inter-group competition involving warfare need to maintain particularly demanding adaptive optima, given that the potential costs of defeat in war are extreme; thus, behavioral systems yielding social and sexual selective pressures that maintain *monomorphic* group-level adaptations—such as high population levels of (in-group) altruism, heroism, and religiosity—by disfavoring whatever sufficiently deviates from those optima, seem essential. Interestingly, there is solid historical evidence that medieval European societies took on strong persecutory attitudes toward non-Europeans, and other "outsiders," and became inclined to ideas of biological group differences when exposed to the perceived threat of conflict with Islamic populations (Epstein, 2009), a phenomenon that may have placed Europeans under group-selective pressures and activated pre-existing group-selected adaptations for inter-group conflict. In contrast to theories that emphasize the role of parasite avoidance in collectivism and groupish behavior (e.g. Thornhill & Fincher, 2014), the theory offered here posits that such behavior may have the effect of preparing groups for inter-group conflict by compressing relevant genetic variance around adaptive means.[16]

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[16] A recent paper has offered experimental evidence allegedly indicating that the "behavioral immune system" in humans has the effect of promoting avoidance of persons carrying pathogens, but not avoidance of ethnic out-group members (van Leeuwen & Petersen, 2018). The results of this work are irrelevant, however, in that the participants in the experiment were not exposed to any sort of stimulus that would be expected to activate psychological adaptations for inter-group conflict. Moreover, with respect to carriers of spiteful mutations as opposed to ethnic out-group members, one should consider that there is evidence that moral judgment and disgust sensitivity may be more deeply related than is ordinarily assumed (Chapman & Anderson, 2014), perhaps due to shared evolved psychological mechanisms partly underlying both phenomena. This possibility suggests that phenotypic signals of spiteful mutations may be mentally processed in ways similar to signals of pathogen stress, which would be consistent with the observation that disgust sensitivity strongly pre-

In light of the SEAM, the sensitivity of evolved psychological mechanisms (mental modules) underlying groupish behavior of this persecutory sort may be placed under rapid directional selection in populations exposed to inter-group conflict, given that social-epistatic amplification of fitness-depressing variants may have large deleterious effects on whole populations (see the simulation in Woodley of Menie, Sarraf, et al., 2017), and that maintenance of group fitness is especially crucial in times of war. Therefore, these modules, activation of which may be dependent on cues of inter-group conflict, may be reasonably termed *social-epistasis control modules.*

Following the collapse of group selection in Western populations, stemming from climatic warming and industrialization that relaxed triggers of inter-group conflict (high morbidity and mortality, resulting especially from resource scarcity), natural, social, and sexual selection redounding to group-level fitness have been profoundly attenuated (Woodley of Menie, Figueredo et al., 2017). We have already argued at length that this relaxation of selection has permitted the accumulation of deleterious mutations. But an important consequence of this process merits attention. Mutation accumulation entails increasing genetic diversity, and indeed reduced opportunity for selection predicts rising morphological variation (a likely consequence of expanding genetic diversity) in European populations over many epochs (Henneberg et al., 1978; more recently, Staub et al., 2018 found evidence of increasing BMI variability in Swiss conscripts, and increasing markers of ill health, consistent with relaxed negative selection).

This "increasing variation of human biological characters" (Rühli & Henneberg, 2017, p. 269) could be a contributor to contemporary Western populations' unique individualism, alongside high levels of *K* (Twenge & Campbell, 2018) and exogamy (MacDonald, 2001; Woodley & Bell, 2013). These factors, together with the breakdown of group selection, may serve as the ultimate bases of the pressure that citizens of "postindustrial" or "late modern" nations put on institutions to achieve greater levels of democratic participation and liberal toleration of an ever-broader set of lifestyles (see Welzel, 2014 for sociological documentation of the drive toward "emancipative values" in the West). The effects of slow life history strategists on this process are of particular note. Those with slow life history strategies have relatively high levels of developmental plasticity and thus may have especially strong motivations to secure

dicts political conservatism (Smith, Oxley, Hibbing, Alford, & Hibbing, 2011), which is associated with aversion to "deviant" behaviors, individuals, and so on.

conditions allowing them the freedom to exploit the niches that maximize their interests (conversely, the behavior of fast life history strategists is more strictly governed by heritable dispositions, suggesting that they should have lower motivations to maximize freedom in niche selection) (Woodley of Menie et al., 2015). This may explain their endorsement of individualistic and hedonistic attitudes, which empower them to pursue whatever objective conditions (niches) that enhance their mental well-being (an ancestral proxy for opportunities to enhance personal fitness, which individual-selected humans should have particularly strong interests in), rather than be relegated by given norms to some predetermined set of circumstances. Moreover, slow life history strategists that do not face the threat of inter-group conflict have little reason to submit to collective or group-level coordinative mechanisms that are needed to ensure a population's survival in war. Rather, given peaceful conditions, a group of genetically diverse (due to mutation accumulation) slow life history strategists will strive for a social order that is basically libertarian, allowing them to radiate into idiosyncratic niches to which they can become developmentally calibrated (deepening their individuality), a process facilitated by their promotion of social institutions that serve mainly to aid and encourage them in this process.

The problem with this particular dynamic favoring the evolution of slow life history strategies is that it lacks a mechanism with which to control mutation accumulation and its negative social-epistatic consequences. Slow life history strategists act to maintain a basically liberal, egalitarian, and irenic social arrangement because this enables stable niche exploitation. Resultantly they (at least the Western variant) seem to be religiously opposed to discriminatory social practices (Rubin, 2015; Twenge, 2017), especially the traditional moral hierarchies that justified punishment and exclusion of those incapable of norm compliance (the behavior of whom may stem ultimately from genetic abnormalities to at least some extent). This should not only weaken selection against carriers of spiteful mutations, but also remove controls that would have traditionally limited their access to positions of power. Such an absence of "filtration" could be considered especially problematic given that the lineages of social elites, by virtue of both greater wealth and delayed parenthood, as suggested earlier, presumably have experienced the longest-running and most thorough relaxation of negative selection and paternal-age-related mutation accumulation, and thus hold the greatest concentrations of individuals possessing "dyscorporate genotypes" (the corrosion of corporate or group-level fitness being the most salient effect of spiteful mutations; note that this would reverse the probable historical tendency for spiteful mutations to predispose to low social status—and while there is little doubt that certain types of deleterious mutations predispose to this outcome in modernized populations, this may not be true of all spiteful mutations with behavioral effects, especially in the case of people who can compensate for the social-status-reducing effects such mutations might have through, e.g., leveraging of high intelligence). We conceive of this dyscorporate type as encompassing those who can broadly be defined as opposed to conditions fostering social cohesion. Through their disproportionate influence on media, business, academia (and education more broadly), government, and so on, these elite dyscorporate types potentially have the power to alter patterns of social epistasis in highly maladaptive ways. And as deleterious mutations come to afflict the public more generally, support for the aims of dyscorporate-type elites should grow, insofar as those mutations might leave such individuals with conditions and behavioral predispositions that lead them to seek a liberal "canopy" that protects them from the threats that traditional belief systems and corresponding behavioral patterns pose to them. Moreover, the developmental plasticity associated with slow life history suggests that slow life history strategists are especially amenable to social-epistatic influence, both negative and positive. All of this implies that social epistasis control modules can become rapidly subverted in Western populations at least, such as to have the effect of *intensifying* rather than *mitigating* negative social epistasis. It also suggests a potential biological basis for conflict over the construction of culture, a process explicated by MacDonald (2009). The cultural constructs that predominate in a population may ultimately (although, of course, not entirely) depend on which individuals are situated to control broad-scale epigenetic influences on behavioral development via social epistasis. Conflict will therefore emerge among individuals with different relevant genetic makeups, and thus interests in favoring and disfavoring the fitness of different genotypes through variable epigenetic rules of development (see Chap. 2's discussion of inclusive fitness). By extension, theories of culture-gene coevolution, which posit that distinct cultures have differential effects on the fitness of genotypes, can also be recast in terms of epigenetic control through social epistasis.

Among dyscorporate-type elites, there may exist a hitherto unrecognized anthropological type that we term the *anti-genius* (see also Dutton & Charlton, 2015). Whereas a genius is a highly intelligent and intellectually creative individual, typically with low personal fitness, whose ideas and innovations deliver (sometimes enormous) benefits to the fitness of their group (Woodley of Menie, Figueredo et al., 2017), an anti-genius, while also possessing high intelligence and intellectual creativity, produces (typically highly anti-normative and atomizing or individualizing) ideas that *depress* the fitness of their group.[17] The intellectual gifts of anti-geniuses may be misdirected, so to speak, as a result of behavior-disturbing deleterious mutations. Among students of human evolution, it is uncontroversial that mutations have the ability to impair psychology and behavior (see, e.g., Keller & Miller, 2006 and associated commentaries). It is thus reasonable to assert that the cultural products of psychology and behavior, such as the ideas of geniuses, while in adaptive contexts fitness enhancing, can be corrupted via the action of deleterious mutations and thereby have the effect of *reducing* fitness. Examples of strains of anti-genius thought can be found on both sides of the contemporary political spectrum. On the left, one might include certain manifestations of Marxism and extreme variants of feminism.[18] The former has tended to yield mass death and social dysfunction for the populations that have officially adopted it (see Courtois et al., 2001; Gregor, 2012)—despite their groupish nature, Communist societies have had a peculiarly self-destructive, maladaptive quality; furthermore, in practice Communism and derivative ideologies have in many instances had dysgenic, specifically g-reducing effects on the populations strongly under their influences, via selective emigration and violence targeting of socially successful individuals who likely had higher-than-average g (Flynn, 2013; Glad, 1998; Sunic, 2009).[19] Intriguingly, Karl Marx suffered with a rare skin condition known to cause psychological disturbances of a sort purportedly consistent with his intellectual output (Shuster, 2007). And even in modernized liberal democracies, factors such as liberal gender attitudes seem to contribute to reduced fertility, net of other factors (Meisenberg, 2010). There is even evidence of morphological and behavioral differences between feminist activists and the broader population of women from which they are sampled, possibly consistent with the former having undergone idiosyncratic developmental trajectories (Madison, Aasa, Wallert, & Woodley, 2014).

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[17] See Murray (2003) for details on the demographics of genius.

[18] We have in mind the strains of third-wave feminist thought that rose to prominence in the 1960s and actively preached violent, socially destabilizing action within those groups that might act on their principles (e.g. Solanas, 1967/2016).

[19] An interesting possible exception to this might have occurred in the German Democratic Republic, where the government actively incentivised the fertility of those with high levels of educational attainment (Weiss, 2000).

Among those individualizing ideologies classified as right-wing in contemporary context, one potential example of anti-genius thought might be found in “Objectivist” libertarianism, which essentially degenerated into a personality cult centered on Ayn Rand (Murray, 2014). According to “the biography [of Rand pupil Barbara Branden] … among Rand’s closest disciples ‘objectivism’ was translated into a radical, and secret, sexual experimentation, including forms of polygamy and polyandry” (Introvigne, 2016, p. 308). Introvigne notes that Rand strongly influenced Anton LaVey, perhaps the foremost proponent of Satanism in the United States. Introvigne (2016) notes that “Rand’s ‘man worship’ is close to the ideology of the Church of Satan” (p. 308). When aspects of ideologies take on truly “extreme qualities,” whatever their nominal political classification, they become non-normative in the context of deep Western social history, and, if highly influential, they may have the potential to disturb group-level adaptations via negative social epistasis, engendering rapid group-level fitness decline.

* * *

The general drift of Western populations into progressively more fitness-depressing ideologies and behaviors offers some evidence consistent with our hypothesis. Individualizing moral foundations (as captured by self-reported liberalism) negatively associate with fertility at the individual (Goldstone, Kaufmann, & Toft, 2011) and, across time and space, group levels, when operationalized as postmaterialism (Inglehart & Appel, 1989; see also Fieder & Huber, 2018, who find evidence that, especially in recent years, rightists are advantaged in reproductive success over centrists and leftists in some Western populations, with more extreme rightism tending to go with greater advantages of this sort—importantly, their findings are robust to a number of controls, such as for education, age, and income). Such moral foundations have clearly been ascendant in the West for decades at least, as indicated by our analysis in Chap. 2 (see also Inglehart, 2018; Woodley of Menie, Figueredo, et al., in preparation). Irreligiosity, as we have seen, potentially positively associates with burdens of deleterious mutations, which is one potential genetic basis for the finding of a nexus linking religiosity to higher mental and physical health (on this nexus, see Flannelly, 2017; Koenig, 2012). Political ideologies associated with individualizing moral foundations seem to be positively associated with irreligiosity (Piurko, Schwartz, & Davidov, 2011), and such political ideologies and irreligiosity exhibit a similar nexus of correlations with undesirable traits—taken together, this all suggests the possibility of a common factor behind this set of associations that is at least in part reflective of an individual's load of deleterious mutations (with more of such mutations leading to higher levels of irreligiosity, individualizing values, and poor health and other markers of poor phenotypic condition).

Congruent with this possibility, when measured as self-reported liberalism, an inclination toward individualizing moral foundations appears to positively relate to a variety of correlates of poor mental health, such as elevated psychoticism (Verhulst, Eaves, & Hatemi, 2011) and neuroticism (McCann, 2014 and references therein; but see Verhulst et al., 2011 and the erratum to their paper in the references), diminished SWB (Okulicz-Kozaryn, Holmes, & Avery, 2014) and meaning in life (Newman, Schwarz, Graham, & Stone, 2019), and lower appearance quality (Berggren, Jordahl, & Poutvaara, 2017; Peterson & Palmer, 2017; appearance quality positively associates with mental and physical health and therefore may be a signal of underlying mutation load; Nedelec & Beaver, 2014). Political ideologies related to individualizing moral foundations may also associate with engagement in non-normative behavior, such as crime (Wright, Beaver, Morgan, & Connolly, 2017). These political ideologies further are associated with openness toward, and thus probably possession of, non-normative gender identities and sexualities that might be linked to developmental instability (Erickson-Schroth, 2013; Swift-Gallant, Coome, Monks, & VanderLaan, 2017), to poorer mental health (Zietsch, Verweij, Bailey, Wright, & Martin, 2011), and, in some instances to autism[20] (Glidden, Bouman, Jones, & Arcelus,

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[20] A puzzle about modern populations concerns their sexual behavior, which on the face of things appears "hedonistic" and promiscuous—not at all what one would expect of a slow life history population. As it happens, however, although average lifetime number of sexual partners in, for example, the United States spiked with the sexual revolution, it has declined since; on the other hand, the percentage of sexual experiences occurring outside of committed relationships has increased (Twenge, Sherman, & Wells, 2015). Additionally, rising participation in sexual activities long considered non-normative (though increasingly less so) has been documented (Brody & Weiss, 2011). This set of trends suggests that while Western people are becoming less sexually active, consistent with slowing life history strategy and with decreasing sexual health and function (Saniotis & Henneberg, 2014), the sexual experiences they do have are more frequently abnormal. One driver of these developments may be autistic-like personality traits, which are potentially growing in prevalence in Western populations (Sarraf & Woodley of Menie, 2017), since they are associated with paraphilias (Schöttle, Briken, Tüscher, & Turner, 2017). More importantly for our purposes,

2016; *cf* Turban & Van Schalkwyk, 2018). Perhaps relatedly, males who self-report greater levels of egalitarianism have lower upper-body strength and social dominance orientation than inegalitarian ones (upper-body strength and inegalitarianism/social dominance orientation in males appear to have a partial common basis, which may be genetic; see Petersen & Laustsen, 2019).

These findings can only be interpreted as tentative support for our hypothesis, but suggest the existence of a common nexus among individualizing moral foundations/irreligiosity, poor mental and physical health/phenotypic condition (perhaps especially apparent in the form of social learning disorders such as autism), and sex-atypical behavior. Our own analysis above has found that trends in church absenteeism and diminished mental health form a well-specified factor that is positively predicted by

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slow life history strategies, of which autistic-like personality is but one extreme variety (Del Giudice, Klimczuk, Traficonte, & Maestripieri, 2014), may be especially predisposed to non-traditional sexualities in the presence of negative social epistasis. As discussed above, Dunne et al. (1997) found that the heritability of one indicator of sexual behavior, age at sexual debut, rose over time; we argue that this was possibly due to the relaxation of social-epistatic controls that reduced variance in age at first intercourse prior to the sexual revolution. If one reason for the lower heritability of behavioral factors observed in slow life history strategists (Woodley of Menie et al., 2015) is the greater influence of social epistasis on trait development in these individuals (e.g. by suppressing the effects of additive genetic variants), the rapid non-normative changes in sexual behavior observed in slow life history populations (at least the Western ones) over the past few decades could be a result of intensifying negative social epistasis.

Importantly, there are indications that efforts to promote non-normative sexuality have been part of efforts to change traditional Western cultures, especially among those of extreme political orientations (Dougherty, 2004), some of whom are prospective anti-geniuses. The radical philosopher Herbert Marcuse is known to have supported the acceptance of "polymorphous perversity" (Lind, 2000), and early Critical Theorists generally sought to thwart supposed incipient fascism through the establishment of an "erotically fulfilled" society explicitly and highly at odds with the defining characteristics of traditional Western life (Gottfried, 2017, p. 7). Certain researchers have argued that disruption of monogamous norms regulating sexual relations between males and females tends to significantly reduce indicators of population fitness (Unwin, 1934; Zimmerman, 1947). Consistent with these expectations, General Social Survey data indicate that females' number of lifetime sexual partners negatively correlates with their reproductive success (Survey Documentation and Analysis, n.d.). This result suggests that, at least in Western groups, monogamous (i.e. high-attachment oriented) behavior is essential to population-level fitness, and thus that efforts to undercut these norms are harmful to fitness, and so potentially have their ultimate source in the influence of spiteful mutations.

developmental instability, and which negatively predicts global population fitness, consistent with the existence of the hypothesized nexus.[21]

The implications of this empirical and theoretical investigation for the future of Western peoples are quite stark. The "soft" existential conditions of the West have permitted the evolutionary and epigenetic development of self-oriented slow life history strategists who favor individualizing moralities. Unfortunately, this may have co-occurred with the buildup of deleterious mutations in the gene pools of Western populations. Slow life history strategists, at least of the Western type, are too humanistic to tolerate the sorts of social mechanisms that originally functioned to limit the influence and presence of spiteful mutations in their groups. Moreover, the high *conditionability*, related to the developmental plasticity, of slow life history strategists leaves Western populations especially vulnerable to the negative social-epistatic influences that seem to have quickly intensified over time. In periods of inter-group conflict, this plasticity is potentially useful if *positive* (fitness-enhancing) social epistasis predominates and helps ensure that individuals are developmentally calibrated for violent competition. But in modernized conditions, the major effect may be to promote individualistic or atomized "drift" from adaptive norms through uncontrolled negative social epistasis, a process which might also generate opportunities for extreme dyscorporate-type individuals and anti-geniuses to potentiate negative social epistasis through their access to elite culture.

This tendency likely attenuates not only global population fitness but also dimensions of quality of life, such as mental health and existential meaning, which, to reiterate, appear to associate significantly with religiosity (religion potentially being an exemplar of a group-selected adaptation; Wilson, 2002) at the individual and group levels (Flannelly, 2017; Oishi & Diener, 2014). Strikingly, there is evidence that belief in "social-moral progress" can function as a surrogate religion and thus offer some substitute meaning in life[22] (Rutjens, Van Harreveld, Van der Pligt, Van Elk, & Pyszczynski, 2014). Therefore, the adverse consequences of negative

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[21] Interestingly, there are possible grounds for synthesizing the SEAM with religious and spiritual perspectives; Beck (2007), for example, considers the implications of genetic and epigenetic science in relation to Christian doctrine, noting that "[t]he human brain and all of man's thinking and feeling [including inner life and religious outlook] are intimately connected with [the epigenetic activation of genes relevant to health]" (p. 67).

[22] Dutton and Dunkel (2019) found evidence that atheists/agnostics are "relatively hedonistic … and less interested in family" (p. 70), consistent with the expectations of the intellectuals discussed in earlier chapters, such as Max Weber, who suspected that modernization,

social epistasis may establish maladaptive feedback loops, whereby further maladaptive behaviors and norms are invested in to escape these problems,[23] that is, they serve as psychological compensatory mechanisms. It is doubtful that these compensatory mechanisms will be successful, since they occur in the context of a generally declining human condition (Lynch, 2016), and because, given their atomizing effects, they are unlikely to satisfy the sorts of needs that may exist to encourage group-fitness-enhancing conditions (intense intra-group binding, sacrifice for one's fellows, shared religious experiences, and the like). This all raises the possibility that negative selection, a phenomenon thoroughly explored in the previous chapter, is actually still quite active in the West, but is occurring at the *group* level, through the negative-social-epistasis-induced fitness collapse of Western populations exhibiting high mutation loads.

The distinctive conditions that generated Western excellence are set to continue deteriorating so long as selection does not favor heroes, geniuses, and saints, but rather "Last Men" (Nietzsche, 1891/1999) whose quest for personal happiness likely cannot sustain a civilization in the long run.

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in undoing public sources of meaning such as religion, would lead people to withdraw into private, self-interested pursuits.

[23] For example, moralized condemnation of those who hold to traditional norms and resist individualizing moralities is a signal aspect of contemporary Western culture (Rubin, 2015).

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