



Defending Biobehavioral Science

THE FAILURE OF ENVIRONMENTALISM

In the Western world at least, it is no exaggeration to say that those academic disciplines concerned with human behavior, even if only obliquely, are in the grip of strong normative biases. More specifically, these fields tend to exhibit biases consistent with a tilt toward individualizing psychological moral foundations¹ among their practitioners. Those with these moral foundations tend to associate with political ideologies on the “left.” (We do not prefer to frame this matter in politically divisive ways, but much of the literature on normative biases in academic research does refer to the sources of these biases in political terms, and, in places, we are forced to follow their approach. Moreover, since political orientation can reasonably serve as a proxy measure for individuals’ moral foundations [Haidt, 2012], and because good data explicitly concerning the distribution of moral foundations in populations are quite limited, while such data on political orientations are abundant, referring to the literature on population distributions of political orientations lets us better ascertain the state of certain normative biases in the academic fields that are of interest to us than we otherwise could.)

¹ Following the work of Haidt (2012), Gladden and Cleator (2018) describe concerns for fairness—which, in light of Haidt’s moral foundations questionnaires, seems largely to reduce to egalitarianism—and harm avoidance, which captures moral inclinations to compassionate or humane behavior, as indicating a latent *individualizing* moral foundation.

Duarte et al. (2015) report that “58–66% of social science professors in the United States identify as liberals, while only 5–8% identify as conservatives”; similarly, “52–77% of humanities professors identify as liberals, while only 4–8% identify as conservatives” (p. 3). (As noted in the Introduction, in European contexts “liberalism” typically refers to the view that government should be neutral with respect to visions of the good, whereas in the North American context, in which Duarte et al. [2015] operate, “liberalism” refers to a brand of social democratic politics; unless otherwise noted, the current authors employ the term and its cognates in the former sense.) A study of the political ideologies of Canadian professors found that 33.3% are broadly leftist while a mere 5.2% are broadly rightist (compared to 24.4% of adults in the Canadian population with at least a B.A. degree who identify as broadly rightist), with involvement in teaching humanities courses and opposition to religion being noteworthy predictors of leftism (Nakhaie & Brym, 2011). There is also evidence of left-wing bias in British academia (Carl, 2017), and given that the political and cultural characters of Western Europe overall are more to the left than, say, those of the United States (Pew Research Center, 2012), one expects that substantial leftist academic bias in Western Europe is not limited to Britain.

Attending just to the figures for the United States given above, it should be noted that in framing the matter in terms of a “liberal” (social democrat)/conservative dichotomy, the numbers likely understate the extent of relevant political/moral homogeneity in the American social science and humanities fields. That is because one struggles to find a mainstream American, and even Western, political party or view that is not, in world-historical perspective, on the left or individualizing in character. Many, probably most, of the American academics who identify as “conservatives” or “moderates” at least nominally share with those identifying as leftists important normative and empirical commitments (Salyer, 2018)—for instance, belief in the moral and biological equality of all human groups, or even persons, across time and space, and support for a liberal as opposed to a perfectionist form of government²; again, within the context

²Note that mainstream American Republicans and “right” libertarians would qualify as leftists in this view.

In the footnoted sentence, “perfectionism” refers to any political view that lacks neutrality with respect to visions of the good, and so would have governments promote the realization of some such vision. But it should be appreciated that the philosophical territory here is more complex than the liberalism/perfectionism dichotomy that we have indicated suggests. For example, some have argued for political views that could be classified as “perfectionist liberal”

of moral foundations theory, we take this to mean that in the modern Western world, the vast majority of academics identifying as on the political left *or* right (or in the center) can reasonably be described as having moral psychologies tilted in an individualizing direction, considered in world-historical context.

But one could argue that it does not follow from the mere fact that individuals with particular political (and/or moral) orientations predominate in certain academic disciplines that the research and scholarship done in those disciplines tend to be biased in ways consistent with those orientations. Nonetheless, evidence for the existence of such bias is apparent in the fact that whenever academics of any notoriety do question or reject beliefs that seem central to individualizing moralities, they are often met with aggressive opposition from fellow academics, administrators, and even students, who, in turn, rarely experience significant disapproval from those with meaningful social influence (Carl & Woodley of Menie, 2019; Nyborg, 2003, 2011; Woodley of Menie, Dutton, et al., 2018; for details on philosophers' often hostile attacks on moral inegalitarians, see Steinhoff, 2015). If those defending, or offering evidence that could support, sufficiently "countercultural" ideas (i.e. those ideas that could be considered to have undesirable implications from the perspective of those with individualizing moralities) in academia strongly tend to experience such serious negative consequences for doing so, at least in the event that they or their work achieves substantial attention, it seems likely that academics will try to avoid those consequences; so one would expect that academics in fields with meaningful bearing on moral and political issues will typically make efforts to ensure that their work does not offend dominant moral and political views, and thus those views will shape the outputs of those fields. (Germane to this point, Carl & Woodley of Menie, 2019, in a study of controversies in the area of intelligence research, observe that "egalitarian [that is, egalitarian] tendencies are more common in individuals on the political left, and it is that political faction from which all the most hostile criticisms of intelligence research have originated" [p. 5]; as one would expect, it is much more challenging to find cases of academics suffering

(e.g. Raz, 1986), and thus the two orientations may not be strictly incompatible. In contrast to us, Reiff (2007) identifies American neoconservatives as representing a kind of perfectionism and distinguishes "hard" from "soft perfectionists," with the former rejecting more of the presuppositions that he takes to define liberalism than the latter, which include neutrality but also, for example, what he calls "toleration"—but the details of these distinctions and precise philosophical concepts are not within the scope of the current work.

serious adverse effects on career or reputation, e.g. job loss, for promoting ideas that fit easily with individualizing moralities, such as the idea that environmental factors entirely determine variation in human intelligence.) Interestingly, and consistent with these observations, it appears that the usage frequencies of a composite of terms associated with individualizing moral foundations (care + harm + fairness + reciprocity) increased, while the usage frequencies of another composite associated with the opposite “binding” moral foundations (loyalty + betrayal + purity + sanctity + degradation + authority + respect) decreased from AD 1900 to 2000 (see Fig. 2.1); these data are taken from Google Ngram Viewer, and indicate changes in the patterns of natural language use, in Anglophone textual corpuses in the case of our analysis, which reasonably are taken to reflect underlying cultural evolution (Michel et al., 2011; trends in Google Ngram Viewer reflect more than changes in academic texts, but of course cultural trends in academia and the broader world are not isolated from one another). There is a high-magnitude (i.e. effect size between 0.5 and 1; Cohen, 1988) and statistically significant negative correlation between

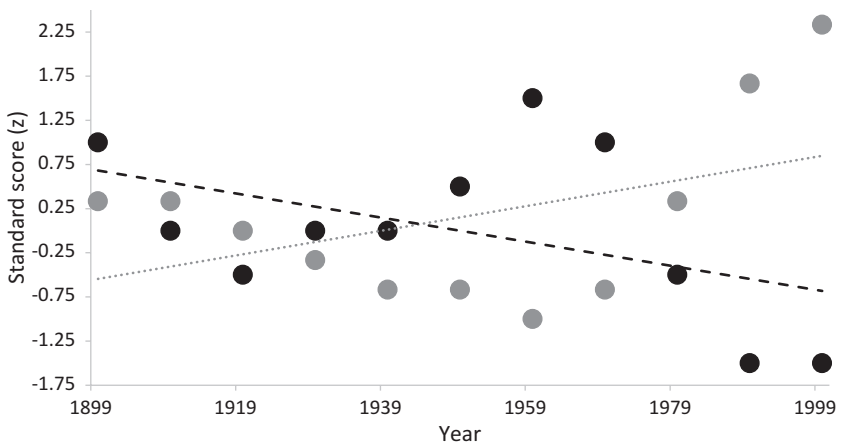


Fig. 2.1 The black dots track the usage frequencies of terms associated with “binding” moral foundations, whereas the gray dots track the usage frequencies of terms associated with “individualizing” moral foundations using Google Ngram Viewer data. The correlation (r) between the two trends is -0.828 ($p < 0.05$; $N = 10$)

the trends time ($r = -0.828$, $p < 0.05$, $N = 10$ decades), evidencing their divergence over this century-long time period.

What is more, these individualizing commitments are so uncontroversial that in the writings of academics they are typically presented as if they were incontrovertibly true. That is to say that most Western academics seem to believe that moral and biological equality, applying over both time and space, are on such solid ground that no case needs to be made in their favor—or that if such a case is to be made, it need do little other than offer individualizing affirmations to the effect that alternative views are so obviously wrong as to barely merit consideration. For instance, legal scholar Edward Rubin (2015), in a recent book devoted to explaining changes in the moral culture of the Western world, notes that “[b]etween the years [AD] 0 and 1000, the privatization process meant that systems of social control became increasingly more violent ... [Later years] reveal an opposite trend ... but that is the result of culture, not biology” (p. 332, n. 74). No evidence or argument whatsoever is provided in support of the final claim—for Rubin, it is seemingly axiomatic that temporal changes in the behavior of human populations can only be due to cultural (and maybe more generally, environmental) factors. Perhaps Rubin would allow that certain behavioral changes and differences of human populations are due, at least in part, to biological changes and differences. But it is unclear what motivated his assertion that only “cultur[al], not biolog[ical]” factors reduced the prevalence of human violence over the given period of time other than a mere assumption favoring cultural determinist models of behavioral explanation and against such models that invoke biology.³

A further example is in the scholarship of the celebrated historian Ian Morris. In his book *Why the West Rules—For Now*, he offers the following in presenting his approach to explaining human population-level behavioral differences: “[B]iology and sociology explain most of the shape of

³It might seem odd that Rubin is inclined to cursorily reject biological hypotheses about human behavioral change, as he elsewhere notes, partly in light of biological considerations, that “equality is not self-evident at all” (2015, p. 181). Importantly, however, he limits this acknowledgment to inter-*individual* inequality (and to the fact that men and women play different roles in reproduction), which some high on individualizing moral foundations will admit exists (though not infrequently with the insistence that the important differences stem from environmental and not biological factors; nothing in Rubin’s account rules out his acceptance of such a view, and his rather explicit individualizing morality makes it likely that he does accept it).

history ... but these biological and sociological laws are constants, applying everywhere, in all times and all places. They, by definition, tell us about humanity as a whole, not about why people in one place have fared so differently from those in another. To explain that ... we need ... geography” (Morris, 2010, p. 29). Morris claims to recognize that a case for biological egalitarianism needs to be made. However, the one that he propounds barely transcends recapitulating the geographical determinism of Jared Diamond—the thrust of which is encapsulated in the passage from Morris (2010) provided above—and tarring opposing views with politically charged invective, the latter move signaling an assumption of the truth of biological egalitarianism from the outset, insofar as it suggests an immediate refusal to treat the matter at issue as truly open to dispute.

As advocates of geographical determinism, Morris and Diamond lose sight of a basic tenet of evolutionary science,⁴ namely that distinct environments and ecologies select for different hereditary traits (something that Charles Darwin grasped even though he lacked understanding of the material basis of heredity, i.e. genetics). And with geographical variation, there is of course variation of ecologies and environments. Morris (2010), for instance, contends that “[n]ature ... is just not fair” since “[a]griculture appeared in the Hilly Flanks thousands of years before anywhere else ... because geography gave [the people there] a head start”; the point here is that such differences of geographical fortune can, at least in principle, explain all inter-population human behavioral variation without any need to invoke biological evolutionary factors (p. 117).

Even setting aside geographical variation, it must be recognized that a human population heavily relying on agriculture for thousands of years will be subjected to different selective pressures than other human populations in distinct subsistence paradigms (as others have noted, e.g. Rushton, 1999) because of the unique challenges associated with agricultural life. Such selective pressures surely conferred to agricultural populations genetic endowments in behaviors that partly determine success in agriculture, and therefore affect the odds of survival and reproduction for agriculturalists, which non-agricultural populations would not have had (in light of the basic principles of evolutionary theory that we just indicated). That these genetic endowments can be ultimately ascribed to the mere

⁴For those who need it, a brief exposition of modern evolutionary theory is provided at the beginning of the second part of this chapter.

luck of agricultural populations' historical environmental and ecological conditions does not make them any less real. By the same token, modern humans' high intelligence relative to all other known organisms depends on the fact that their ancestors happened to encounter certain environmental and ecological conditions. That does not somehow render this cognitive endowment non-biological today.

The very fact that Morris uncritically recites Diamond's geographical determinism thesis when it has faced rather severe critique, which should at least be addressed (see, e.g. Clark, 2007; Cochran & Harpending, 2009; Figueredo, 2009; Rushton, 1999), intimates an assumption of biological egalitarianism out of hand. It is telling that Morris (2010) even includes Cochran and Harpending's book *The 10,000 Year Explosion* (2009) in the "Further Reading" section of the very same work in which he extols Diamond's geographical determinism; but he does not discuss the critique of Diamond that Cochran and Harpending present. Morris even goes so far as to assert, absent any citation of supporting evidence, that "[o]ur dispersals out of Africa in the last sixty thousand years wiped the slate clean of *all* the genetic differences [among human populations] that had emerged over the previous half million years" (Morris, 2010; emphasis added). This claim is entirely inconsistent with evidence from Cochran and Harpending (2009), who document a number of such differences distinguishing modern human populations. In more recent years, many population and behavior geneticists, evolutionary psychologists, physical anthropologists, behavioral ecologists, and the like have offered further evidence of socially significant genetic differences among human populations, as well as evidence of evolutionary-genetic changes within certain populations over just the past few thousand years (some predicted by Cochran & Harpending, 2009), which the unique environmental circumstances of those populations likely caused, probably leading to genetic divergence from other populations (see Kirkegaard et al., 2019; Lasker, Pesta, Fuerst, & Kirkegaard, 2019; Piffer, 2019; Winegard, Winegard, & Boutwell, 2017; Woodley of Menie, Younuskunju, Balan, & Piffer, 2017). Despite these and other shortcomings in Morris' book, the current authors failed to find any high-profile academic who has taken him to task for them. Rather, *Why the West Rules—For Now* has won more or less universal acclaim. It would appear that tendentious research is permissible among the academic establishment so long as its imperfections align with individualizing pieties.

One could think that Morris and Rubin are exceptions to a more balanced academic consensus on the role of biology in human behavioral variation. But more systematic evidence is available, suggesting that they are firmly within the mainstream. Geher and Gambacorta (2010) and Horowitz, Yaworsky, and Kickham (2014) both examined academics' views about the relation of biology to human behavior, though the latter only probed the beliefs of sociologists. The former study, based on data from 268 adults, reached a number of striking conclusions: leftism (or "political liberalism," as the authors call it) is associated with the belief that human sex differences are environmental rather than genetic in origin; academic employment, especially in the departments of sociology and women's studies, is also associated with belief in the foregoing environmentalist⁵ view; finally, employment as an academic is associated with the belief that "behavioral differences between *roosters and hens*" (emphasis added) are functions of environmental rather than biological factors (Geher & Gambacorta, 2010, p. 32). The latter study, based on a survey of 155 "sociological theorists," found, echoing the former, that "liberal-minded," that is, likely individualizing, sociologists are more opposed to "evolutionary biological" ideas than those probably higher on the opposite cluster of psychological moral foundations, that is, those high on Haidt's "binding" orientations that stress loyalty, authority, and purity or sanctity (i.e. a tendency toward disapproval of activities traditionally considered disgusting) (Horowitz et al., 2014).

Particularly striking is the fact that of the 151 sociologists who responded to a question about their general "attitude toward applying evolutionary biological ideas to human social behavior and organization," only 13.2% selected the response indicating that they "embrace" such ideas, whereas 62.9% selected responses indicating skepticism or hostility toward them (Horowitz et al., 2014, p. 495). It must be stressed that resistance to such biological ideas may leave one unable to accept, without logical inconsistency, even the evolutionary origins of humanity itself, insofar as there seem to be very limited options for coherently reconciling denial of the relevance of evolutionary biology to human behavior with the belief that the human species emerged through evolutionary processes.

⁵We will use the term "environmentalism" more broadly to refer to the belief that human behavioral variation is primarily or entirely determined by non-genetic environmental variation.

Perhaps the clearest evidence of distinctively individualizing tendency among sociologists is in their response pattern to a question concerning a prototypical politically sensitive matter, namely the origin of human behavioral sex differences, compared to other questions. Whereas 81.2% of surveyed sociologists were willing to recognize the plausibility or high plausibility of the idea, discussed in more detail later in this chapter, that genetic differences for “intellectual potential” exist among individuals (though nearly a fifth were either uncertain about this or thought it unlikely or very unlikely), only 42.8% were approving of the claim that certain average differences in social and cognitive skills between men and women have a biological basis (Horowitz et al., 2014, p. 497). Unsurprisingly, Horowitz’s team found that political radicalism, that is, a kind of ideology that probably attracts those very high on individualizing moral foundations, and feminism significantly negatively predicted sociologists’ approval of evolutionary or more broadly biological accounts of human behavior. Since inequality between individuals is less offensive to those with strong individualizing sensibilities, in light of their political preferences, than inequality between the sexes or other groups, it is unsurprising that sociologists were particularly hostile to biological explanations of sex differences.

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Hopefully it is now clear that, at least in the West, individualizing bias is generally and strongly present in those academic disciplines concerned with human behavior. Further, there is evidence (albeit less robust) that this bias is associated with opposition to genetic explanations of human behavioral variation, especially between-group variation. We refer to these biological explanations collectively as “hereditarianism.”⁶ Of course and although we have already made clear that we reject it, anti-hereditarianism, whatever the motivations for maintaining it, may encompass true empirical beliefs, even if, for example, Morris and Diamond have argued poorly for it. In other words, anti-hereditarianism may be true in part or whole—

⁶To be sure, “hereditarianism” is concerned with scientific explanations made in reference to heritable factors, specifically genetic ones. There are various non-genetic biological approaches to explaining human traits and trait variation, but the genetic approaches in particular seem to be unwelcome among those on the political left (see Furnham, Johnson & Rawles, 1985) and proponents of environmental explanations (environmentalists), and thus our focus is on hereditarianism.

the mere fact that arguments made on its behalf are often weak, and are probably often morally/politically motivated, does not exclude this possibility. Reasons to challenge political/moral biases in academia would not be very strong if the only beliefs that they favor rejection of are false anyway.⁷ And what appears to be bias could in fact be principled moral and political rejection of a paradigm that sound empirical inquiry has (seemingly) authoritatively discredited, especially if acceptance of that paradigm carries certain dangers.

Anti-hereditarians often seem to think that their approach exhibits just this sort of scientific integrity. For instance, paleontologist Stephen Jay Gould and population geneticist Richard Lewontin, though both committed Marxists,⁸ inveighed relentlessly against evolutionary psychology, behavior genetics, and psychometrics for allegedly scientific reasons.⁹ Indeed, Gould stridently criticized hereditarians for their “a priori prejudice,” which, he contended, was the cause of the supposedly manifold errors in their research (1996, p. 59). By contrast, then, it would seem that Gould believed his work to be at least better and less biased than the hereditarian research he attacked as poor science. Yet, his own output

⁷Although note that it is generally accepted that sound scientific practice treats all empirical beliefs as, in principle, defeasible. This is needed to avoid dogmatic commitment to theories and beliefs that may impede further advancement of science. There is, then, always some reason to criticize moral and political biases that *compromise* scientific research. But it is necessary to find evidence that such biases have had a corrupting effect before concluding that some particular bias is problematic. It seems certain that no researcher is entirely free of extra-scientific biases, and we are not exceptions. The point is that the mere presence of biases on the part of a researcher, which, as just indicated, are seemingly ubiquitous, does not constitute sufficient basis to dismiss their scientific work (so in the above in this chapter, for example, we have endeavored to draw associations between apparent biases and verifiable scientific errors or other problems). For the zealous anti-hereditarian Stephen Jay Gould, this evidently was not the case: so long as he could even *speculate* that a scientist, such as Samuel George Morton, was operating under unconscious biases, Gould felt entitled to claim that that scientist’s work really was distorted by bias, provided, apparently, that the scientist offered results that Gould found morally disagreeable (see Lewis et al., 2011; Ruse, 1989; Sesardic, 2005, pp. 39–40). Even worse, and as will be discussed in the main text, it appears that Gould entered distortions into his own re-analysis of Morton’s work to offer evidence of faulty research where none in fact existed.

⁸One can debate whether Karl Marx was or was not a hereditarian of some sort. But this is not very relevant. In practice, Marxism has been an overwhelmingly anti-hereditarian ideology.

⁹Though Lewontin was at times quite open about the fact that his “scientific” work was a means of pushing a political agenda (see Wright, 1998).

clearly expresses strong moral and political biases—revealed, for instance, where he makes apparent that his most famous critique of hereditarianism, the ostensibly scientific *The Mismeasure of Man*,¹⁰ is in no small part a moralistic protest against various forms of European “supremacy” (e.g. Gould, 1996, p. 144) and their harmful alleged consequences (p. 263; see also Ruse, 1989).

More importantly, a number of the attacks that Gould leveled against hereditarian scientists in this work were subsequently shown to be nothing more than defamatory and possibly willfully deceitful misrepresentations, which seemingly originated in his own just mentioned biases. The most prominent such case is Gould’s allegation that physician Samuel George Morton was led to produce inaccurate data on human skull size differences consistent with his alleged racial prejudices. It has since been shown that Morton’s measurements were sound (Mitchell, 2018) and that, if

¹⁰Nonetheless, Gould tirelessly attempted to refute criticisms of his work, an effort facilitated by the characteristic slipperiness of his writing, namely his tendency to explicitly state that he does or does not do or believe some particular thing, but make apparent that the opposite is true at another point in the same work. Alcock (1998) provides an example of this trick of Gould’s: “In *The Diet*, after having caricatured persons studying the mating tactics of men and women as genetic determinists, [Gould] writes, ‘Perhaps I have caricatured this position, but I don’t think so, having read so many articles of support. In fact, I don’t even think that the basic argument is wrong.’ But Gould then goes on to explain that the basic argument *is* wrong because it supposedly cannot cope with the reality that human behavior is influenced by cultural factors” (p. 325; emphasis in original). This tactic allowed Gould to conveniently respond to critiques of his work by denying that he did what his critics accurately claimed he had done, citing as proof the false characterizations of his own writings peppered in them: “These apparent concessions ... enable Gould to deflect criticism by pointing piously to his rare, against-the-grain comments when confronted by someone who is responding to the basic negative nature of his attacks. Thus, when Maynard Smith ... attempted to rebut ‘Gould’s curiously ill-tempered review of Helena Cronin’s *The Ant and the Peacock*’ ... Gould replied by pointing to a benign sentence in an otherwise hostile review” (Alcock, 1998, p. 325).

The same tactic is evident in the work of Gould’s colleagues and fellow Marxists Richard Lewontin, Steven Rose, and Leon Kamin. In this trio’s infamous anti-hereditarian book *Not in Our Genes*, it is argued that science is never free of political bias. In so arguing, Lewontin et al. (1984) seem to preempt charges that their far-left orientation to science is just as politically biased as they allege hereditarianism to be (just in the opposite direction); and yet, in the book as a whole, they go ahead with ferocious attacks on hereditarians for their supposedly politically warped research. Thus, Lewontin et al. (1984) expected readers to accept both that political bias in science is ubiquitous *and* that hereditarian researchers are worthy of unique scorn for doing politically biased scientific work. The hypocrisy is obvious and indicates merely an attempt of Lewontin, Rose, and Kamin to have their cake and eat it too.

anything, *Gould* deliberately manipulated Morton's numbers to create the false impression that the latter was a biased scientist (Lewis et al., 2011). Perhaps more damning, however, is the fact that an anthropology student, John Michael, re-measured a portion of the skulls in Morton's collection and determined that Morton's results were not biased *before* Gould produced the second edition of *The Mismeasure of Man* (Cofnas, 2016, pp. 486–487). Even though Michael sent Gould a copy of the paper reporting his corroboration of Morton's measurements, Gould left his scurrilous claims about Morton's research in *Mismeasure's* revision (Sesardic, 2005, p. 42, n. 14).

It is an unfortunate truth that a great deal of academic work with an anti-hereditarian bent is uncharitable to its targets (so the phenomenon is in no way limited to Gould's output). Philosophers of science Neven Sesardic (2005) and Nathan Cofnas (2016) have copiously documented not only a welter of errors in the work of Gould (see also Alcock, 1998) and researchers of a similar bent, but also, more troublingly, the tendency of more contemporary academics to uncritically parrot the long-discredited arguments and claims of these scientists.

This tendency is still apparent even in very recent years. Endocrinologist Barbara Demeneix's *Toxic Cocktail* (2017) is a case in point. Demeneix offers an explanation of the rising prevalence of a number of behavioral and psychological problems in developed countries, for example, increasing rates of autism, in purely environmental terms. More specifically, she blames toxins and pollutants of various kinds for this growing psychobehavioral damage. Other researchers, however, have presented strong empirical evidence and/or theoretical considerations indicating that some of these changes are due, at least in part, from genetic factors (e.g. D'Onofrio et al., 2014; Kong et al., 2017; Liu, Zerubavel, & Bearman, 2010; Lynch, 2016; Woodley of Menie, Figueredo, et al., 2017).

Demeneix is aware of at least some of this research but chooses to dismiss it on the basis that it "smacks strongly of biological determinism and genetic determinism or the overriding influence of genes compared to that of the environment. Many authors have written excellent critiques of biological determinism, including Richard Lewontin, Steven Rose, and Leon Kamin" (2017, p. 87). This is not a sensible counter to hereditarianism for a number of reasons. In the first place, the only "critique" of "biological determinism and genetic determinism" (an apparent pleonasm) that Demeneix cites was over three decades old at the time of her book's publication. That critique, the openly Marxist *Not in*

Our Genes (1984), has been met with more or less universal rejection from the relevant scientists who have considered it (for an especially cutting review of this book, see Dawkins, 1985), and so it is odd that Demeneix treats it as an uncontroversial basis on which to reject biological or, more narrowly, genetic theories of recent human behavioral change. One critic (Wright, 1998) has even gone so far as to characterize *Not in Our Genes* as a work of “slander” (Wright, 1998, p. 199), further contending that it offers nothing but familiar arguments that already had been (e.g. Jensen, 1982) and continued to be “refut[ed],” though without any acknowledgment by anti-hereditarians (Wright, 1998, p. 198; see also Sesardic, 2005; Sarraf & Woodley of Menie, 2021; Woodley of Menie & Sarraf, 2021). Indeed, the terms “genetic determinism” and “biological determinism,” which not just Demeneix but also Lewontin, Rose, and Kamin employ, are mere terms of abuse that only reflect ignorance of hereditarian research (see Sarraf & Woodley of Menie, 2021) since “there is literally no one who ever subscribed to genetic determinism,” that is, “the doctrine that an organism’s phenotype is determined by genotype alone”¹¹ (Sesardic, 2005, p. 14).

Even when setting aside its most unreasonable theses, it remains true that none of the central arguments of *Not in Our Genes* has fared well in the course of time—for example, that the concept of general intelligence is illegitimate and that “[s]trong performance on IQ tests is simply a reflection of a certain kind of family environment” (Lewontin, Rose, & Kamin, 1984, p. 94). By point of fact, all efforts to undermine the theory of general intelligence, that is, that the validity of intelligence tests is primarily a function of the degree to which they tap a single mental factor (general intelligence or g), have failed—it is a simple fact that one statistical psychometric factor accounts for much of the variance in and most of the validity of IQ test scores, consistent with the predictions of g theorists (Bouchard, 2014; Ganzach & Patel, 2018; Jensen, 1998; Johnson, te Nijenhuis, & Bouchard, 2008). There is hardly a serious psychometrician left who rejects g theory given the strength of such results, and the most extreme alternatives, such as Howard Gardner’s theory of multiple intelligences, have lost virtually all support from relevant experts (Waterhouse, 2006).

The most spectacular failure of all is perhaps Lewontin, Rose, and Kamin’s (1984) effort to argue that “family environment” is the decisive

¹¹Demeneix’s understanding of “genetic” or “biological determinism” is perhaps more tempered than this, but Lewontin, Rose, and Kamin’s (1984), to which she refers, is not.

determinant of IQ test performance (p. 94). Roughly a century of scientific work on the genetics of intelligence has left little doubt that, by adulthood, family environment explains just about *none* (0%) of the variation in IQ scores (Plomin, 2018), whereas genetic factors explain about 70–85% of the variation (Bouchard, 2004; Plomin & Deary, 2015; *g* potentially has an even higher adult heritability of 86%, according to Panizzon et al., 2014, who modeled it explicitly as a latent factor, reaching 91% when corrected for measurement reliability, according to Woodley, te Nijenhuis, & Murphy, 2014). (The percentage of variation in a phenotype, or some life outcome, in a population for which variation in genetic, and perhaps other heritable, factors accounts is called “heritability.”) It is unknown what factor(s) accounts for the residual 20–30% of unexplained variance in IQ test performance, but it may be primarily measurement error and random developmental noise—genetic (and perhaps other biological) error, in other words, with perhaps some contribution of random environmental events (Jensen, 1998; Sarraf & Woodley of Menie, 2021). Recently, work on the heritability of intelligence has ramified into the realm of molecular genetics, meaning that specific genetic variants, or variants that are “nearby” in the genome to the causal ones, have now been causally implicated in individual-level cognitive and related phenotypic variation in humans (Lee et al., 2018; Sniekers et al., 2017; Trampush et al., 2017; Zabaneh et al., 2017). This is reasonably construed as a deathblow to the “not in our genes” thesis.¹²

¹²Some critics, such as Ken Richardson and Jay Joseph, deny these implications of behavior-genetic research. For a detailed response to arguments of the sort that they offer, see Sarraf and Woodley of Menie (2021). In brief, it is worth noting that these and other critics tend to focus narrowly on problems alleged to pertain specifically to twin studies, problems that they argue inflate heritability estimates. Their complaints are very probably incorrect, however, since the heritability estimates of twin studies have been replicated in non-twin behavior-genetic analyses specifically aimed at determining if the results of twin studies could be validated (e.g. Schwabe, Janss, & van den Berg, 2017). Moreover, there is evidence that certain errors that some such critics highlight in twin studies in fact tend to downwardly, not upwardly, bias those studies’ heritability estimates (although the degree of this bias is associated with the heritability of the trait; see, e.g., Liu, Molenaar, & Neiderhiser 2018). Some have noted that molecular-genetic studies tend to deliver far lower estimates of trait heritability than classic (non-molecular) behavior-genetic studies, and take this to be evidence of upward bias in those studies of classic design. But this “problem of missing heritability” is unsurprising in light of the fact that these molecular methods are quite new and imperfect—for instance, they are poor at detecting the probably substantial contribution of rare genetic variants to the heritabilities of traits and life outcomes; Kendler et al. (2016), given the results of their non-twin behavior-genetic study, note that they found no evidence that twin

A more complete assessment of the hereditarian and environmentalist paradigms is attempted later in this chapter. But here it is worth asking why there is such limited sophistication in efforts to defend anti-hereditarian (or environmental determinist or environmentalist) views. Too often, opponents of hereditarian science systematically depend on misrepresentation and omission of theory and fact for their arguments to achieve any apparent plausibility. Worse still, and as noted earlier, environmentalists seem unable to abstain from concerted efforts to intimidate and defame their ideological enemies (Carl, 2018, 2019; Carl & Woodley of Menie, 2019; Cofnas, 2016; Davis, 1986; Hunt, 1998; Meisenberg, 2019; Nyborg, 2003, 2011; Scarr, 1987; Sesardic, 2005; Segerstråle, 2000; Walsh, 2014; Woodley of Menie, Dutton, et al., 2018; Wright, 1998). Their resistance to hereditarianism, or even mere isolated findings that are at odds with broadly individualizing moral commitments, is rarely without a great deal of passion. Walsh (2014) recounts the story of anthropologist Charles Leslie, who left an editor post at the academic journal *Social Science and Medicine* in protest “after it published an article documenting the large overrepresentation of Africans and people of African descent among AIDS patients” (p. 6). Leslie issued a statement explaining his motivation for resigning, in which he averred that “[n]on-social scientists generally recognize the fact that the social sciences are mostly ideological ... Our claim to be scientific is one of the main academic scandals ... By and large, we believe in, and our social science was meant to promote, pluralism and democracy” (quoted in Walsh, 2014, p. 6). For a serious scientist, an admission anything like that offered by Leslie would be an occasion for embarrassment. But Leslie somehow seems to have been proud of the fact that his life ostensibly as a scientist has not been about generating empirical knowledge at all, but instead has been a very refined and opaque¹³ form of politicking.¹⁴

There is not space here to document the countless instances of academic behavior akin to Leslie’s, but they are largely united insofar as they are highly emotional and often clearly motivated by individualizing ide-

studies provide upwardly biased heritability estimates, and so conclude that biases in twin studies are not a plausible source of the missing heritability problem.

¹³Leslie certainly does not announce his extreme bias so transparently in each of his scientific publications.

¹⁴One also has to wonder what value this sort of moralistic refusal to accept certain facts has in the “real world.” If some demographic suffers from a higher rate of HIV infection, ignoring this will only prevent the development of policy initiatives that might save lives.

ologies. Evolutionary psychologists who attempt to scientifically explain the phenomenon of rape in humans are libelously portrayed as “silly ... narcissistically self-aggrandizing [fantasists] who justify sexual coercion” (quoted in Palmer & Thornhill, 2003); psychometricians investigating the effects of immigration to developed nations on population-level intelligence (e.g. Nyborg, 2012) are wrongfully (see Vernon, 2015) accused of scientific misconduct (it seems that Nyborg’s experience in this case was an extension of earlier attacks he faced from Marxist academics; Nyborg, 2011, pp. 250–251); behavior geneticists studying the relative effects of genetic and environmental factors on variation in intelligence are maligned and “threatened and attacked, both verbally and physically” (Scarr, 1987, p. 224); and so on. In recent years, neurobiologist Adam Perkins, who has argued that welfare claimants tend to manifest an “employment-resistant personality profile,” had a talk at the London School of Economics canceled in response to pressure from activists (Foster, 2016), and the political scientist Charles Murray was assaulted by protesters at Middlebury College for his supposedly “bigoted” views (Krantz, 2017).

In face of all of this, one has the impression that environmentalists, and those of an individualizing moral bent more broadly, are driven by fear and paranoia in their antagonism of hereditarians. They are, seemingly on the whole, unwilling to tolerate even the conditions in which hereditarianism *could* gain traction in academic or wider Western culture. A hypothesis explored later on in this book posits that this behavior is itself the product of biosocial factors. But for now, it is sufficient to note that these reactions are probably consequences of the fact that political and social ideologies associated with individualizing moral orientations often strongly depend on certain empirical beliefs, and these beliefs in turn have been seriously challenged by many strains of evidence that have been accumulating in the biobehavioral sciences for decades.

Some may be skeptical of the idea that biobehavioral science has political implications at all. But such skepticism is unwarranted. For example, leftism is principally defined by *egalitarianism*; some have even suggested that all forms of leftism take “universal equality” to be the “highest good” (Paul Gottfried quoted in Hawley, 2016, p. 11). But what distinguishes the political-moral left from right is perhaps somewhat more subtle. Leftism seems to overwhelmingly involve, in its various manifestations, commitment to the realization of equality in at least one morally salient domain (typically political, economic, or hedonic) among all persons in a national society, or even among all persons on Earth or among all sentient

creatures; leftists might treat such equality as a feature of the correct moral theory (as when certain utilitarians posit that all persons' pleasure must be regarded as "counting" equally) or might have some vaguer reason for regarding equality of whatever sort(s) as *intrinsically* good or right. To the extent that leftists come down from moral abstractions and take equality in concrete, empirical spheres of life to be realizable, and its realization to be a goal that ought to be urgently pursued, the findings of biobehavioral science threaten their moral-political mission. Certain persons on the left have acknowledged this fact—take, for example, Cordelia Fine's (2017) assessment of the relevance of empirics to the sex-egalitarian objectives of feminists: "Although scientific claims don't tell us how our society ought to be ... they can give us strong hints as to how to fulfil those values, and what kind of arrangements are feasible ... if the sexes are essentially different, then equality of opportunity will never lead to equality of outcome" (p. 17). Those inclined to politics informed by individualizing moral commitments are of course at liberty to await the day that technology can eradicate genetic human or even animal inequality (an issue to be considered later [see Chap. 8]), so obviously biobehavioral science does not challenge their values *as such*. But in the same way that standard economics has shown socialism¹⁵ to be an impracticable political-economic project, given certain general facts about human limitations (see Gintis, 2018) that do not seem realistically surmountable, biobehavioral science has done much to show that equality for humans, let alone for all animal life, is not achievable in the world as it is.

Unsurprisingly, then, those of individualizing moral psychologies are at pains to deny the relevance of genetic variation to human behavioral variation. They are forced to adopt a *sociological*, *sociocultural*, or (most general of all) *environmentalist paradigm*, according to which, even if biology can explain *universal* features of human behavior, only social, cultural, and/or environmental facts figure in explanations of behavioral differentiation. This skewed perspective has far-reaching and mostly untenable implications. It must deny, for instance, that individual behavioral differences have heritable bases and are targets for (natural, social, and/or sexual¹⁶) selection, which seems to exclude the possibility of human behavior-genetic evolution in the first place, in addition to the

¹⁵At least in the context of industrial and "postindustrial" societies.

¹⁶See Figueredo et al. (2017) for an elucidation of this categorization of forms of biological selection.

possibility that such evolution is ongoing (despite the fact that it manifestly is; Kong et al., 2017), and by extension an evolutionary basis for differences in behavior between humans and other primates (given that modern evolutionary theory assumes that there is heritable phenotypic variability among organisms with consequences for fitness,¹⁷ and that humans and other modern primates descended from archaic hominids). Moreover, it leads anti-hereditarian academics to offer particularly dubious explanations of social phenomena, such that these academics are far more often guilty of the scientific failings that they frequently impute to hereditarians than are hereditarians themselves. An exemplar of this hypocrisy is in anti-hereditarians' frequent complaint that evolutionary psychologists engage in "just-so story" telling in their research, that is, that evolutionary psychologists merely generate hypotheses about the ultimate biological origins of behaviors without ever offering good reasons to accept them or even advance them beyond the level of speculation (*cf* Confer et al., 2010; Figueredo & Berry, 2002; Woodley of Menie & Sarraf, 2021). The current authors are yet to see the "just-so story" criticism directed at anything but evolutionary science, especially evolutionary psychology. Yet the work of anti-hereditarian social scientists and humanists is *rife* with just-so stories that are far more egregious than almost anything one can find in the whole corpus of evolutionary research.

For the sake of illustrating this point, consider the following inventive explanation of the origin of human behavioral sex (though in this case called "gender") differences found in the work of noted feminist philosopher Sally Haslanger (apparently inspired in part by the writing of an even more illustrious feminist academic, Catharine MacKinnon):

[W]e can usefully model one process by which gender is constructed roughly as follows: The ideal of Woman is an externalization of men's desire (so-called Woman's Nature is what men find desirable); this ideal is projected onto individual females and is regarded as intrinsic and essential to them. Accepting these attributions of Womanhood, individual women then internalize the norms appropriate to the ideal and aim to conform their behavior to them; and, in general, behavior towards women is "justified" by reference to this ideal. This, in turn, *is responsible for significant empirical differences between men and women.* (2012, p. 93; emphasis added)

¹⁷"Fitness" refers to the replicative success of one's genes; a more elaborate treatment of the concept is offered in the second part of this chapter.

This explanation is highly implausible, and the author provides no serious empirical evidence to support it. First, the existence of sex roles across animal taxa,¹⁸ arising from variation in behavioral and physical traits, is an established fact, one most parsimoniously explained through *sexual selection theory*¹⁹ as opposed to theories invoking “environmental factors or chance” (Janicke, Häderer, Lajeunesse, & Anthes, 2016); there is simply no rational basis on which to expect that humans would be the one sexually reproducing species to which this rule does not apply:

we find it hard to believe that social role theory, even the “biosocial” version, retains any scientific credibility at all in the twenty-first century. To us, social role theory is a vestigial remnant of human exceptionalism. Given the overwhelming preponderance of comparative evidence for sexually selected sex differences in intraspecific aggression across such a broad diversity of species, it does great violence to the principle of parsimony to invent a special explanation for exactly the same phenomenon in our own species. Surely, such special pleading cannot be considered sound scientific theorizing.²⁰ (Figueredo, Gladden, & Brumbach, 2009, p. 278)

Haslanger (2012) ignores the voluminous literature on the evolution of behavioral (and other) sex differences, the findings of which do not align with her social constructivist thesis.

Second, even if one were to grant that her a-biological theory accurately describes relations between the sexes that held at some point in the very distant human past, its account implies that sexual selection would have favored those women most naturally compatible with, and thus most able to embody, the ideal of “Woman’s Nature” (e.g. through greater relative physical femininity and the like). In the absence of countervailing selective pressures, this process of sexual selection would have produced and/or deepened genetically based behavioral (and physical) sex differences in the long run. It would thus be incorrect to think that even the process that Haslanger outlines would not give rise to genetically based differences in behavior between the sexes.

¹⁸Note that some animals reproduce asexually.

¹⁹Sexual selection refers to variation in reproductive success (fitness) that occurs as a result of mate choice and competition for mates.

²⁰Figueredo, Gladden, and Brumbach’s (2009) assessment was applied specifically to the case of sex differences in aggression, but their view is clearly relevant to behavioral sex differences generally.

Third, it makes no sense that a sexually reproducing species would have arbitrary mate preferences. Haslanger seems to think that men's sexual tastes are matters of purely contingent social norms, unrelated to the biology of men or women. But she never convincingly explains why men constructed the "ideal of 'Woman's Nature'" in the first place. Her book gives the impression that the explanation would have something to do with this ideal helping to facilitate the oppression or domination of women by men, but this only moves the problem back a step—why, as Haslanger's own view posits, do men but not women tend to have an interest in socially dominating, and overall success (as a group) in so dominating, the opposite sex, and why are women acquiescent to male efforts at such domination (see Haslanger, 2012, pp. 41, 58–60); why is this general dominance/submission dynamic between the sexes so rarely reversed, especially at the group level, over time and space, and what non-genetic basis could the *ultimate origin* of this dynamic, with its high generalizability across environments, reasonably have?²¹

The standard evolutionary view of mate preferences is that they encourage reproduction with individuals who are likely to produce fit offspring, through the genetic traits and/or resources that they will prospectively bequeath to those offspring (Geary, 2010)—these preferences likely evolved because of this fitness-enhancing function. Mate preferences vary with a number of factors such as phenotypic condition (Cotton, Small, & Pomiankowski, 2006) and sexual relationship types (e.g. whether the relationships are prospectively short or long term—see Figueredo et al., 2017, p. 50—although this distinction is not free of controversy). Nevertheless, universal mate preferences in humans have also been noted, such as for

²¹ Moxon (2016) maintains that "[a]ny adherence to a notion that at root is 'social conditioning' is a naive position born of failing to appreciate that there is an infinite regress to biology.... The social constructivist view of the sexes is a self-contradiction ... [that] cuts no ice in psychology. The sexes are supposed identical, yet, at the very same time, one sex is held somehow to 'oppress' the other in some foundational way, through the nebulously envisaged structure or dynamics of 'patriarchy' No sense can be made of putting these two groundless, non-scientific positions together. It would be impossible for males to somehow conspire putatively to 'oppress' in their 'patriarchy' ... and for females not to do likewise if there were no such thing as sex difference" (p. 4; emphasis in original). While one likely could not find a notable feminist academic who would argue that the sexes are "identical," absent qualification, Moxon's argument is quite effective against feminist claims of genetic *behavioral* sameness, more often called equality, between the sexes.

more as opposed to less symmetrical faces and bodies²² (Geary, 2010, pp. 193, 208; *cf* Graham & Özener, 2016). Features regarded as attractive associate positively with health (Nedelec & Beaver, 2014), suggesting that they indicate relative freedom from deleterious mutations—indeed, evidence supports the idea that humans have evolved dispositions to find these traits attractive because they signal “good genes” that would benefit the fitness of prospective offspring (Geary, 2010, pp. 192, 209–210). Moreover, to the extent that mate preferences vary, this variation is under substantial genetic control (Zietsch, Verweij, & Burri, 2012). All this is to say that human mate preferences are not at all arbitrary or mere “social constructs” and furthermore that it is not sensible to think, in the light of the basic evolutionary theory, that they would be—given that there is variability in all fitness-relevant traits, and that some of this variability is heritable, it is unreasonable to expect that humans’ mate choices would be hostage to social and cultural conventions; rather, the sound expectation is that they have reliable heritable tendencies to favor mates who will likely advantage the fitness of their offspring, as their fitness would be seriously jeopardized if they lacked these tendencies. Since Haslanger’s theory of the origin of human behavioral sex differences rests on the premise that men’s sexual preferences in women are purely socially contingent constructs, it is implausible. It is more reasonable to maintain that the ideal of “Woman’s Nature” exists because it corresponds to the most prospectively fitness-enhancing ensemble of female traits. Together with the foregoing considerations provided, this makes clear that Haslanger’s “theory” is in fact a mere “just-so story.”

With the scientific research immediately above in mind, it should not surprise anyone that general aspects of biological theory sometimes become the critical targets of those oriented to individualizing moral foundations. An example of this that has proven harmful to the academic, and possibly public, understanding of biology is seen in the work of Stephen Jay Gould and Richard Lewontin (1979), specifically their attempt to minimize the role of selection and adaptation in the evolutionary history of life on Earth. Again indicative of Marxist influence, made so explicit in *Not in Our Genes* in the case of Lewontin and elsewhere in the case of Gould (see Ruse, 1989), the hope seemed to be that biological

²²This is not to imply that individuals never choose other desirable traits in mates *over* symmetry—they do. Rather, the point is that, *all else being equal*, people overwhelmingly tend to prefer more rather than less symmetrical sexual partners.

evolution could be interpreted as an essentially communistic process. Marx himself, at least once, scorned Darwin's selectionist theory of evolution, casting it as a mere ideological artifact of England's capitalistic milieu: "It is noteworthy ... how Darwin rediscovers his English society with its division of labor, competition, the opening up of new markets, 'inventions,' and the Malthusian 'struggle for existence,' among the animals and plants" (quoted in Gasman, 2004, p. 110). Gould and Lewontin (1979) appear to capture something of the spirit of this critique in their salvo against adaptationism and selectionism (theories invoking the "struggle for existence"), in keeping with Gould's belief that the "minimiz[ation]" of "alternative [non-selective] evolutionary agents" in biology such as "random drift," that is, random as opposed to selective changes in the frequency of genetic variants in a population, was undesirable (Beatty, 1984, p. 113). To a great extent, their arguments turned on a failure to understand what an adaptation actually is (see Figueredo & Berry, 2002) and a curious lack of awareness of the fact that their anti-adaptationism was merely another species of the "just-so story" that they saw everywhere in selectionist and adaptationist thought (Andrews, Gangestad, & Matthews, 2002; Figueredo & Berry, 2002 coined the term "just not so story" in reference to "[uncritical acceptance] of any alternative explanation as long as it is *not* an adaptationist hypothesis" [p. 517]). Importantly, the history of science indicates that adaptationism has fared far better than its alternatives: "The exaptationist research program [Gould and Lewontin's preferred anti-adaptationism], if there is anything even worthy of the name, has yielded very little new knowledge in comparison [to the adaptationist program] because of its inability to make novel predictions" (Figueredo & Berry, 2002, p. 518; see also Krasnow & Truxaw, 2021 and Woodley of Menie & Sarraf, 2021). Nevertheless, the ideas of Gould and Lewontin seem to have succeeded in sowing plenty of confusion (Alcock, 1998, 2001; Wright, 1998), especially in the social sciences (on Gould specifically, see Carroll, 1995).

All this aside, the fatal problem for the sociocultural/environmental paradigm is its poor explanatory power relative to its biobehavioral counterpart. There are too many regularities of human behavior that the latter can adequately explain, but the former cannot, to avoid the conclusion that the biobehavioral paradigm is superior. One highly persuasive testament to this fact is Clark and Cummins' (2018) study of a very large English pedigree, covering the years 1750 to 2017 (and therefore an enormous amount of social, cultural, and economic change), finding that variation in wealth,

educational, and occupational outcomes is almost entirely genetically determined. This result could hardly be more at odds with sociological views that insist on the overwhelming role of social “structures and processes” in producing socioeconomic status differences (see, e.g. Butler & Watt, 2007; it should be stressed that work offering such environmentalist assertions very rarely even attempts to measure genetic effects and compare their importance to non-genetic ones, preferring to sweep such considerations away as irrelevant with liberal use of, for example, the terms “essentialist” and “determinist”). Beaver and Walsh (2011) cover the poor explanatory performance of environmental/sociocultural theories of crime, noting that even when a statistical model includes variables from more than one environmentalist criminological theory, it will usually explain much less than 30% of the variance in the phenomenon of interest (p. 3); biologically informed approaches to the study of crime, while still relatively new, are already offering more impressive empirical results and more comprehensive and parsimonious theories (e.g. Figueredo et al., 2018). Quite damning findings for environmentalists come from Sariaslan (2015), who analyzes the relationship between neighborhood socioeconomic conditions and violent crime, substance use problems, and mental health problems in unusually large nationally representative samples of the Swedish population; his results indicate that neighborhood socioeconomic conditions likely have no causal effect on any of these outcomes, whereas genetic factors probably do, in complete contradiction to the structural-sociological approach.²³ Furthermore, Sariaslan (2015) found that variable exposure to “family income” among genetic full siblings may have no effect on the probability of participation in violent crime or of developing substance use problems. These findings are consistent with the typical results of behavior-genetic studies, which indicate that family environment has no lasting effect on psychological and behavioral traits (as indicated above in the case of intelligence) (Plomin, 2018).

Behavior geneticists have accumulated a tremendous amount of highly replicable evidence (see Plomin, DeFries, Knopik, & Neiderhiser, 2016)

²³ An environmentalist could object that this result may be contingent on the unusually high standard of living (in world-historical context) that the vast majority of Swedes enjoy. But the fact that Clark and Cummins (2018) found that genetic variation has been overwhelmingly determinative of social outcome variation over more than two and a half centuries in England bodes very poorly for this environmentalist counter, since eighteenth-century England, which Clark and Cummins’ data partly cover, had a remarkably bad standard of living by contemporary Western standards (Clark, 2007).

that genetic factors have a very substantial role in generating human psychological and behavioral variation. As noted above, variation in intelligence or IQ, which is robustly related to general success in life (Strenze, 2015), is probably about 70–85% determined by genetic factors in adulthood (Bouchard, 2004; Plomin & Deary, 2015²⁴). Environmentalists will in all likelihood have to accept the fact that “environmental factors have a more limited impact on individual differences in success than some theories suggest” (Moreau, Macnamara, & Hambrick, 2019).

²⁴Some, such as Turkheimer (2016), deny that behavior genetics has demonstrated much more than that correlations between genetic and phenotypic/life outcome variation exist. The idea is that behavior-genetic research is inadequate to support causal claims about the role of genetic differences in generating phenotypic/life outcome differences. But the force of this argument depends on the highly implausible view that there probably are hidden environmental factors strongly confounding these associations and that may be causally responsible for them (see Sarraf & Woodley of Menie, 2021).

Research on the generalizability of heritability estimates across populations and over time within populations, as well as on gene-environment interactions that might modulate heritability, are relevant here. While more of this research is needed on other phenotypes and life outcomes, it does appear that IQ, and especially general intelligence, hardly varies in its heritability as a function of population, socioeconomic status, or time period (Sarraf & Woodley of Menie, 2021; Woodley of Menie, Sarraf, et al., 2018; Woodley of Menie, Pallesen, & Sarraf, 2018; Toto et al., 2019 found an unusually low heritability of IQ in one population, but this is likely due to the low validity of the IQ test for the population on which it was used—for relevant discussion, see Wicherts, Dolan, Carlson, & van der Maas, 2010). Similarly, the heritability of social status seems minimally variant across populations (Clark, 2014) and, in the case of England, over time (the same was found for other measures of social success as well; Clark & Cummins, 2018). Consistent with these results, studies of gene-environment interactions generally tend either not to find the predicted interactions or to find that they have weak effects, at least in humans (Culverhouse et al., 2018; Dudbridge & Fletcher, 2014; Duncan & Keller, 2011; McGue & Carey, 2017), which does not bode well for hopes of finding large differences in trait and outcome heritability across human populations as a function of environmental variation. Further, there are substantial genetic influences on which environmental factors individuals are exposed to, given, for example, that genetic predispositions influence the environments into which people sort themselves (Kendler & Baker, 2007). Therefore, even when considering traits and outcomes variation in which is under non-trivial environmental control, it may be challenging to alter the distribution of environmental exposures through, for example, policy initiatives.

Nonetheless, certain traits and outcomes of organisms, especially those exhibiting relatively low additivity (which is not true of general intelligence or, in all probability, social status), may be substantially influenced by epigenetic effects stemming from the genomes of other organisms (see Chap. 7). To what degree epigenetic effects of this kind, which we call social-epistatic effects, influence trait/outcome variation within populations as opposed to absolute levels of traits/outcomes of whole populations is currently unclear.

When personality traits are well measured, they can exhibit heritabilities of around 85–90% (Riemann & Kandler, 2010). A general factor of life history speed (a phenomenon given more attention in the following section), subsuming personality, health (mental and physical), insight, planning, and self-control, is probably about 65% heritable (Figueredo et al., 2006). These are all critical human traits, the high heritability of which carries many implications that would be foolish for social scientists to ignore. Indeed, failure to recognize the role of genetic factors in variable behavioral outcomes frequently leads to spurious sociological explanations of important phenomena. For example, the association between exercise and subjective well-being (conceptualized as happiness or satisfaction with life) may not be causal at all, despite the advice and claims of countless doctors, therapists, and social scientists—rather, they may be positively associated only because common genetic factors contribute to both of them (Stubbe, de Moor, Boomsma, & de Geus, 2007). Similarly, genetic as opposed to environmental factors may entirely explain the association between non-heterosexuality and proneness to poor mental health, and not discrimination as sociocultural theorists often suppose (Zietsch, Verweij, Bailey, Wright, & Martin, 2011; but see also Bailey, Ellingson, & Bailey, 2014; Timmins, Rimes, & Rahman, 2018).

It should be noted that not only human behavioral variation but also *invariance* can seemingly be well-explained only with biologically informed science. To return to the earlier example of sex differences, it is unclear how a sociocultural or otherwise non-genetic theory could parsimoniously account for: (1) universal cognitive and behavioral human sex differences within different populations (see Ellis, 2018); (2) universal human mate preferences and the genetic associations of preferred traits with other fitness-relevant traits such as physical and mental health (see again Nedelec & Beaver, 2014); and (3) consistent behavioral sex role differences throughout the animal kingdom that align with those found in humans (Janicke et al., 2016). We contend that no purely environmentalist theory can adequately explain these phenomena, whereas evolutionary theories positing the distinct fitness challenges—and consequently different selective pressures—experienced by men and women, the fitness-enhancing function of mate preferences, and the genetic relatedness of all earthly lifeforms can easily accommodate them.

Non-genetic, or more broadly non-biological, perspectives on human behavior can be declared dead with great confidence. While theories of this sort occasionally correctly identify proximate, as opposed to ultimate,

causes of human behavior and its variation, there are no obstacles to integrating such proximate-level theorizing into biobehavioral theories (e.g. Figueredo et al., 2018). There is thus no apparent value in continued pursuit of entirely non-genetic/biological behavioral science, given that there is not a single apparent aspect of human life on which biology does not bear in some way, and also given the manifest deficiencies of this approach. As far as we can tell, non-biological behavioral science continues largely for extra-scientific reasons. Evolutionary theorizing was in fact quite well integrated with behavioral science for some time prior to the twentieth century, when politically motivated egalitarians started to make (ultimately successful) aggressive efforts to oust biological ideas from these disciplines (MacDonald, 1998; Nyborg, 2003, 2011). Evidence of this process is found in the substantial increase in the frequency with which the words intelligence/IQ and certain terms of political abuse are used in the same sentence in Anglophone texts published from 1965 to 2000 (Woodley of Menie, Dutton et al., 2018). In our view, the rising use of moral and political values to distort scientific research is one of the more concerning cultural trends of the past century.

ELEMENTS OF A BIOBEHAVIORAL FRAMEWORK FOR UNDERSTANDING HUMAN SOCIETAL AND PSYCHOLOGICAL CHANGE

Among the relevantly informed, it is uncontroversial that biological evolution via selection has substantially shaped human behavior; though some argue that, for various reasons, it is not possible to gain insight into the selective pressures that shaped human behavioral evolution (without denying that this evolution occurred), these claims are not sound (Andrews et al., 2002; Woodley of Menie & Sarraf, 2021). The common approach to criticizing evolutionary behavioral science, or biobehavioral science more generally, is *philosophical*; in critiquing evolutionary psychology in particular, critics typically stress the supposed insufficiency of methods at researchers' disposal to reconstruct the conditions that determined human behavioral evolution (e.g. Pigliucci, 2010). But critiques of this sort are entirely blind to the enormous predictive success of human evolutionary behavioral science (see, e.g. Buss, 2005, 2015a, 2015b; Laland, 2017). Science is generally conducted such that the emphasis in theory building is not on ensuring the absolute purity and correctness of theoretical premises prior to empirical work, but rather on conducting appropriate *empiri-*

cal tests of predictions derived from those premises. If a hypothetical model of human behavioral evolution implies certain predictions, and if sound tests of those predictions support the latter, then acceptance of that model is usually (though not necessarily) justified unless an alternative is shown to better account for the relevant data. Critics of evolutionary behavioral science tend to ignore the countless successful predictions of their target, preferring to attack the theoretical level alone; and when radical alternatives to well-established evolutionary models are offered, they are typically weak, even obviously wrong (Machery & Barrett, 2006).

Arguments throughout this book draw extensively on biological and biobehavioral science, especially evolutionary theory, mainly for the purpose of explaining human social and cultural change over time. Having offered the reader a sense of the virtues of a biological perspective on human behavior, and of the explanatory poverty of non-biological alternatives, we presently turn to the task of introducing some of the concepts that are especially crucial for the remainder of the book.

We have so far assumed that readers have a basic familiarity with the concept of evolution by selection. Nonetheless, a statement of the idea “in a nutshell” may be useful for some. Modern evolutionary theory posits that organisms exhibit variation in phenotypic traits—behavioral, physiological, anatomical, and so on—at least in part because organisms vary genetically, that is, with respect to the information governing phenotypic development and maintenance encoded in deoxyribonucleic acid (DNA), a molecule that consists of sequences of four bases: adenine, thymine, guanine, and cytosine. The total genetic material of an organism is called its *genome* (a term sometimes used interchangeably with *genotype*).²⁵ In the case of humans, the genome (typically) is contained in 23 pairs of chromosomes, which are coiled DNA molecules, the structure of which is supported by histones (a type of protein). Specific sites on chromosomes can be identified, which contain sequences of DNA with particular functions—these sites are called *genetic loci*, and the associated sequences of DNA are called *genes*. Variant DNA sequences at particular genetic loci among organisms in a species are referred to as *alleles* or *genetic variants*. Importantly, genomic variation occurs not only because of allelic variation, but also as a result of variation in chromosomal structure (structural variants) and chromosome count (within a species, the phenomenon of atypical chromosome counts is called aneuploidy; aneuploidy often involves serious medical problems in humans, but the finding of aneu-

²⁵ Sometimes, the term “genome” is used to refer to the total genetic material of a species.

ploidy in certain cells of the body, such as brain cells, is evidently normal; Rehen et al., 2005).

Phenotypic variability, arising in part from genomic variation, co-occurs with variability in organismal *fitness* partially²⁶ as a function of the environmental conditions to which organisms are exposed. Fitness typically refers to the relative replicative success of genetic variants, that is, the number of copies of these genetic variants made through organismal reproduction compared to other variants in a population. A phenotypic trait is usually deemed fit, or adaptive, if it increases the relative replicative success of the genetic variants that underlie it. But fitness can be defined more generally at the level of the genotype and the total phenotype of an organism—fitness in these cases is the relative reproductive success associated with a phenotype or genotype, respectively. Fitness can also be defined prospectively—an organism, say, might have high fitness in this sense if it lacks deleterious mutations that impair organic function; in other words, if an organism exhibits high genetic quality or genomic integrity. *Selection* simply is the phenomenon of certain genetic variants, genotypes, or phenotypes (depending on one’s focus) having greater relative replicative or reproductive success than others. The pathways of selection (e.g. natural, social, and sexual) and patterns of selection (e.g. directional, disruptive, negative, stabilizing, correlational, and frequency-dependent) are complex—but generally when it is said that, for example, a phenotype is “selected for,” this merely means that it is associated with high relative reproductive success, and when it is said to be “selected against,” it is associated with low relative reproductive success.

To simplify matters, an organism is deemed fit if its phenotype is associated with relative reproductive success in its population. Such relative reproductive success, or fitness advantages, sustained over time should lead to the genetic variants underlying favored phenotypes to become more common in a population. Given that the process of DNA replication is imperfect, it gives rise to new genetic variants, or mutations, that will either harm or (far less frequently) benefit organismal fitness through their phenotypic effects, and thus tend to become more or less frequent in populations over time. Biological evolution by selection in the modern sense

²⁶We say “partially” because phenotypic variability relevant to fitness is clearly affected by non-environmental factors. For instance, an organism that is infertile because of a genetic defect cannot have any personal reproductive fitness, regardless of its environmental circumstances.

therefore can be summarized as heritable phenotypic variation subject to selection and mutation. (In this simple overview, we have said nothing about other processes through which evolutionary change occurs, such as genetic drift, but these are not particularly relevant to the key arguments of this book.)

KEY BIOLOGICAL CONCEPTS

The Levels of Selection Debate

The levels of selection debate is a long-standing feature of evolutionary biology (Okasha, 2006), and is of special interest in human sociobiology (the biology of social behavior; Gintis, 2017; Richerson et al., 2016) and biobehavioral science. The dispute holds primarily between those who believe that selection acts exclusively at the individual (organismal) or even genic level (or that, even if selection occurs at higher levels of biological organization, it has had little to no meaningful effect on human and perhaps other animal evolution), and those who believe that selection acts not only at the genic and individual levels but also at the level of groups of organisms²⁷ (and perhaps even species), simultaneously and potentially in consistent or opposing directions at these different levels. The former camp can be termed individual-selection theorists and the latter multilevel-selection theorists. It should be emphasized that the contending parties in this debate are not in disagreement about the fact that selection is ulti-

²⁷ Some controversy in the levels of selection debate seems to concern the “groups” to which group selection is relevant. While it is true that, as we have noted above, multilevel selectionists at least sometimes maintain that selection may act even at the species level, it is mostly the reality of selection among or between “groups” that is debated, and what is meant by “groups” here is not always apparent. Generally, the “groups” referred to seem to lie in complexity anywhere between networks of close kin and subspecies (while potentially including the latter), and would therefore include tribes and perhaps nations.

Salter and Harpending (2013) cut through much of this confusion in making clear that for evolutionarily relevant group selection to occur, it must merely be the case that two or more populations exhibit a certain degree of genetic dissimilarity, with such genetically dissimilar populations being the groups of interest. Sufficient inter-group genetic dissimilarity allows individuals to receive substantial inclusive fitness benefits (a concept discussed below) from intra-group cooperation in a context of *competition* with other groups. Competition is facilitated by frequent contact such as when sharing a territory. Salter and Harpending also make clear that there is enough genetic variation among human biogeographic ancestry groups to permit group selection among them.

mately meaningful insofar as it affects gene frequencies (setting aside, for example, certain models of cultural group selection). Rather, the debate concerns the levels of biological complexity at which selection acts to affect gene frequencies. The levels of selection debate is relevant to the current work because the latter posits that group-selection dynamics have played a substantial role in (relatively) recent human behavioral evolution. It is therefore appropriate to make some effort to defend group-selection models of such evolution against what we consider the most important critique that they have received.

As indicated above, the most distinctive and controversial aspect of multilevel-selection theories is that they posit that selection can act on groups of organisms, favoring some of these groups over others, rather than on individual organisms (or genes) alone, favoring certain individuals over others. At least since Darwin's (1871) *The Descent of Man*, the concept of group selection has enjoyed intuitive plausibility as a potential explanation for the evolution of the highly cooperative and prosocial behaviors observed in humans (although Darwin did not use the term "group selection," the concept with which that term is associated is clearly present in *The Descent of Man*). Darwin reasoned that groups composed of individuals able to act for one another's benefit were likely to outcompete and replace groups composed of individuals acting without regard for the interests of other group members. This analysis implies that when groups are in conflict, selection should favor populations the members of which are aggregately advantaged over competitors with respect to levels of positive other-regarding (in-group) behaviors. The paradigmatic other-regarding behavior, or set of behaviors, is altruism: an organism acts altruistically when it enhances the fitness of at least one other organism at the expense of its own (i.e. personal) within-group fitness.

While intuitively plausible, it seems difficult for this group-selection model of the evolution of other-regarding traits to explain how altruism becomes selectively favored within groups, that is, how selection against altruism within groups is not insurmountable. If altruists invest in others at the expense of their own relative fitness, it is *prima facie* unclear how genes that code for altruistic behaviors ever manage to reach high frequencies within groups. This problem for multilevel-selection theories is still raised in the contemporary literature: "Genes for altruism or cooperation ... though helpful for the group, tend to reduce the fitness of individuals that behave [in altruistic and cooperative ways]" (Baum, 2017, p. 406); "altruists will generally fail to reproduce as much as the less altruistic

members of the group that benefit from the presence of self-sacrificing individuals. The effects of differences in the survival and reproductive success of groups must exceed that of differences in the inclusive fitness of individuals within groups [for altruism to be selectively favored]” (Alcock, 2017, p. 388).

A common solution to this problem among multilevel-selection theorists invokes various cultural processes that may have the effect of advantaging the fitness of individuals that behave prosocially, that is, for the benefit of others, relative to those who are less prosocial or are selfish (e.g. Boyd & Richerson, 1992). If groups construct culture such that fitness penalties accrue to those that behave selfishly and fitness benefits accrue to those that behave prosocially, for example, through systems of punishment, reputation, and morality, it seems obvious that genes coding for positive other-regarding behaviors could reach high frequencies in human populations. Unfortunately, theories of this sort are insufficient to explain the evolution of altruism in the standard sense, which, by definition, entails that altruism *harms* the personal fitness of organisms, all else equal (although, as we will argue, such theories might nonetheless play a critical role in explaining the evolution of altruism). Indeed, theories of the kind that Boyd and Richerson (1992) present sometimes indicate, implicitly or explicitly, that altruism, as defined above, simply does not exist, at least in humans. But claims of this sort seem inconsistent with the existence of certain human behaviors, such as a soldier jumping on a grenade to save the lives of his comrades.

Inclusive fitness theory, the favored paradigm in sociobiology among individual-selection theorists, seemingly best explains most cases of altruistic behavior—though multilevel-selection theorists generally do not deny the reality of inclusive fitness dynamics in human evolution (Gintis, 2017). Inclusive fitness theory posits that organisms act to increase the population frequency of copies of genes that they carry; contrary to original formulations of the theory, which depend on an “identity by descent” qualification, it is irrelevant in what organism(s) these copies reside (Hamilton, 1975; those unaware of the foregoing paper often mistakenly equate the concept of inclusive fitness with kin selection, when the former is in fact “more general” [pp. 140–141] than the latter, in the words of Hamilton, since it does not depend on the concept of identity by descent). An organism can sacrifice its own fitness, or individual or personal fitness, to improve the fitness of others carrying copies of its genes, its inclusive fitness, and ultimately yield a fitness payoff equivalent to that of producing

a certain number of offspring through its own reproduction (the offspring equivalent of the inclusive fitness payoff of course depends on the organism's success in boosting the fitness of related others and those others' degree of genetic similarity to the organism).

It should be emphasized that whether and how inclusive fitness theory and multilevel-selection theory are distinct is not always clear, and is in many respects controversial (Gintis, 2017; Hamilton, 1975; Harpending, 1979; Okasha, 2016; Salter & Harpending, 2013). It is widely believed that inclusive fitness theory and multilevel-selection theory are formally equivalent (Birch & Okasha, 2014), but that they nonetheless are not interchangeable as theoretical frameworks (Okasha, 2016). For example, Gintis (2017) believes that neither multilevel-selection theory nor inclusive fitness theory is independently adequate for sociobiological analysis, arguing that the former is “structural” and the latter “atomistic” as theoretical orientations (a point on which we elaborate below); thus, in his view “[t]he correct way of thinking is to embrace both atomistic and structural approaches and analyze the corresponding interplay of forces” (p. 192). To appreciate the conflict between multilevel-selection theorists and inclusive fitness theorists, it is perhaps best to ask what those who identify as inclusive fitness theorists and those who identify as multilevel-selection theorists tend to argue about. The most striking basis of disagreement lies in the fact that whereas multilevel selectionists tend to believe that prosocial behaviors that benefit members of entire groups equally can be adaptive, inclusive fitness theorists are wont to reject this idea, searching instead for ways that prosocial behaviors advantage the inclusive fitness of those carrying genes for such behaviors over the inclusive fitness of *others within their group* (Alcock, 2017).

Unsurprisingly, then, inclusive fitness theorists typically deny the existence of altruism that does not boost the intra-group inclusive fitness of those carrying altruistic genes, which is here termed extreme altruism. Alexander (1989), for example, speculates that those that sacrifice themselves in war may enhance the intra-group fitness of their surviving kin through the reputational benefits associated with having a heroic relative (see discussion in Alcock, 2017, which though favorable to Alexander's explanation fails to improve on it in any way). In other words, apparent extreme altruistic behaviors are alleged to in fact have the effect of generally raising within-group inclusive fitness, and thus are merely altruistic behaviors as opposed to extreme altruistic ones. This explanation is unpersuasive, however, since it is far from clear that the mere fact of having an

altruistic relative will do anything to, say, advantage an individual in sexual selection. Since fitness varies substantially even within families, it seems reasonable to suppose that among individuals, selective outcomes for any individual depend more on its own traits than the traits of others with which it is tenuously associated via reputation.²⁸ Therefore, it is not obvious that apparent extreme altruism can be explained as an inclusive-fitness-boosting behavior.

The failure of inclusive fitness theory to explain extreme human altruism reflects the former's most critical general deficit, which is its failure to model the "social" quality of the genome (this is the reason Gintis [2017, p. 192] characterizes inclusive fitness theory as "atomistic"): "[I]nclusive fitness theory applies to a *single gene* in the organism's genome, or to several *non-interacting genes*. But the evolutionary success of an organism depends on the way the various genes *interact synergistically*. Claiming that inclusive fitness theory explains societies is like claiming that the analysis of word frequency in a book is sufficient to comprehend the book's meaning" (Gintis, 2017, p. 190; emphasis in original). The blindness of inclusive fitness theorists to intra-genomic interactions implies that they generally will not model the role of adaptive function in human evolution with adequate sophistication. Instead, they often prefer to theorize in terms of the effects of "genes" as such on fitness, rather than in terms of traits or adaptations, which involve the interactive effects of many genes, as well as the epigenetic²⁹ up- and downregulation of them. This narrow focus on genes may lead inclusive fitness theorists, and population geneticists generally, to effectively assume that genetic factors have highly stable

²⁸ One might object here that even granting all of our claims, it could still be that associations with kin of good reputation advantage fitness, all else equal, but probably only slightly. Ultimately, this uncertainty cannot be resolved without appropriate empirical investigation, which has not yet been conducted (as far as we know).

One possibility is that such association-based fitness advantages vary among populations as a function of individualism/collectivism, with collectivists more attuned to the family backgrounds of prospective mates than individualists. Nonetheless, one could doubt that information about deceased relatives tends to be salient and well-preserved enough to meaningfully affect mate choice, even in collectivist populations (of course, we have in mind those dying through altruistic sacrifices).

²⁹ Although its meaning is broader than this, we use "epigenetics" and cognate terms to refer to processes that suppress or activate genes, thereby allowing or disallowing their phenotypic effects. Social epistasis, a phenomenon introduced in Chap. 1 and that is especially important in later chapters (7 and 8), simply is epigenetic change of gene activity ultimately caused by a gene, or more than one gene, of at least one organism other than the one undergoing such change.

fitness effects across environments—genes that code for altruistic behavior should, then, “generally” harm the fitness of individuals within groups (Alcock, 2017, p. 388). In the world of actual adaptive behavior, however, assumptions of this sort are not always correct. For example, general intelligence was, a mere few centuries ago, highly advantageous for the fitness of groups and individuals in the West, but since roughly the mid-nineteenth century has had a role in greatly reducing the fitness of such individuals and possibly groups (Woodley of Menie, Figueredo, et al., 2017). Clearly, then, a trait’s effect on fitness, and so the effects of the genes underlying that trait, can vary dramatically with environmental context.

If one theoretically models extreme altruistic behavior as a multilevel selectionist, and so conceives of evolutionary phenomena in “structural” as opposed to “atomistic” ways (Gintis, 2017, p. 192), at least two facts become salient. First, in the context of inter-group conflict, the presence of extreme altruists will benefit group fitness (a fact not even individual-selection theorists deny; Alcock, 2017). Therefore, second, the groups that will be most successful in conflicts with other groups in the long term will, *ceteris paribus*, be able to consistently generate large subpopulations of extreme altruists for inter-group conflicts. Inter-group conflict, likely the greatest source of group-selective pressure in human evolutionary history, should therefore have selectively favored not only the evolution of extreme altruism, but also mechanisms through which high frequencies of extreme altruists could be maintained in populations. Call realization of this condition the adaptive problem of inter-group conflict, or simply the adaptive problem.

If genes coding for extreme altruism must generally produce behaviors that reduce the fitness of those that carry these genes, it seems unlikely that any group could solve the adaptive problem, except under rare circumstances. But if the adaptations underlying extreme altruistic behavior only generate such behaviors under conditions of inter-group conflict, there is no necessary obstacle to solving the adaptive problem. Since inter-group conflict in humans is a recurrent, as opposed to a constant, phenomenon (Harpending & Harris, 2016; MacDonald, 2001), there would certainly have been times in the histories of human groups to produce high frequencies of extreme altruists without immediately losing large fractions of them to inter-group conflict. This could have potentially occurred if in times of peace, selection favored, or has favored, individuals that give signals of the ability to engage in extreme altruism, in the same way that signals of high g , such as humor, can enhance *prospective* indi-

vidual fitness (Miller, 2000; even if in modernized populations, β tends to lower realized individual fitness—see Chap. 8). Indeed, the sorts of mechanisms elaborated by Boyd and Richerson (1992), among others, may have had the effect of shifting sexual and social selection such that they favored those giving off these signals of high levels of altruism, potentially bringing altruism into genetic correlation with general intelligence and general fitness (that is, the degree to which a genome is free of deleterious mutations), thus further facilitating heightening population-levels of altruism—evidence in fact suggests that altruism is correlated with general fitness (Miller, 2000). As such, in times of peace occurring in a broader context of recurrent inter-group conflict, selection within human groups may have strongly favored the proliferation of adaptations underlying the ability to engage in extreme altruism since this would have enhanced prospective group fitness in inter-group conflict. While individuals with these adaptations would have typically been selectively disadvantaged in times of inter-group conflict, insofar as they would have tended to perform acts of extreme altruism, when cues of inter-group conflict were absent, those high in genetic potential for extreme altruism may have simply enjoyed the substantial favor of social and sexual selection. Evidence generally supports this possibility, given that mate preferences for altruism (in seeking long-term mates) are apparent and substantial in both men and women (Farrelly, 2013), and may be at least moderately heritable (Phillips, Ferguson, & Rijdsdijk, 2010). Nevertheless, this possibility depends on the assumptions that the genetic potential to engage in extreme altruism can be signaled through behaviors that do not penalize fitness, and that extreme altruism occurs on the broader spectrum of altruistic behavior (so, for example, those finding altruism sexually attractive should be especially attracted to those that signal the potential for extreme altruism).

Extreme altruism could thus be understood as a group-selected adaptive response to the recurrent challenge to group fitness of inter-group conflict: in the same way that recurrent fitness challenges have given rise to unique traits that enable adaptive engagement with multiple environmental contexts at the individual level (e.g. general intelligence, covered in the next section, which allows humans and other species to cope with environmental novelty), so adaptations may have evolved with the same characteristics via group-level selective pressures. The adaptations underlying extreme altruism may be one example.

A potential problem for our model concerns the possible evolution of behavioral morphs that signal extreme altruism, but actually lack any tendency to engage in extreme altruism when exposed to relevant environmental cues. In other words, these morphs would enjoy all of the benefits of signaling extreme altruism, but suffer none of the costs of being extreme altruists, which would necessarily advantage their fitness over extreme altruists, *ceteris paribus*. However, inter-group conflict should favor those groups that develop “honest” signalers of altruism that can be targeted for positive social and sexual selection (on the concept of honest signals, see Biernaskie, Grafen, & Perry, 2014). Groups wherein “fake” extreme altruistic morphs were not effectively distinguished from actual extreme altruists would have tended toward defeat in inter-group conflict, since they would have lacked high frequencies of extreme altruists. An interesting implication of our model, then, is that group-selective pressures issuing from inter-group conflict should have shaped the social and sexual selective mechanisms that partly determine intra-group gradients of selection. Many inclusive fitness theorists would likely predict the evolution of such morphs, given not only their atomistic focus but also their tendency to assume that organisms maximize inclusive fitness; however, social organisms typically fail to maximize inclusive fitness (Gintis, 2017, p. 190); instead, they “interact strategically in a complex manner involving collaboration, as well as enhancement and suppression of gene expression” (Gintis, 2017, p. 209), which results in and sustains arrangements where organisms generally do not maximize inclusive fitness.

General Intelligence (g) and Its Evolution

General intelligence or *g* is the mental ability that underlies performance, to varying degrees, on all cognitive tasks, and that explains most of the validity of IQ tests (Ganzach & Patel, 2018; Jensen, 1998). It was originally discovered through the observation of the positive manifold of correlations on diverse cognitive tests (Spearman, 1904), meaning that individuals who do well on one cognitive test have an increased probability of doing well on others. Insofar as *g* exhibits *domain generality* with respect to the tasks on which it positively predicts performance, it has been argued that *g* is the basis of novel problem-solving ability and so was likely selected in species frequently encountering novel problems, that is, problems for which there was, and perhaps still is, no evolved specialized system (MacDonald & Woodley of Menie, 2021).

A number of considerations support the view that g corresponds to an evolved neurological system. For instance, g is not limited to humans but has been observed in other primates (Burkart, Schubiger, & van Schaik, 2017; Hopkins, Russell, & Schaeffer, 2014), other (non-primate) mammals, such as dogs, cats, mice, and rats (Galsworthy, Arden, & Chabris, 2014), and non-mammals such as ravens (Pepperberg, 2017). Moreover, interspecific differences in intelligence are concentrated on g , as opposed to domain-specific abilities (s), suggesting that the evolution of cognitive ability has primarily involved selection for g (Fernandes, Woodley, & te Nijenhuis, 2014). Furthermore, the abilities that show the strongest affinity for g , in both humans and non-human mammals, are also the most heritable and phenotypically variable, and show the greatest additive genetic variance, indicating that they are the most evolvable (González et al., 2019; Woodley of Menie, Fernandes, & Hopkins, 2015). Within humans, g correlates with a number of biological variables, such as velocity of nerve conduction and brain metabolism parameters (Rushton & Jensen, 2010) and white matter tract integrity (Penke et al., 2012). Taken together, these findings leave little doubt that g is a substantive biological and evolutionary phenomenon, and not merely a statistical artifact as some have contended (e.g. Gould, 1996).

g is relevant to the study at hand in that a population's average level of the trait may substantially determine its well-being and cultural vigor, and because population levels of g have not been temporally stable (Woodley & Figueredo, 2013; Woodley of Menie, Figueredo, et al., 2017; see also Chap. 8). As indicated in Chap. 1, it is also substantially through g that inter-group conflict and resultant group-level selective pressures are relevant to this book, in that such pressures may be the primary determinant of population levels of g , with greater such conflict placing fitness premiums on the collective ability of groups to develop innovations that advantage them in competition (Hamilton, 2000; Woodley of Menie, Figueredo, et al., 2017).

Life History Theory

Life history theory describes and explains the tradeoffs that organisms make among diverse fitness domains, that is, components of their phenotypes related to fitness³⁰ (Figueredo et al., 2006). Sets of phenotypic traits

³⁰Life history theory applied to individual differences has recently been challenged (see Zietsch & Sidari, [in press](#)). For a response to this challenge, see Sarraf, Woodley of Menie, and Luoto ([In preparation](#)).

resulting from these tradeoffs are coordinated ensembles of adaptations, called strategies. As applied to humans, life history theory posits that variation in life history strategies occurs along a continuum of what is called life history speed, ranging from *slow* to *fast*, which is captured by variation in a general psychometric factor called *Super-K* (to be explained below). The term “speed” is used to indicate the fact that this variation in life history strategies tracks the length of the time horizon over which organisms are adapted to pursue fitness. In humans, slow life history strategies are those adapted to the pursuit of fitness over a long time horizon, and thus involve relatively late achievement of developmental milestones, such as pubescence, reproduction, and senescence. The opposite is true of fast life history strategies. Theory and empirical evidence indicate that both the type and level of environmental harshness (i.e. morbidity and mortality) and the temporal stability of these factors (environmental stability) to which organisms are exposed determine the evolution and, to a lesser degree via epigenetic effects, ontogenetic development of life history strategies (Figueredo et al., 2006). Environments in which harshness is relatively low and/or intrinsic (i.e. controllable by the organism to some degree) and/or environmental stability is high, or at least where environmental instability is predictable, typically select for slower life history speeds; environments in which environmental harshness is relatively high and/or extrinsic (i.e. uncontrollable) and/or environmental instability is high and unpredictable typically select for faster life history speeds.

Slow life history organisms are high on *Super-K*, a higher-order general psychometric factor that captures variation in three subordinate general factors of personality, health (mental and physical), and insight, planning, prosociality, and self-control, respectively (Figueredo et al., 2007). Thus, slow life history strategists are relatively healthy and have relatively high levels of broadly desirable personality traits: extraversion, emotional stability (the opposite of neuroticism), agreeableness, openness to experience, and conscientiousness—variation in all of which is captured by a general factor of personality (GFP) (Figueredo et al., 2007). Further, those with slow life history strategies are relatively future-oriented and prosocial, and thus biased toward the development of enduring and mutualistic social, sexual, and parenting relationships; they are generally sexually restrained and favor monogamy over multi-partner sexual and romantic arrangements. They typically have small numbers of offspring but invest heavily in the fitness of the offspring that they do have, as well as in others to whom they are genetically similar (thereby boosting inclusive fitness). (Nevertheless, there are contexts

in which slow life history strategists will tend to have larger numbers of offspring than fast life history strategists; Woodley of Menie, Cabeza de Baca et al., 2017.) The greater longevity of slow life history strategists, a function of their relatively high health, increases their opportunities to invest in genetically related conspecifics, including offspring. This approach to fitness enhancement is viable for slow life history strategists because they usually either face few risks of early incapacitation and death or can buffer against the risks that they do face. The specified package of slow life history traits is a proximate consequence of the fact that in developmental time, slow life history strategists invest heavily in fitness domains governing somatic development and parental and nepotistic behavior, but minimally in the fitness domain related to mating success (i.e. the acquisition and retention of short-term sexual partners³¹; Fernandes, Kennair, Hutz, Natividade, & Kruger, 2016; Figueredo et al., 2006).

Conversely, fast life history strategists are low on Super-*K*, and thus tend to be relatively unhealthy and short-termist, and to exhibit personality profiles generally considered to be socially undesirable. Their social schemas and interactions with others tend toward antagonism as opposed to mutualism, such that fast life history strategists generally have relatively few lasting or mutually beneficial relationships. They are typically less sexually restrained and seek multiple sexual and romantic partners. Resultantly, fast life history strategists are adaptively inclined to the reproduction of many offspring, but they typically invest minimally in the latter. Moreover, fast life history strategists sexually develop and reproduce early, as this lowers the probability that environmental hazards will kill or incapacitate them before they can reproduce; the health of fast life history strategists is relatively low because their fitness does not depend on long-term survival. The specified package of fast life history traits is a proximate consequence of the fact that in developmental time, fast life history strategists invest heavily in the fitness domain related to mating success, but minimally in the fitness domains related to somatic development and parental/nepotistic behavior (Figueredo et al., 2006).

³¹ Figueredo et al. (2006) define “mating effort” (i.e. investment in the mating domain of fitness) as related to success in both acquiring *and* keeping sexual relationships. But the second part of this claim does not fit with the observation that fast life history strategists, who are high in mating effort, seem to have adaptations to end sexual relationships relatively quickly after they begin (see Fernandes et al., 2016, who define mating effort more narrowly, and in our view more accurately, as “the amount of energy, time, or other key resources invested in competing for and retaining *short-term mates*” [p. 222; emphasis added]).

Among the more interesting phenomena related to life history are cognitive differentiation and integration effort (CD-IE) and strategic differentiation and integration effort (SD-IE) (Figueredo, Woodley, Brown, & Ross, 2013; Woodley, 2011; Woodley, Figueredo, Brown, & Ross, 2013). Cognitive differentiation effort (CDE) is the hypothesized causal basis of the observed weakening of the manifold of g at progressively slower life history speeds, and cognitive integration effort (CIE) is the hypothesized causal basis of the observed strengthening of the manifold of g at progressively faster life history speeds (effects predicted by Woodley, 2011 and empirically corroborated by Figueredo, Woodley, et al., 2013, and Woodley, Figueredo, et al., 2013). Strategic differentiation effort (SDE) is the hypothesized causal basis of the observed weakening of the manifold of the Super- K factor and its three lower-order factors at progressively slower life history speeds, and strategic integration effort (SIE) is the hypothesized causal basis of the observed strengthening of the manifold of the Super- K factor and its three lower-order factors at progressively faster life history speeds (Figueredo, Woodley, et al., 2013). Slow life history strategists are thought to invest in the cultivation of specialized cognitive abilities and other behavioral traits through CDE and SDE³² because the stable environments in which they are typically found have correspondingly stable niches, to which slow life history strategists can adapt themselves through behavioral specialization. Additionally, specialization should reduce competition for access to niches, and this reduced intraspecific competitive pressure should in turn facilitate the execution of the broadly prosocial behaviors of slow life history strategists (Figueredo, Woodley of Menie, & Jacobs, 2015). By contrast, fast life history strategists must contend with variable fitness challenges as a function of the instability, unpredictability, and uncontrollability of the environments in which they evolve and develop. This places a fitness premium on their ability to adapt to a variety of niches over the life course, and so favors behavioral generalism as opposed to specialism, and therefore a relatively equal investment in behavioral domains through CIE and SIE (Figueredo, Woodley, et al., 2013; Woodley, 2011).

Importantly, the ability to adaptively specialize through SDE and CDE has been hypothesized to require greater developmental plasticity³³ in

³²In both cases, this is done through the greater allocation of time, calories, and other resources to the development of brain regions associated with specific cognitive and other behavioral traits.

³³Developmental preparedness is “the degree to which an organism is genetically predisposed toward a particular developmental trajectory,” whereas developmental plasticity is “the

slow life history strategists, as reflected in lower trait heritability (Figueredo et al., 2006). It has not yet been determined whether slow life history strategists exhibit lower heritabilities of cognitive abilities. But it has been confirmed that the heritability of life history traits and slow life history speed are negatively associated (Woodley of Menie, Figueredo, et al. 2015).

As we will explain in subsequent chapters, the life history traits of populations substantially bear on the societies and cultures that they develop and maintain. Furthermore, a certain syndrome of slowing life history speed, falling g , and minimal (or absent) inter-group conflict may characterize modernized populations generally and serve as key explanatory variables of their distinctive behavioral and cultural characteristics (see Chaps. 3, 7 and 8).

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