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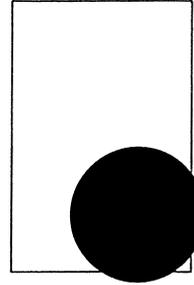
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What a tangled web he weaves

Race, reproductive strategies and Rushton's life history theory

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Abstract

The last decade of the 20th century experienced a resurgence of genetically based theories of racial hierarchy regarding intelligence and morality. Most notably was Herrnstein and Murray's *The Bell Curve* (1994), that claimed genetic causality for long-standing racial differences in IQ. In addition, it raised the time worn argument that the over-reproduction of genetically deficient individuals within our population would lead to a serious decline in average American intelligence. These authors provided no specific rationale for why these genetic differences should exist between human 'races'. Instead, they relied heavily on the work of Canadian psychologist J. Philipe Rushton (in *The Bell Curve*, 1994, Appendix 5: 642–3). Rushton has advanced a specific evolutionary genetic rationale for how gene frequencies are differentiated between the 'races' relative to intelligence. He claims that human racial differences result from natural selection for particular reproductive strategies in the various racial groups. Rushton's theory is based entirely on the concept of r- and K-selection, first explicitly outlined by MacArthur and Wilson in 1967. This article examines both the flaws in the general theory, and specifically Rushton's application of that same theory to human data. It concludes that neither Rushton's use of the theory nor the data that he has assembled could possibly test any meaningful hypotheses concerning human evolution and/or the distribution of genetic variation relating to reproductive strategies or 'intelligence', however defined.

Key Words

human races • IQ • life history theory • pseudoscience • psychometry • r- and K-selection • racism

INTRODUCTION: THE TANGLED WEB . . .

In 1994, The Free Press published Richard Herrnstein and Charles R. Murray's *The Bell Curve*. This book claimed that the 'black' race was genetically deficient in intellect and

that this deficiency was responsible for their social stagnation in American society. Few people realized that this claim was heavily influenced by the racial ideas of Canadian psychologist J. Philippe Rushton. Many view Rushton as a respectable scholar who has raised important questions concerning how evolutionary theory allows us to understand the significance of race in modern society. In reality, he is a spider spinning a pseudo-scientific web of incorrectly stated hypotheses supported with dubious evidence. His ideas have not graduated beyond those of the anthropologists of the early 20th century. They were convinced that race was a key explanatory variable in the evolution of human society. For example, in 1929 the biologist Edward East claimed that gene packets of African origin were not of any value when added to genes of European origin (East, 1929: 181). Others claimed that the gap between the 'advanced' and 'retarded' races would only increase. Even Franz Boas felt that Blacks were slightly inferior to Whites on average in intelligence, due to a 'defective ancestry'. Yet, he also felt that this slight difference did not justify discrimination against African Americans. To rectify this injustice, he set about throughout his career to generate new facts on which anti-racist claims could be based, to question racist explanations of facts, and finally to remove racial markers by re-labeling supposedly racial traits as universal human traits (Williams, 1996). Boas's initial misconception that 'Blacks' had defective ancestry was the result of the belief that legitimate races exist within the human species. This belief resulted from the common practice of raising specific phenotypic markers to greater significance than others in classifying populations. For example, some consider all African populations 'black', even though we now realize that the genetic difference between Pygmies and Ethiopians is greater than the genetic distance between Ethiopians and southern Europeans. Furthermore, these misconceptions result from the common practice of thinking that genetic processes are directly revealed by phenotypic differences. This article continues in the Boasian tradition by laying bare the nature of J.P. Rushton's explanation of life histories and their relationship to the formation of the so-called human races.

RACE, EVOLUTION AND BEHAVIOR

During the 1970s and 1980s, important developments in evolutionary genetics occurred that were directly relevant to the race concept in anthropology. In particular, the measurement of the amounts of genetic variation that actually existed within and between populations would greatly erode the legitimacy of racial classification in humans. A year ago I described how despite these developments, anthropology, social science and psychology were slow to integrate these data into their views of race (Graves, 2001). Some fringe elements in these disciplines actively ignored the significance of these results.

In 1999, Transaction Publishers released an abridged version of J. Philipe Rushton's *Race, Evolution, and Behavior: A Life History Perspective*, the unabridged version having originally been published in 1995. The new, abridged version has been sent to a number of scholars, particularly anthropologists at universities throughout Canada and the United States. It has been hailed by all the leading proponents of genetically determined racial hierarchy: Arthur Jensen, Thomas Bouchard, Linda Gottfredson, Hans Eysenck, and Richard Lynn. They champion Rushton's views because their program lacks any specific or credible evolutionary genetic rationale that could possibly explain why 'race' specific differences in IQ should exist. One reviewer of the pamphlet makes this point clearly:

> Rushton's *Race, Evolution, and Behavior* . . . is an attempt to understand [race] differences in terms of life-history evolution . . . Perhaps there ultimately will be some serious contribution from the traditional smoke-and-mirrors social science treatment of IQ, but for now Rushton's framework is essentially the only game in town. (Harpending, 1999: 2)[1]

If indeed Rushton's explanation of 'race' differences is the only 'game' in town, it is one being played with a crooked deck. There are insurmountable problems with the application of Rushton's theory of human life histories, in particular his reliance on the concept of r- and K-selection (see later in the article). Chief amongst these problems is the fact that r- and K-selection theory is now considered virtually useless. Biologists who study life history evolution began to falsify this idea in the late 1970s. Since that time, multiple experiments have failed to corroborate the core premises of r- and K-selection theory. It would have been impossible not to notice this event (sort of like an elephant walking into your living room). In addition, even if the theory itself were reliable, Rushton has applied it incorrectly to describe the supposed genetic tradeoffs he wishes to explain. This can be demonstrated by examining the following:

1   the history and formulation of density dependent selection theory;
2   the critical experiments that falsified the central predictions of r- and K-selection theory;
3   the attempt of Rushton to apply r- and K-theory to human life history evolution;
4   the inadequacy of Rushton's data to test any specific hypothesis concerning the evolution of human life histories.

The Bell Curve relied heavily on Rushton and cited him 11 times in its bibliography. Herrnstein and Murray wrote in Appendix 5:

> Rushton argues that the differences in the average intelligence test scores among East Asians, blacks, and whites are not only primarily genetic but part of a complex of racial differences that includes such variables as brain size, genital size, rate of sexual maturation, length of menstrual cycle, frequency of sexual intercourse, gamete production, sexual hormone levels, the tendency to produce dizygotic twins, marital stability, infant mortality, altruism, law abidingness, and mental health. For each variable, Rushton has concluded that the three races – Mongoloids, Caucasoids, and Negroids – fall in a certain order. (Herrnstein and Murray, 1994: 642)

On the face of it, *Race, Evolution, and Behavior* presented a seamless argument for evolutionary origins of modern racial differences. However, its arguments rely on a series of dubious, if not absurd, assumptions. First, we must question whether r- and K-selection theory is a valid model for understanding life history evolution; secondly, whether human populations can be legitimately grouped into the 'racial' categories described in this book; and finally, whether the way Rushton collected and organized his data actually tested genetic hypotheses concerning human life history variation. The answer to all of these questions is no. J.P. Rushton's program purportedly explaining human 'racial' variation is a case study in how *not* to investigate evolutionary

explanations concerning life histories. Ironically, Rushton and his supporters have attempted to seize the 'evolutionary and scientific' high ground in defending these theories (see, for example, Rushton, 1998). Actually, we must vigorously oppose Rushtonism due to his blatant distortion of the methods of evolutionary biology in general and life history theory in particular. Rushton is not alone in attempting to apply r- and K-selection to human biology. Lee Ellis, for example, utilized the same rationale to explain the supposed greater rape potential of African and African-American males as compared to males of other 'races' (Ellis, 1987, 1989).

HABITAT, LIFE HISTORIES AND THE VERBAL THEORY OF R- AND K-SELECTION

Life history evolution concerns itself with biological traits that impact an organism's Darwinian fitness (reproduction and survival). The principal life history traits are listed in Table 1. The cornerstone of life history theory is the necessary existence of tradeoffs in life history features, in particular tradeoffs which reflect costs of reproduction (Roff, 1992; Stearns, 1992; Graves, 1993b). These tradeoffs result from the fact that the energy input of all organisms is limited and therefore they must often apportion this energy input between competing demands. Table 2 lists some potential life history feature tradeoffs.

Charles Darwin might be considered the originator of the study of life history evolution. For example, he speaks about the evolutionary factors involved in the molding of species' life spans in Chapter VII of *The Origin of Species* (1859). The *Origin* actually deals with many topics that anticipate the development of a mature theory of life history evolution. Darwin also suggested that life history evolution might have been involved in the development of the intellectual and moral faculties of human beings.[2] However, he doubted that there was a straightforward relationship between reproduction rates and the formation of intellect (Darwin, 1981 [1871]: 328).

Modern evolutionary life history begins in the 1940s. Skutch (1949) and Dobzhansky (1950) first suggested that habitat, life style, and life history might be correlated (Stearns, 1992). Cody (1966) reiterates this theme, and Pianka (1970) cites the Dobzhansky article in the formulation of his ideas concerning r- and K-selection (henceforth to be described as the verbal theory of r- and K-selection; after Mueller, 1988; Graves and Mueller, 1993). Dobzhansky (1950) suggested that in any lineage different life histories

Table 1. Principal life history traits (after Stearns, 1992: 10)

1 Size at birth	5 Number, size, and sex ratio of offspring
2 Growth pattern	6 Age- and size-specific reproductive investments
3 Age at maturity	7 Age- and size-specific mortality schedules
4 Size at maturity	8 Length of life

Table 2. Central life history tradeoffs (after Stearns, 1992: 10)

1 Current reproduction and survival	3 Number, size, and sex of
2 Current reproduction and future reproduction	offspring

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are found in tropical and temperate habitats, because the tropics are more predictable. This would appear in r- and K-selection theory as the prediction that stable habitats should be K-selecting (i.e. the tropics) and unstable habitats should be r-selecting (the temperate zones). This specific point will gain much importance in later examining the formulations of r- and K-selection used by Rushton and his co-workers to explain 'racial' differentiation in human evolution.

MacArthur and Wilson (1967) presented the basic argument that became known as r- and K-selection (also called density dependent selection). According to this argument, catastrophic weather in temperate and arctic regions causes periodic crashes in resident populations with little regard to genotype. These population crashes are then followed by long periods of population increase during which adaptations that increase the exponential growth rate (r-) are favored. The parameter 'r-' is called the intrinsic rate of increase, and it is equal to the instantaneous rate of birth–the instantaneous rate of death. The verbal theory predicted that small (r-) would be increased by greater fecundity and early maturity. On the other hand, in more stable tropical environments, where populations fluctuate little, populations should remain near the limit imposed by resources (called the carrying capacity, or K-), and adaptations that improve competitive ability and efficiency of resource utilization are selected. The distinction between temperate and tropical patterns popularized the term 'r- and K-selection' in the scientific lexicon (MacArthur and Wilson, 1967; Pianka, 1970). On a closer examination of the regions labeled as temperate and tropical, it is clear that there exists considerable temporal and spatial variation in climatic and biotic variables within them. For example, under contemporary conditions the region known as the tropics contains warm, moist evergreen forest, tropical monsoon forest, tropical rain forest, savanna, semi-desert, desert, and mountain biomes. The temperate zones contain desert, semi-desert, temperate grasslands, chaparral, warm, moist evergreen forest, temperate evergreen, temperate deciduous, mountain zones, taiga, and tundra. Thus, even within climatic zones, there is room for considerable difference in habitat selection parameters.

Pianka (1970) proposed a list of traits associated with the poles of the r- and K-continuum (Table 3). No experimental rationale was ever given for the assignment of these traits to either category, hence the use of the term 'verbal theory' in this article (after Mueller, 1988). One immediate problem with this typology is that in ectotherms (organisms that use environmental energy to regulate their temperature) and, to a lesser extent, endotherms (organisms that use metabolic energy to regulate their temperature), development time, size at maturity, and fecundity are inter-correlated (Roff, 1992;

Table 3. Species traits historically associated with the r- and K-selection continuum (after Pianka, 1970)

r-selected traits	K-selected traits
Rapid development	Slow development
High rate of increase	Low rate of increase
Early reproduction	Delayed reproduction
Small body size	Large body size
Single reproduction	Repeated reproduction

Stearns, 1992). This means that natural selection may not be acting on each of these traits separately, but on a few traits, with the others essentially coming along for the ride (e.g. as demonstrated in Rose et al. 1990). Pianka (1970) used this scheme to correlate the body length of vertebrates and insects to their generation times.

Bonner (1965) presented a similar set of correlational hypotheses, and that table is reproduced in Rushton (1995) as evidence for the validity of r- and K-selection. The comparison of vertebrate and invertebrate life history features in this way is meaningless. Differences between taxa as widely separated as these are undoubtedly due to a number of causes. In addition, the statistical validity is compromised by the fact that these species are not independent observations (Harvey and Pagel, 1991; Garland and Carter, 1994; Leroi et al., 1994). That is, they share common evolutionary histories, and hence their genetic architecture could result from either selection or genetic drift. It is therefore literally impossible to infer a particular adaptive hypothesis by the examination of patterns of life history data alone (Reznick, 1985). A correct approach requires the genetic analysis of different genotypes or populations within a species. This point has been made both in theory and with experiments, as in Templeton and Johnson (1982); Reznick (1985); Mueller (1988); Rose et al. (1990); Roff (1992); Stearns (1992); Lauder et al. (1993); Garland and Carter (1994); Orzack and Sober (1994); and Leroi et al. (1994).

In addition to broad assumptions about environmental variability and fluctuations in population size, r- and K-selection theory depends on an implied tradeoff between genes favored under conditions of high population growth rate, and those favored under conditions of crowding and low resources. During its heyday in the 1970s, r- and K-selection theory prompted hundreds of papers. These studies analyzed life history data, attempting to fit them into the pattern predicted by the verbal r- and K-selection theory. However, not a single study demonstrated a correlation between population fluctuation and adaptation. Nor was a genetic tradeoff between r-selected and K-selected traits ever proven (Ricklefs, 1977; Roff, 1992; Stearns, 1992). In the rush to apply r- and K-selection theory to real organisms, it became evident that several different definitions of r- and K- were employed by researchers, sometimes even within the same paper! Parry (1981) reviewed hundreds of studies and ascertained that there were four major definitions implied within the literature. The first three definitions suggested a relationship between life-history parameters and the environment, while the fourth definition merely described a life-history parameter. He states that the problem arose from the incorrect use of the variables r- and K-, as either labels or as implied evolutionary explanations. In addition, he questioned whether there is truly a relationship between total reproductive expenditure and the packaging of offspring (e.g. whether high reproductive effort actually necessitates a large progeny number). In an excellent study of the impact of K-selection on the frequency of a specific allele (abnormal abdomen in *Drosophila mercatorum*), Templeton and Johnson (1982) showed that K-selected conditions (drought) actually increased the frequency of the abnormal abdomen allele. The abnormal abdomen allele was pleiotropically (one gene that impacts several characters) related to phenotypes that, from the classic definition, were r-selected. Hence, selection for K-conditions resulted in phenotypic correlations with r-predicted life history features. Pleiotropy thus makes it a necessity that you understand the genetic basis of the traits under selection before predicting the types of life histories that will evolve

under certain ecological conditions. It is precisely our grasp of the genetic basis of human life history that is missing, indicating that Rushton's program is hopelessly untestable, as it is currently formulated.

THEORETICAL AND EXPERIMENTAL TESTS OF r- AND K-LIFE HISTORIES

By the late 1980s, r- and K-selection was clearly an antiquated paradigm. Not only were there definitional problems, but there were also problems with the biological significance of this line of reasoning. For example, the use of r- and K- as descriptors of population regulation had been confused for their use as mechanisms of selection that acted on individuals (Stearns, 1992). An examination of the best studies claiming to support r- and K-selection (Solbrig and Simpson, 1974; McNaughton, 1975; Law et al., 1977) shows there is never a mode of population regulation established, while studies that strive to use r- and K- as a method of life history classification show only 50 per cent accuracy in species from which reliable data were collected (Stearns, 1977).

The most powerful evidence dismissing the validity of the r- and K-selection paradigm, however, has been the experimental work testing its predictions. The mechanisms of r- and K-selection by definition infer that there are costs incurred in relation to reproduction in high- or low-density conditions. Reznick (1985) outlined the criteria by which we could test any cost of reproduction argument:

1   Phenotypic correlations based on field or laboratory observations of unmanipulated situations.
2   Experiments in which organisms were manipulated to vary the amount of reproductive effort (virgin v. mated, or manipulations of clutch size in birds).
3   Genetic correlations, obtained by sib-analysis, between reproduction and some component of fitness, such as survival.
4   Genetic correlations, demonstrated by a correlated response to selection either on the age schedule of reproduction or the correlated response of this schedule to selection on a component of fitness.

Resnick argued that since evolution can only proceed if there is genetic variation for the traits in question, only scenarios 3 and 4 represent a definite proof of the existence of a tradeoff of evolutionary significance. Rushton's analysis only represents the evidence that one can obtain from the type 1 scenario. This, of course, assumes that his observations and data sources are unbiased (Graves, 2002, demonstrates that we cannot safely make that assumption). An early experiment (Mueller and Ayala, 1981) gave some weak support for the type of tradeoff predicted by the r- and K-paradigm. However, since then there has been an avalanche of experiments falsifying the core premises of r- and K-selection. Table 4 shows that these studies are inconsistent with the predictions of r- and K-selection theory. That is, in each study, some key life history variables would not conform to the predictions of the theory. For example, Taylor and Condra (1980) found that r-selected populations of *Drosophila pseudoobscura* had a shorter egg-to-adult development time, lower pre-adult viability, and shorter adult life span than K-selected populations. However, contrary to theory, body size, fecundity, time to first oviposition, intrinsic rate of increase, and carrying capacity did not differ between the

Table 4. Some experimental studies contradicting r- and K-theory

Authors	Year	Organism
Snell & King	1977	rotifer, *Asplanchna brightwelli*
Kerfoot	1977	cladoceran, *Bosmina longirostris*
Luckinbill	1979	protozoan, *Paramecium caudatum*
Luckinbill	1984	bacterium, *Escherichia coli*
Taylor & Condra	1980	fruit fly, *Drosophila pseudoobscura*
Templeton & Johnson	1982	*Drosophila mercatorum*
Barclay & Gregory	1981/82	*Drosophila pseudoobscura*
Mueller & Sweet	1986	*Drosophila melanogaster*
Mueller	1988	*Drosophila melanogaster*
Bierbaum et al.	1988	*Drosophila melanogaster*
Joshi & Mueller	1989	*Drosophila melanogaster*
Joshi & Mueller	1993	*Drosophila melanogaster*
Mueller et al.	1991	*Drosophila melanogaster*
Guo et al.	1991	*Drosophila melanogaster*
Mueller et al.	1993	*Drosophila melanogaster*
Templeton et al.	1993	*Drosophila mercatorum*
Hollocher & Templeton	1994	*Drosophila mercatorum*

r- and K-populations. Similar results were found in Bierbaum et al. (1988). These inconsistencies have led several authors to conclude that no simple predictions concerning the nature of life history tradeoffs can be made a priori. For example, according to Templeton, 'no general prediction can be made about which aspect of the tradeoff will be favored by selection' (Templeton, 1983: 69–70). He further stated that r- and K-selection cannot be legitimately thought of as opposite ends of a continuum and that it is impossible to specify a single phenotype that is 'optimal' under one and not the other (Templeton, 1983: 70). Mueller came to similar conclusions (1991: 28). Rushton's analysis of life history theory is precisely in opposition to these data and reasoning. That is, Rushton relies on the validity of the r- and K-'continuum' and then utilizes it incorrectly to infer the life history features of human 'races'.

It could be argued that since these studies were conducted with invertebrates this is not sufficient reason to discard the theory for mammals. However, organisms like fruit flies, rotifers, cladocerans, and microorganisms are best suited for testing hypotheses concerning life history evolution. The key to evolutionary tests of theories of life history is the ability to distinguish between phenotypic and genetic correlations (Stearns, 1992). Phenotypic tradeoffs may exist that are not the result of genetic tradeoffs, and phenotypic tradeoffs may often be opposite in sign from the underlying genetic tradeoffs (Rose, 1984; Roff, 1992; Stearns, 1992). For example, Graves and Rose (1989) point out that much of the confusion concerning the nature of genetic correlations in *Drosophila* experiments results from factors such as gene $\times$ environment interaction, inbreeding depression, and confounded selection regimes. Organisms such as *Drosophila* have the advantage of small body size, rapid growth, ease of maintenance of large populations and suitability for genetic analysis, and thus have well-studied genetics. These are essential qualities required for the proper experimental investigation of population

and quantitative genetic hypotheses. The *Drosophila* populations were exposed to density dependent selection under controlled environmental conditions with large population sizes. Thus, these experiments represent our best information on the validity of the r- and K-selection paradigm. Finally, comparative data in eutherian mammals (Harvey et al., 1989; Promislow and Harvey, 1990) suggest that the *Drosophila* experiments accurately describe the inability to apply simplistic life history theories to explain mammalian diversity.

These theoretical and experimental failures of the paradigm have led evolutionary biologists to dismiss r- and K-selection theory. This is evident from its current absence from the literature in evolutionary life history theory. Stearns (1992: 207) points out that from 1977 to 1982 there was an average of 42 references per year on r- and K-selection within the BIOSIS literature search service. From 1984 through 1989, however, this average had dropped to 16, and it continued to decline over time. In 2001, I ran a search on BIOSIS, using r- and K-selection as keywords for the period of 1995 to 2001, and found only one article. This appeared in the *Journal of Environmental Biology*, rather ironically concerning algal diversity in treated versus untreated sewage. Stearns (1992) and Roff (1992) presented r- and K-theory as a once useful heuristic that no longer serves any purpose in the discussion of life history theory.

It should be noted that their conclusions appeared three years before Rushton published his analysis of human 'racial' variation, with r- and K-selection as its cornerstone. It is hard to understand how any serious student of life history evolution could have missed these developments in the theory. In fact, I had the opportunity to present these same observations to J.P. Rushton personally. This occurred at a panel discussion held at the John Jay College of Criminal Law, City University of New York, 20 March 1997. Yet his newly released abridged version of *Race, Evolution, and Behavior* would still claim that r- and K-life history theory was 'a basic principle of modern evolutionary theory'.[3] This would indicate that either Rushton does not agree with the theoretical and experimental work invalidating r- and K-theory, does not understand the argument, or has consciously chosen to ignore it. If the first possibility were true, then we would expect some theoretical justification to appear in his work that addresses these specific criticisms. Yet the absence of such a response only supports my view that Rushton does not understand life history theory. Thus he employs it incorrectly and through this error his work serves racist ideological agendas.

DISMANTLING RUSHTON'S r- AND K-THEORY

a. Testability of the theory

In *Race, Evolution, and Behavior* Rushton presented a modified summary of r- and K-life history features (see Table 5). Rushton theorized that the survival of early human migrants from Africa, proto-Mongoloids and Caucasians, necessitated an increased cognitive ability to survive the predictable harshness of the colder climate.[4] The additional cognitive ability was achieved through selection for K-related life history features that would have been genetically correlated to features allowing an increase in brain size. Genetic correlation can occur due to either pleiotropy (alleles with effects on multiple characteristics or genetic linkage, resulting from loci impacting both traits being physically linked on chromosome segments). In Rushton's interpretation of r- and K-theory,

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Table 5. From Table 10.1 in the chapter 'Life History Theory' (Rushton, 1995: 203)/Some life history differences between r- and K-strategists

r-Strategist	K-Strategist
Family characteristics	
Large litter size	Small litter size
Short birth spacing	Long birth spacing
Many offspring	Few offspring
High infant mortality	Low infant mortality
Little parental care	Much parental care
Individual characteristics	
Rapid maturation	Slow maturation
Early 'sexual' reproduction	Delayed 'sexual' reproduction
Short life	Long life
High reproductive effort	Low reproductive effort
High energy utilization	Efficient energy utilization
Low encelphalization	High encelphalization
Population characteristics	
Opportunistic exploiters	Consistent exploiters
Dispersing colonizers	Stable occupiers
Variable population size	Stable population size
Lax competition	Keen competition
Social system characteristics	
Low social organization	High social organization
Low altruism	High altruism

Modified from Pianka (1970), Wilson (1975), Eisenberg (1981) and Barash (1982)

'The racial differences in intelligence, law abidingness, health, and longevity . . . seem similarly ordered by r-K theory' (Rushton, 1995: 214). To be genetically based, therefore, Rushton's theory requires that loci that influence these traits are physically linked or are populated by alleles that have multiple pleiotropic effects on these characters. He predicts that Orientals or Mongoloids (Asians) should be most K-selected (hence have genetically greater intelligence and the lowest fecundity rates), while Negroids (Africans) are most r-selected (thus should have the lowest intelligence and the greatest fecundity), and Caucasians (Europeans) should be intermediate in these traits. To this end, he reports brain size as the basal factor determining life history traits, including generation time, gestation time, rate of maturity and body size (Rushton, 1995: 230–1).

The central difficulty facing Rushton's hypothesis is the absence of any evidence supporting the r- and K-continuum within our species. He conveniently skips over elementary procedural points in formulating his argument. For example, he does not ever establish the specific relationship between phenotypic variables he measures and their relationship to differential fitness in the human species. Establishing this relationship is crucial to testing adaptive hypotheses (such as r- and K-selection). For if these traits are unrelated to fitness they will not be acted on by any specific model of natural selection.

Alternatively, if they are related to fitness by a mechanism different from that proposed by the adaptive mechanism in question, genetic correlations might result in opposition to the theory. In Table 1.1 of the unabridged version (1995: 5), Rushton lists a variety of traits that he implicitly asserts are related to fitness and differentiated between the human 'races'. He lumps a number of observations together in a category that he calls 'reproductive effort'. Some of these characters could conceivably be linked to fitness, such as hormone levels, size of genitalia, secondary sex characteristics, or intercourse frequencies. However, no specific mechanism is ever experimentally established between these traits and fitness (thus adhering to the verbal approach of earlier r- and K-theorists). One could easily imagine alternative relationships between any of these traits and fitness. For example, he suggests that great 'Black' reproductive effort is related to greater rates of sexually transmitted diseases (he spends considerable time on AIDS in Chapter 8 of the unabridged addition). The relationship of STDs (sexually transmitted diseases) to fitness, however, seems in opposition to his r- and K-continuum. AIDS, for example, might have various impacts on individual fitness. Certainly it lowers later age fitness due to increased mortality rate probability, although it might initially increase one's sexual activity (patients with AIDS-related dementia are often hypersexual). Indeed, passing the HIV virus on to one's offspring cannot be considered to increase that offspring's viability. Furthermore, AIDS as a disease is undoubtedly irrelevant to the evolution of modern human life histories, since as an epidemic it has only existed for one or at most two human generations. More likely we would want to examine bacteria or protozoans that have been related to STDs for many generations. If so, we are still left with more questions than answers. Should there not have been selection for resistance to such pathogens in an 'r-' selected population? *Chlamydia trachomatis* may be such a pathogen. Currently it is probably the largest venereal cause of infertility in humans. Yet infection rates in African-Americans are higher than in Euro-Americans (Ellen et al., 1995; Mertz et al., 1998). This would tend to lower African-American fitness. Neither is this 'racial' dichotomy uniform, because rates of infection higher than those found in African-Americans occur in 'Caucasian' populations (Joshi et al., 1994; Vizitiu and Badescu, 1996). There is no reason to propose any specific relationship between a venereal pathogen and fitness (although it is likely that most would be negative). Solving these problems would require population screening and demographic analysis in excess of what is currently available. This again speaks to the 'verbal' character of Rushton's hypothesis. The failure of verbal just-so adaptive arguments in evolutionary biology is legend. For example, one of the mainstays of the just-so approach, the 'kamikaze' sperm hypothesis, just fell to a very simple experiment (Moore et al., 1999).

At a deeper level, Rushton does not present any evidence of the existence of pleiotropic loci, or of allelic variation capable of explaining his reputed tradeoff categories. He presents no evidence of genetic linkage, other than suggesting that the loci responsible for skin pigmentation must also be those controlling the morphological and behavioral traits he has differentiated for the so-called 'races'. In addition, he does not grasp the importance of gene $\times$ environment interaction in interpreting any phenotypic data that would be used to support a genetic hypothesis. He clearly does not understand the limitations of data collected from populations with uncontrolled environmental influences on genetic variation for testing hypotheses of life history variation.

Finally, he does not adequately explore alternative hypotheses that could explain his 'data'. Phenotypic correlations created by specific environmental factors can easily be altered by changes in those same factors. For example, at the turn of the 20th century, it is likely that African-Americans suffered low fertility, high infant mortality, and high rates of age-specific adult mortality relative to Euro-Americans. This can be gathered by looking at medical reports concerning the general health and status of African-Americans in this period (e.g. Rice and Jones, 1990). However, by the mid-century, African-American fertility values had surpassed, but the infant and age-specific adult mortalities were still higher than, Euro-Americans (Graves, 2002). These changes could not have been genetic. It would be impossible to change gene frequencies in a large population sufficiently to achieve this end in one generation.

b. Discussion of Rushton's use of r- and K-theory

The second fatal flaw in Rushton's thinking about the evolution of human life history patterns is that he confuses the supposed pattern of phenotypic correlations engendered by a specified pattern of selection (r-characteristics, K-characteristics) with the specific patterns of selection (r-selection, K-selection). For example, in his defense of his theory in the chapter entitled 'Challenges and Rejoinders: Is r-K theory correct?', he criticizes Barash (1982) thusly:

> Barash, however, is incorrect. Predictability is the ecological necessity for K-selection. This can occur in either a stable environment or a predictably variable one. What has apparently been misunderstood is that subtropical savannahs, where humans evolved, because of sudden droughts and devastating viral, bacterial, and parasitic diseases, are less predictable for long-lived species than are temperate and especially Arctic environments. Although the Arctic climate varies greatly over one year, it is highly predictable, but harsh, over many years. (Rushton, 1995: 249)

There are many things wrong with this formulation. First, there is no evidence cited from the ecological, life history, population, or environmental literature that support his claim that arctic, in particular glacial, environments are more predictable than tropical environments. There is absolutely no reason to believe this assertion. The problem here is that Rushton is comparing apples to oranges. All environments contain the complex interaction of both biotic and physical components. To compare the general predictability of an environment (and here we are talking about it being relative to sources of human mortality or factors that influence fertility or viability), we would need to have accurate information about both the biotic and physical sources of variability and compare them. In this paragraph, Rushton compares biotic sources of mortality (viruses and so on) to non-biotic sources in the Arctic. He makes these comparisons without citations from the scientific literature to validate either claim. Finally, we would have to be able to establish causal relations between these sources of variability and their relationship to variations in fitness within the human species. None of this is provided in this analysis, nor are relevant studies of this problem provided. Finally, r- and K-selection never explicitly dealt with environmental predictability. This is more in the domain of 'bet-hedging' hypotheses (as described in Stearns, 1992). Bet-hedging theory generally does not yield the same predictions concerning the evolution of life histories as r- and K-selection. Again, Rushton simply has these concepts confused.

In his Table 10.1 of r- and K-life history differences, Rushton (1995: 203) gracefully ignores some of the major assumptions intrinsic to r- and K-theory, such as the whole issue of density dependence. If K-selection happens in high-density conditions, it is unlikely to occur in a newly colonized area. He also contends that K-selected species should have a low infant mortality rate when, in fact, it should be the opposite according to the literature. If Rushton had a scientific reasoning behind this disagreement with the prior literature, he would have provided an explanation, as he did with the assigning of r- and K-labels to particular 'races'. The absence of such an explanation seems suspect. One could just as well argue that if K-selected species live near the asymptote of the logistic growth curve and competition is severe, the rates of early mortality are going to be high due to the difficulty of initial establishment. On the contrary, it is r-selected organisms that exist in the 'ecological vacuum' where there is little competition, and early mortality rates should be low. He also neglects to mention that K-selection should predict large body size on his table of r- and K-correlates. Body size is a critical assumption of r- and K-selection due to its energy allocation implications. Rushton suggests (1995: 200) that there is a negative correlation between body size and reproductive allocation, but then contradicts this by his own data and citations (e.g. Hegmann and Dingle, 1982). According to his interpretation of Table 6.4, large size is negatively correlated with total reproductive allocation (Rushton, 1995: 122). The table shows that, in the US Army, 'Negroid' females have an average height of 163 cm and weight of 62.2 kg and 'Mongoloid' females have an average height of 158.1 cm and weight of 58.6 kg (sample for enlisted, 1206 and 116 respectively). In Table 8.1 he then rates 'Blacks' as consistently highest and Asians consistently lowest in reproductive potential (Rushton, 1995: 166). Yet, his own analysis suggests that because the 'Negroids' are larger than 'Mongoloids', they should have lower reproductive values. These data do not explain the blatant contradiction in his findings, purporting that Africans have higher reproductive allocations. These are also inconsistent with comparisons of modern birth rates per 1000 in Africa and Asia. These data show that 'Mongoloid' and 'Caucasian' figures exist that are as high as those exhibited in Africa and higher than those shown by US 'Blacks' (Agarwala, 1977; Murdoch, 1980; China Financial and Economic Publishing House, 1988).

Worse still is the fact that Rushton makes his entire argument about the nature of selective forces that lead to racial differentiation in life history features utilizing hypothetical arguments about the nature of the predictability of Pleistocene temperate versus tropical environments. The argument proceeds that the environments that existed in Europe and Asia required greater intelligence to survive than those in the tropics. Hence genotypes with greater intelligence left more progeny than those without. This in turn would lead to directional selection for greater intelligence at the cost of alleles contributing to early reproductive success. This, of course, is not an r- and K-selection argument in reality. It simply asserts that intelligence is negatively genetically correlated with reproduction. He then proceeds to test his version of differential r- and K-selection theory in early humans, utilizing data he gathers from modern human populations! Thus, in reality he is asserting with this method that all features of human life history patterns were fixed in the Pleistocene! This formulation is essentialist (as is the Linnean conception of race utilized to construct his argument). For this procedure to make any sense whatsoever it is necessary for density-dependent selection regimes facing human

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'racial' groups to have remained constant, both temporally and spatially, over the range of years our species has existed (for *Homo habilis* through to *Homo sapiens*, about 1.75 million years). Such a proposition is absolutely ludicrous. If we assumed 30-year generation times (15 years to age of first reproduction, and 15 years to raise offspring), we could calculate between 4000 to 3000 generations have passed since the Pleistocene environments Rushton utilizes to found his thesis.

In addition, what little we know about the evolution of 'intelligence' in hominids seems to argue directly against his thesis. It is possible that around 300,000 years ago *Homo erectus*, *Homo sapiens*, *Homo heidelbergensis*, and *Homo neanderthalensis* were extant in different regions of the world. It is not clear whether these were true species, or geographic races of the same species (in ways that we do not have 'races' in modern *Homo sapiens*). The evidence seems to suggest that in Europe *Homo sapiens* and *Homo neanderthalensis* coexisted between 40,000 to 30,000 years ago. Most evidence suggests that *Homo sapiens* originated in Africa and when it invaded Europe it brought with it culture, art, wind instruments, record keeping, symbolic and ritualistic beliefs, and a constant pattern of organization and technical improvement. The contact between *Homo sapiens* and *Homo neanderthalensis* seemed to always lead to the short-term replacement of the latter by the technologically advanced former (Tattersall, 2000). Why does this observation contradict Rushton's thesis? Simply, because it was the Neanderthals who should have been living under Rushton's K-selection regime and the culture of the *Homo sapiens* resulted from the r-selected tropical environment. We know, for example, that the Neanderthals had larger cranial capacities than *Homo sapiens* (Neanderthal cranial capacities: 1524–1640 cc for males, and 1425–1270 cc for females, as opposed to around 1325–1166 for early *Homo sapiens*, in Poirer and McKee, 1999). We should compare these differences with the within-species values reported by Rushton. In his Chart 1 of the abridged version (1999: 19) he shows 1267, 1347, and 1364 cc for Blacks, Whites, and Asians respectively. This amounts to a 7.2 per cent difference between Blacks and Asians, while if we utilize the midpoint for Neanderthals and early *Homo sapiens* we would calculate a 15 per cent advantage for Neanderthals! These observations fly in the face of two of Rushton's predictions: first that harsh winter climates should select for greater intelligence, and secondly that cranial volume should be correlated with intelligence. All available evidence suggests that the Neanderthals were less 'intelligent' than modern *Homo sapiens* that had smaller crania and evolved in the tropics.

It is also clear that humans have not faced uniform demographic regimes throughout our history as a species (thus we have experienced different density-dependent selection regimes). These differences were also manifested spatially, so that patterns even within Africa, Asia, and Europe would not have been uniform at any given point in history. Rushton's analysis has also lumped comparisons of intelligence and reproductive potential of several African populations, and African-Americans, even though these groups have very different population growth and genetic histories. Not only do these populations have different genetic composition (for example, African-Americans are a hybrid population with about 20–30 per cent European and about 10 per cent American Indian admixture), they also have lived in a broad range of environments. In reality, Rushton implicitly accepts the socially constructed rule of genetic hypo-descent (the one drop rule) as the basis of a biologically valid racial classification scheme. This is tantamount

to saying that the six to eight loci responsible for skin pigmentation are also the repository for all important genetically based life history variation.[5] However, we know that this cannot be true, because skin pigmentation also shows discordant geographic variation (melanic populations exist within the so-called Caucasian, Asian, and Australoid 'races' also). Neither do we have any idea what genetic loci are truly related to any substantial normal genetic variation in life history (or intelligence) in humans. Thus Rushton's project, even if r- and K-selection theory were valid (and remember it is not), would simply not be testable. The type of information concerning the nature of population densities, life history, and behavioral variables simply does not exist at a sufficient level of detail to test the properly formulated hypothesis. Studies that relate to early history of world population all agree that insufficient data exist to accurately measure birth and death rate statistics (Vinovskis, 1976; Cipolla, 1978; Murdoch, 1980; China Financial and Economic Publishing House, 1988). Finally, in fossil data, genetic and environmental sources of variation are almost impossible to disentangle (Erwin et al., 1987; Jablonski and Bottjer, 1990; Wagner, 1996).

c. Dismissal of the concept of human races

The most obvious and serious flaw in Rushton's application of r- and K-selection to explain the behavioral features of human races is that at present there are no biologically definable 'races' in the human species. This point has been appreciated since Darwin's *The Descent of Man* (1981 [1871]), and amplified by numerous results from biologists and anthropologists over the last century (for a summary see Graves, 2002). Numerous authors have summarized why there do not exist any objectively definable races in the human species. The term 'race' here is defined as a subspecies. A subspecies is considered a locally adapted population that significantly differs in average gene frequencies, chromosomal arrangements, or has a distinct evolutionary history from other subspecies level populations (Montagu, 1974; Brown, 1980; Cann et al., 1987; Nei and Livshits, 1989; Graves, 1993a; Cavalli-Sforza et al., 1994; Diamond, 1994; Brace, 1995; Owens and King, 1999; Templeton, 2002).

The fact that there is no biological reality to the socially constructed term 'race' is the most serious blow to Rushton's thesis. For example, given the measurement of the genetic composition of human populations, it is entirely unreasonable to expect that agents of life history evolution have acted in a consistent way to differentiate groups in the way Rushton describes. For example, one could just as well search for life history variation along the r- and K-continuum within African, Asian, or European populations. Sub-Saharan Africans have greater genetic diversity than any of the other populations found in the human species (Cavalli-Sforza et al., 1994; Jorde et al., 1997; Kaessmann et al., 1999; Owens and King, 1999), and the African continent contains a wide variety of habitat regimes. There is absolutely no credible intellectual reason to suspect that genetic variation in life history characteristics should not also be distributed in a similar fashion to other human genetic variation. If this were true, we would expect genetic variation for life history variation in humans to be overlapping and no necessary genetic correlation between these loci and those that have been used to socially define human 'races'.

Note that the argument that there are only small genetic differences between human populations does not mean that there need not be phenotypic differences between

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them. Phenotypes for complex traits are determined by genetic, environmental, gene and environment, and the covariance of genes and environment (e.g. Graves and Johnson, 1995; Graves and Place, 1995; Falconer and MacKay, 1996). The problem here is whether any examination of phenotypes alone can reconstruct the nature of the genetic variation responsible for the observed phenotype, or for the nature of the selective regimes that were responsible for the proposed genetic changes. The simple answer is no. Thus, any claim to a scientific assignment of genetic determination of complex phenotypes is flawed. The fact that we see this argument made so consistently with regard to humankind is strongly linked to the persistence of 19th-century racist ideology.

d. Misrepresentation of legitimate research
Graves (2002) summarizes the many areas of legitimate research that are misapplied to support Rushton's ordering of human 'races' along the r- and K-continuum. These include theory and data concerning:

1   Experimental results relative to testing r- and K-theory, such as Taylor and Condra (1980) and Hegmann and Dingle (1982).
2   Correlation of body size, brain size, IQ, and life history variation, including errors in utilizing original data (such as from Broman et al., 1987).
3   Dubious interpretations of hormone biology and variation of such between human 'races'.

Graves (2002) examined Rushton's use of original data from Broman et al. (1987). This appeared in his book in Table 2.3, p. 40. The data in this table are the result of lumping all of the IQ cognitive classes for each race reported in the original study. (In a personal communication Rushton explained how the figures in his Table 2.3 were calculated. I was originally under the mistaken impression that they had been miscopied.) The children in this study were assigned to the following cognitive classes: severely retarded, mildly retarded, borderline, average, and above average. The figures in Table 2.3 were calculated from Tables 6.10, 9.28, 9.34, 9.41, and 9.54; pp. 104, 220, 226, 233, and 161 respectively in Broman et al., 1987.

While on the surface, lumping all the children by socially identified race may seem reasonable, it is an error in statistical reasoning that favors his thesis of the greater head size of 'whites'. He arrived at the figures shown in Table 3.8 by using a weighted average for all of the cognitive classes at each of the age groups shown. An examination of the original data shows that for each of the age groups the 'blacks' in the study had 2–3 times more children assigned to the severely retarded, mildly retarded, and borderline groups. For example, the figures at birth were for whites: 26, 167, and 2331 and for blacks: 58, 825, 8079 respectively. Thus, the weighted means of the white sample were equivalent to the means of the average cognitive group, but the weighted mean of the black group became less than the mean of the average cognitive group for each age category. It is not an appropriate statistical operation to calculate a weighted mean from groups that have not been drawn from the same population (Zar, 1999: 130). Therefore it makes no sense to lump the categories of children classified as severely retarded, mildly retarded, borderline retarded, normal, and above average into the same group

(this conclusion is supported by the analysis reported by Broman et al., 1987 for each age group in this study.) Finally, the equating of head size alone to intelligence is compromised when no analysis is presented of the relationship of head to body size in the two populations in question. Broman et al. (1987) did report data that suggested that the body sizes of the 'black' and 'white' children in their cognitive class groups were not equivalent. Rushton did not mention this in his discussion of the study. For example, when head size is normalized by body weight in the data for four-month-old children, the black head circumference/body weight ratio is actually bigger than that for white children in all the cognitive classes (head circumference, Table 6.10, p. 104; body weight, p. 109; black ratio 7.03, 7.01, 6.672, 6.50, 6.25 and white ratio 6.86, 6.66, 6.51, 6.33, 6.23 respectively.) A similar pattern emerges when we examine body size data from the other age groups reported in this study.

There are many other examples. Rushton's technique of misrepresentation of legitimate research is similar to the tactics utilized by creationists when they assault evolution. Typically the creationist will present a large number of distortions of scientific fact, such that if the evolutionary biologist were to address them all, the audience would simply get lost in the details. Thus, it is necessary to first dismantle the core assumptions of Rushton's work, i.e. r- and K-selection theory. Having accomplished that, it becomes easier to understand how he has misrepresented biological data to fit his bankrupt hypothesis. In addition, much of his social science data has been collected by dubious means. Thus, Rushton argues genetic causality for racial differences utilizing a discredited theory and questionable data.

CONCLUDING REMARKS

J.P. Rushton's view of human evolution suffers from the use of antiquated and simplistic theoretical models concerning life history evolution. In addition, his methods of data analysis, results, and data sources call into question the legitimacy of his research. In the unabridged version of his book, he claims 'to have reviewed the international literature on race differences, gathered novel data and found a distinct pattern' (Rushton, 1995: xiii). This is fallacious on many accounts. Although the scope of the literature is international, to an extent, the data are not novel and the pattern he 'found' is hardly distinct from common racist stereotypes. He has only spun a tangled web of disingenuous construction speculations, in which:

1   He failed to grasp the history and formulation of density dependent selection theory.
2   He failed to review the critical experiments that falsified the central predictions of r- and K-selection theory.
3   He incorrectly applied r- and K-theory to explain human life history evolution.
4   He has presented data that are woefully inadequate to test any specific hypothesis concerning the evolution of human life histories.

Rushton's technical failings also reveal the larger ideological predispositions that drive his research agenda. He sees himself in the tradition of the London School of Psychometry founded by Sir Francis Galton (Rushton, 1995: xvii). Sir Francis Galton held, without scientific proof, that Negroids were intellectually inferior to other races. He even went so far, in *Hereditary Genius* (1869), as to rank the intelligence of various

breeds of dogs higher than that of some Englishmen and most Africans! Galton's tradition is also that of Gobineau, Davenport, Laughlin, and other eugenicists who thought that American democracy could not withstand the untrammeled reproduction of the genetically unworthy types (Chase, 1977). J.P. Rushton's work on race and life history fits well within the racist political agenda that now seeks to reverse the democratic gains made by African-Americans, Hispanics, and American Indians over the last half century. The new philosophers of race attempt to disguise their assault on the gains of non-European minorities behind 'objective scholarship and race neutrality' (Ladd, 1997). To this end, they rely heavily on work like that of Rushton (1995). What I hope I have accomplished here is, at the very least, the dismissal of this work as reasoned, objective science. Unfortunately, the history of the philosophy of 'race' in America has shown that adherence to scientific methodology was not required when one reified the inferiority of 'Blacks' to the American public. One can observe the use of Rushton's work to influence popular opinion by visiting www.duke.org, the website of the former Louisiana Klansman David Duke. The use of pseudoscientific justifications for racist policy will probably continue for some time. As long as it does, there will be reason to write articles such as this one. Indeed, it is a tangled web; fortunately, however, there is no correlation between its convolution and its strength.

Acknowledgements

Notes

1   The special abridged version of *Race, Evolution, and Behavior* begins with accolades from the genes, race, and IQ axis, including Charles R. Murray, Mark Snyderman, Harry Harpending, Arthur Jensen, T.J. Bouchard, Linda Gottfredson, Hans Eysenck, and Richard Lynn.

2   Thus the reckless, degraded, and often vicious members of society tend to increase at a quicker rate than the provident and generally virtuous members. Or as Mr. Greg puts the case: 'the careless, unaspiring Irishman multiplies like rabbits: the frugal, foreseeing, self-respecting, ambitious Scott, stern in his morality, spiritual in his faith, sagacious and disciplined in his intelligence, passes his best years in struggle and in celibacy, marries late, and leaves few behind him. Given a land originally populated by a thousand Saxons and a dozen Celts – and in a dozen generations five-sixths of the property, of the power, of the intellect, would belong to the one-sixth of the Saxons that remained. In the eternal "struggle for existence" it would be the inferior and less favoured race that had prevailed – and prevailed by virtue not of its good qualities and but of its faults.' (Darwin, 1981 [1871]: 326)

3   The panel featured J.P. Rushton of the University of Western Ontario, Todd Disotell, a molecular anthropologist, and Walter Stafford, a political scientist, from New York

University, and myself. The quotation is from J.P. Rushton (1999) *Race, Evolution, and Behavior*, special abridged version, page 82.

4   It seems that Rushton's thesis for the role of harsh winter climate playing a major role in the evolution of intelligence is an old theme. For example, Huntington (1925) presents an analysis of the role of glaciation in the acquisition of European intelligence in his chapter entitled 'Glaciation and the Supremacy of Europe'. Here Huntington outlines Rushton's present argument:

> The contrast between the action of tropical and non-tropical environments, whether through natural selection or through stimulation of mutations, seems to be one of the most important causes of differences in racial character. It appears to be a biological law that a tropical environment, because of its uniformity, tends to perpetuate primitive, unspecialized forms. Since man split off from the apes his specialization has been in the size, complexity, and functioning of the brain. Other specializations, such as changes of complexion, stature, and hair, have been of minor importance. In equatorial regions the mental type of specialization has apparently been slow, largely because there have been no really great changes throughout man's history, not even during the severest glacial epochs. That, presumably, is one of the chief reasons why it is so difficult to impose upon equatorial people anything more than the outer husk of northern government, northern religion, northern ideals, and northern culture. (Huntington, 1925: 50)

Huntington goes on to describe the type of characters that natural selection would favor in this new climate:

> This brings us to what I believe to be another highly important step in understanding the evolution of racial character. In Northern Asia, as well as in Northern Europe, the approach of the ice age would cause three things to happen. First, some of the inhabitants, presumably the most adventurous and intelligent, would migrate southward to milder regions. Second, a large percentage of the population, though not a large number as we count population, would be exterminated from generation to generation. Third, the remnant which survived would go through a process of regressive selection, whereby the survivors would be those in whom passive qualities of resistance to hunger and discomfort were most highly developed. The nervous, active types who lead the march of human progress would be at a disadvantage compared with those of a more phlegmatic constitution. (Huntington, 1925: 52–3)

Thus Huntington gives Rushton an entire rationale for the selection of higher intelligence in Europeans and Asians.

5   There may be even fewer loci controlling skin pigmentation than previously thought. See for example Ranaa et al. (1999) and Schioth et al. (1999).

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