COULD r SELECTION ACCOUNT FOR THE AFRICAN PERSONALITY AND LIFE CYCLE?

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Summary—Rushton has shown that Negroids exhibit many characteristics that biologists argue result from r selection. However, the area of their origin, the African Savanna, while a highly variable environment, would not select for r characteristics. Savanna humans have not adopted the dispersal and colonization strategy to which r characteristics are suited. While r characteristics may be selected for when adult mortality is highly variable, biologists argue that where juvenile mortality is variable, K characteristics are selected for. Human variable birth rates are mathematically similar to variable juvenile birth rates. Food shortage caused by African drought induce competition, just as food shortages caused by high population. Both should select for K characteristics, which by definition contribute to success at competition. Occasional long term droughts are likely to select for long lives, late menopause, high paternal investment, high anxiety, and intelligence. These appear to be the opposite to Rushton's r characteristics, and opposite to the traits he attributes to Negroids.

Rushton (1985, 1987, 1988) has argued that Negroids (i.e. Negroes) were r selected. This idea has produced considerable scientific (Flynn, 1989; Leslie, 1990; Lynn, 1989; Roberts & Gabor, 1990; Silverman, 1990) and popular controversy (Gross, 1990; Pearson, 1991, Chapter 5), which Rushton (1989a, 1990, 1991) has responded to.

Rushton (1988, p. 1019) modifies Pianka's (1970) list of r selected traits, to obtain a list of r traits which includes large litter size, short spacing between births, many offspring, high infant mortality, low degree of parental care, rapid rate of maturation, early sexual reproduction, short life, high reproductive effort, high energy utilization, low intelligence, opportunistic exploiters of environment, dispersing colonizers, variable population size, competition variable, often lax, low degree of social organization, and low amounts of altruism. One is impressed by the length of the list of traits whose distribution can apparently be explained. K selected organisms are the opposite. He documents that the human races can be ordered for most of these traits such that Negroids are the highest, Caucasians next, and Mongoloids last.

Rushton's critics attacked him for calling attention to racial differences, questioning whether they really exist, or whether they have a genetic basis. However, this paper will accept his description of the facts. After reviewing many of his sources, he appears to have read the literature correctly, although it is far from conclusively shown that many of the racial phenotype differences reflect genotype differences. Most of the traits have been shown within populations to have a genetic component, but little work has been done to determine if differences between populations are genetic or environmental. This paper will argue that the biological selection mechanisms in the area in which Negroids emerged would not have selected for the characteristics Rushton reports. Thus, his data may be correct, but his theory appears incorrect.

Among other objections to Rushton's theory, Weizmann, Wiener, Wiesenthal and Ziegler (1990) argued the tropical rain forest is actually a low variability environment. In fact, it is the biologists standard example of where K selection should occur. However, Rushton (1991, p. 39) responded that the African origin for Negroids was most likely the dry sub-tropical Savanna, as he had earlier suggested. The Savannas (here taken to include the Sahel) are the dry grasslands area between the Sahara and the tropical rain forest.

The Bantu language group, which is spoken over half of sub-Saharan Africa, is argued on the basis of linguistic evidence to have emerged near the Northern Cameroon (Phillipson, 1977). If the wide spread of the Bantu language groups reflects migration of an agricultural people into an area previously only occupied by hunter–gatherers, it is likely that the genetic constitution of this very important Negroid group was shaped by Savanna conditions. The Bantu expansion is believed to

have begun about 100 B.C., which would have allowed relatively little time to change gene frequencies. Most of non-Bantu Africa consists of savanna or Sahel. The West African rain forest would be the principal exception, and it very likely became densely inhabited only after agriculture emerged.

The Negroid's dark skin is much more consistent with a grassland's intense sunlight than with a tropical rain forest where both clouds and a tree canopy protect the skin from direct sunlight. There is also some question as to whether early man could have survived in the tropical rain forest only by hunting and gathering. The Sahel and Savannas are variable environments, subject to dry periods of many years duration.

Rushton follows many biologists in arguing that in a highly variable environment, a relatively r strategy would be optimal. Certainly, during a period of favorable conditions, the genotype with high r will experience the highest population growth, causing r selection. In population theory r is the steady state population growth rate. In r/K theory, it is the growth rate in favorable, low density conditions. Thus, by the definition of r, populations of animals with high r grow more rapidly in favorable conditions.

In the long run, the population is neither growing nor shrinking, but constant. Thus, r is often conceptualized as the rate of growth that would be observed when the population is low enough that competition between individuals does not cause high death rates from food shortage, or other forms of density dependent mortality competition.

THE IMPORTANCE OF THE ANNUAL CYCLE IN PIANKA'S THEORY

A reading of Pianka's (1970) original short paper reveals that the annual weather cycle plays an important role, with winter kills leading to r selection for many northern animals. Rushton's argument obviously does not depend on winter kills of humans. If winter kills were of importance (by holding the population to resource ratio down for the rest of the year), it would select for r characteristics in northern populations, causing Mongoloids to be the most r selected. Imagine a hypothetical Martian biologist unfamiliar with the data on human races but familiar with the Pianka paper. Such a biologist would predict that the most r selected human populations would be found in the coldest areas, where the winter kills were largest. This, of course, is opposite to the conclusion Rushton reached.

Rushton is not very clear how he applies the very general ideas of Pianka, written with the annual climatic cycle in mind, to humans who live through many annual cycles. However, he has apparently generalized Pianka's argument to much longer periods of time over which some human populations may be exposed to occasional catastrophic episodes which cause heavy loss of life. After such a catastrophe, the population should be well below the environment's carrying capacity, and the survivors would be selected for fast population growth. This is to say they would be selected for r characteristics. The populations Rushton regards as exposed to such occasional catastrophes are those originally inhabiting the Savannas of Africa, or the Negroids.

There appear to be two issues. One is whether such catastrophes are really more common in Africa than in the colder regions where other races evolved? The other issue is whether or not Rushton's application of the theory is valid, and should one really expect r selection in Savanna populations? Let us start with the first issue.

It is doubtful that the conditions in Africa are that much more variable than other continents, judging from three separate studies. Dunn (1968) examined the causes of mortality among hunter–gatherers. He states that in general starvation occurs infrequently. He argues it has been rare in tropical and temperate regions of moderate to heavy rainfall. In contrast, "In the arid tropics only an unusually prolonged drought may be expected to imperil the food supply, but failure of the water supply may select out the aged and sick before gross food shortages can have an effect. In the arctic and subarctic winter, on the other hand, starvation has probably always been a relatively important cause of death." One might very well expect the Arctic peoples to have become more r selected if periods of starvation were more frequent. Admittedly, Dunn does not state that the periods of starvation are due to climatic variations in the Arctic rather than merely individual hunters' bad luck, but one would expect individual luck to average out.

To see if conditions of prolonged multi-year food shortage were peculiar to Africa, a tabulation

(Murdock & Morrow, 1970, p. 307) was examined to discover where the food resources were described as being "markedly variable from year to year owing to extreme annual differences in rainfall or other recurrent but unpredictable climatic vicissitudes," (coded O, P, or Q). In sub-Saharan Africa there were 4 such cultures out of 39 (the Lozi, Wolof, Bogo, and Kenzui Nubians). Outside of Sub-Saharan Africa there were other examples (the West Punjabi, Siamese, Iban, Gilyak, Saulteaux, Zuni, Aztec and Inca). Although the data include mainly agricultural people, the climatic conditions that lead to variability in crop yields would also lead to variability in the abundance of wild plants and animals. Notice, the areas that have experienced multi-year food shortages appear well distributed around the globe, and do not appear to be limited to the African Savanna and Sahel. There appears to be no obvious basis for asserting that unusually variable environments affected the evolution of one race more than another.

Ember and Ember (1992) reported whether famine was reported as having occurred within a 25 year period in 186 cultures, the Standard Cross Cultural Sample of Murdock and White (1969). Four of the cultures (Hausa, Fulani, Teda, Nubians) were in North African areas similar to those where Negroids appear to have evolved. The percent of the African cultures reporting famine within 25 years (coded 3 or 4, out of those for which information was available) was 32% (9 of 28), vs 33% for West Eurasia (5 of 15), 29% for East Eurasia (4 of 14), and 25% for Insular Pacific (8 of 28) (the regional definitions were from the maps in Murdock & White, 1969). Thus, a history of famine does not appear to be peculiar to Africa. Again, although many of the cultures were agricultural, the weather that led to agricultural famine might have also been expected to lead to famine in pre-agricultural conditions.

Thus, three different studies fail to show that the ancestral homes of the Negroid race were any more exposed to famine than the ancestral homes of other races. Admittedly, the tests are weak, and disputes about just where one locates ancestral homes might make a difference. Let us grant that the African Savanna is indeed more variable than the areas where other races emerged, and turn to the second question: Would this variability have selected for r characteristics?

STRATEGIES FOR AVOIDING EXTINCTION DURING ADVERSE PERIODS

Biologists (whom Rushton follows), do talk of a variable environment as selecting for r characteristics (see Cody, 1966; MacArthur & Wilson, 1967; Pianka, 1970). However, close examination of the species often used as examples shows that most fall into one of two categories. In both cases, the r selection in favorable periods is associated with a supplemental strategy for avoiding extinction during the adverse periods.

One common strategy for avoiding extinction during adverse periods is to have a second life phase designed to insure that the genes survive during the adverse period. These are seeds, spores, hibernation, etc. The typical examples are plants and animals that experience an annual cycle.

Is it just nit-picking to emphasize the K part of the strategy? No, humans do not have seeds, spore, or similar protective devices in their behavioral repertoire. The r strategy works for annuals only because they can survive the periods of adversity in another state. If the species (or strictly speaking the genes) had to survive the adversity without changing form, considerably less r strategy would be optimal. Much more energy would go into building up reserves to carry it through the winter, and less to offspring production. This is why the annual plant is a poor model for humans.

If one averages the r characteristics of the growing organism and the K characteristics of the seed or spore, such organisms are considerably less r selected than results from considering the growing organism alone.

Now let us look at another strategy frequently used for surviving periods of adversity. This is dispersal and colonization. Many of the r selected species in nature are such colonizing organisms. Bush fires and tree falls create clearings in vegetation which are rapidly filled by r selected plants. Among mammals rodents appear to follow such a colonizing strategy.

It is certainly correct to describe such colonizing organisms as selected for a variable and fluctuating environment. The dispersal works because the adversity (often caused by competition) is limited to only certain areas. If the gene can transport itself to a new, more favorable area, growth can be resumed.

Thus, it is correct to say that highly variable environments often lead to selection for r

characteristics in some part of the life cycle. However, on closer observation the r characteristics are only part of the full story. The r characteristics are beneficial during the favorable periods, permitting the organism to rapidly increase its population. However, these r characteristics are coupled with one or more supplemental strategies for surviving adversity. These are either to enter a K selected state, or to disperse in the hope that some offspring will reach a more favorable environment. Of course, both options are frequently used. Seeds or spores are created, which both serve to survive adversity, and to permit dispersal. In r selected species the r characteristics are only part of the story.

ARE HUMANS COLONIZING SPECIES?

Does the human use either strategy? Clearly he does not form seeds or spores. Clearly, he is capable of at least some dispersal. Could dispersal be his strategy for surviving adverse periods in certain environments? In theory, yes. Such spatially uncorrelated variability is at least conceivable. However, the droughts in the African Savanna affect the whole area (i.e. are spatially correlated) making dispersal and recolonization impractical.

However, even if practical, a dispersal strategy need not select for r characteristics in humans. Variability can easily be imagined to lead to migration, but not to r characteristics. Humans, being intelligent and mobile, typically try different environments. If one environment proves unsuitable, humans try another. Plants, in contrast, are stuck with where they sprout. If anything, variability might select for intelligence (which Rushton makes a K characteristic), since that would be at a premium if it was frequently necessary to colonize new areas. Indeed, Geist (1978, p. 137), who even uses the vocabulary of r and K selection comments (p. 137), "Under conditions of superabundance of forage, normally encountered only by individuals colonizing a vacant or new habitat, it is adaptive to prepare individuals for a relatively great diversity of situations as well as to make them opportunisitc." This seems to imply that humans that frequently colonize new areas should be more intelligent.

Possibly a series of tropical islands exposed to hurricanes might lead to r selection for humans. At different times the population would be extinguished on any single island. Humans would avoid extinction by recolonizing such islands after the hurricanes. A more r selected race would have an advantage since it could colonize more islands. Once on a hurricane depopulated island, the new arrivals could populate it rapidly. A lack of K characteristics would not slow the population growth, since the conditions on the newly colonized, low population density island would be favorable. This island example is the very type of conditions that MacArthur and Wilson (1967) had in mind when they wrote their book on island population theory, from whence came the concepts of r and K selection. (Colonizing plants and animals that colonize clearings can be thought of as colonizing such "islands".) Unfortunately, such an island story does not sound realistic even for the Pacific Islands, and certainly not for the African Savanna. When conditions are unfavorable in one place, they are likely to be unfavorable in any adjacent areas accessible to walking hunter–gatherers.

COMPETITION FOR FOOD DURING FAMINES

The chief form of environmental fluctuation in the Savanna is the prolonged droughts that occur at intervals. The effect of these is to reduce the food supply, intensifying competition for the remaining food. The intensified competition caused by a reduction in the food supply would appear to be essentially the same as the competition that occurs in stable environments when population rises to near (or even in excess of) its carrying capacity. In such conditions, selection would be for the very characteristics that cause certain genotypes to do better when population nears its carrying capacity. By definition, these are K characteristics. There is no logical distinction between the selection for K characteristics caused by a population having grown to the carrying capacity, and the carrying capacity having been reduced to the population. For instance, intelligence and the ability to work in groups might be selected for during times of food shortage, perhaps more strongly than in normal times when food was merely scarce.

Just as periods of unusually favorable conditions are argued to select for r characteristics, periods

of unusually unfavorable conditions are argued to select for K characteristics. By definition, an expanding population is selected for r characteristics. A shrinking population is argued by biologists to be K selected. What happens in variable conditions? In variable conditions, r and K selection would alternate. What would be the net effect? In general this would depend on whether the selection for K conditions in decline was greater than the selection for r condition in growth.

This does not apply to the colonizing species since they are r selected to facilitate colonization. However, humans are not colonizing species, but ones that survive adversity in place. Surviving adversity in place calls for K characteristics. They are the characteristics that contribute to successful competition during resource scarcity.

EXTINCTION AVOIDING STRATEGIES

Long run survival in an area such as the Savanna is determined by the ability to survive the occasional very adverse periods. If extinction occurs, there is no long run survival. Conversely, avoiding extinction assures survival.

A mathematical point is worth remembering. The product of many numbers is always zero if any of the numbers is zero. The probability of the product being zero is determined by two factors: how often zero occurs and how many numbers are in the series. A long life span reduces both the probability of zero offspring in any one generation, and the number of generations required to span any given period of time. In contrast, if a colonizing species goes extinct on any one area, it is no great loss because it will be recolonized from elsewhere.

Rushton's basic insight was that biological life cycle models can be applied to humans, but models designed for colonizing species do not appear to apply to humans. However, another possibility is that biological life cycle models can be applied to humans, but Rushton selected the wrong model from the set of models available. Let us examine that possibility.

BET HEDGING MODELS AND CHILDHOOD SURVIVAL VARIABILITY?

Bet hedging models (see Stearns, 1976, p. 16, 1977, p. 154) imply that where there is variability in adult survival, variability in mortality does indeed select for r variables, notably numerous offspring. However, where the variability is greater in juvenile mortality than in adult mortality, variability selects for the K variable of long life (Murphy, 1968; Schaeffer, 1974). In essence, long life permits the gene pool to survive occasional adverse periods for juvenile mortality.

Consider an animal that has to decide on the optimal number of offspring before future conditions are known. If it overestimates, none of the offspring may survive and the parent's own survival is imperiled. If it underestimates, at least some offspring survive. In a fluctuating environment, the optimal number of offspring is smaller than in a stable environment. This would argue for a K type strategy with few offspring for the Savanna.

In humans, it appears that juvenile mortality is normally more variable than adult mortality. The mother's death often results in death of her dependent offspring. However, the reverse is not true. Thus, the childhood variance in mortality should be greater. Also, childhood mortality normally exceeds reproductive period mortality, which would suggest (but not demonstrate) higher juvenile variability. It is true that epidemics often have their greatest mortality among the very old (as in the 1918 influenza epidemic), but the old have passed their reproductive years, and variability in their survival has relatively little selective importance.

Mathematically, models with variability in birth rates are similar to those with variability in juvenile survival. It makes little difference whether a juvenile is born and then dies, or is never born. In humans, one of the responses to difficult environmental conditions is loss of female fat. This in turn leads to a loss of fertility (Frisch, 1989). An early effect of a Savanna famine would be female weight loss, and fewer births. Population would decline. The shorter a woman's reproductive years, the higher the percentage of her potential children that will be prevented by a prolonged famine. Alternatively, a long period of child bearing diversifies the risk of reproductive failure over a longer period of time, and this increases the number of children per generation. Thus, long period random environmental fluctuations, such as those in the Savanna, should select for the K characteristic of prolonged child bearing, rather than the r characteristic of a short period.

WOULD THE SAVANNA SELECT FOR r CHARACTERISTICS?

Let us abandon high theorizing and consider in detail the characteristics that would be selected for in the African Savanna, the area whose human population is argued by Rushton to have been r selected. Would a high r strategy work in the Savanna? Probably not. The droughts that have affected the Sahel have been widespread, affecting most of it (Rasmusson, 1988). The adverse conditions cannot be defeated by dispersal in search of a new area where conditions are better. An r selected population dispersing into an already populated area, also experiencing adversity, would be at a disadvantage compared to a K selected population already inhabiting the area, or trying to move into it.

Indeed, close consideration of the conditions in the Sahel suggests that K characteristics, not r characteristics would have been beneficial, and would have been selected for.

Let us look now at some differences between r and K selected individuals. Consider the benefits and disadvantages of a short life cycle. In favorable conditions, short generations imply faster population growth. Thus short generations are selected for, and the r selected individuals become more frequent.

Now suppose there is a drought of many years. Food is scarce, and females have difficulty reproducing. Suppose a female with a reproductive life of 20 years reaches maturity just as a drought starts. After 20 years of drought there is again sufficient food. Alas, she has reached menopause and cannot reproduce.

Now consider the K selected individual with a 30 year reproductive life. When conditions finally turn favorable, she still has 10 years of fertility left. A long lifespan is an advantage in environments with long periods of adversity.

Humans appear to be unique (or almost unique) in having menopause. The evolutionary advantage of this is usually given as freeing a female to devote her efforts to assisting the earlier born children and grandchildren, rather than trying to raise one more child, who would probably not reach maturity before the mother died (see Diamond, 1992 for a popular exposition). In the usual exposition, a late born child is equivalent to an early born child (actually in a stable environment the late born is worth even less because the present value of its offspring are less). However, if the problem is to survive prolonged adversity, a late born child may be worth considerably more than an earlier child. This is because the later child is insurance against a long period of adversity which prevents the birth of earlier children, or kills them.

If a long period from birth to menarche is necessary for a long period from menarche to menopause (i.e. if all parts of the life cycle must increase in proportion), this argument would lead to selection for a later start of reproduction. This is a specific application of Mountfort's suggestion "of retaining a certain proportion of progeny with delayed reproduction in order to minimize the risk of extinction" (Stearns p. 29).

Geist (1978, p. 263), the only other author besides Rushton to apply r/K theory to humans, has commented in a discussion of human evolution, "In fluctuating environments with marginal habitats for a species, longevity may be selected for, since it permits individuals to take advantages of rare unpredictable opportunities to reproduce." Geist's comment appears eminently sensible.

If one way of achieving a long period from birth to the start of reproduction is slow growth, and slow growth demands less food, genes for slow growth might actually aid in survival during difficult times by reducing the need for food, as well as delaying the start of the next generation.

Now consider another aspect of r vs K selection, the optimal period between offspring. A short period permits bearing more offspring. This increases the rate of population growth and increases r. However, it also leaves little time between offspring for the mother to restore her fat reserves. The short period between offspring also implies the offspring are competing for their mother's support while growing up.

What happens when conditions turn adverse in the next drought? Mothers who have conceived before rebuilding body fat reserves are at a disadvantage and may not survive. Mothers with large families lose more offspring. The K selected individuals, (long spacing between children), leave more survivors of the famine. The above is very similar to the bet hedging argument in the theory of optimal clutch size (see Stearns, 1976, p. 16), discussed above.

A closely related question is how much to invest in offspring. Generally devoting more energy

to investing in offspring implies having fewer offspring (the essence of the r vs K tradeoff). Consider the wisdom of the K strategy of high investment in offspring. In favorable times a high per offspring investment implies fewer children and slower population growth (reducing r). However, in adverse times, the offspring receiving more parental investment survive, while those whose parents withdrew support perish early. Thus, the K characteristic of high parental investment is selected for in adverse times.

Consider the advantage of reaching reproductive maturity early. Such individuals can start families early, but parental provisioning is likely to have been withdrawn early (as is suggested by their being r selected). In adverse conditions they are likely to experience far higher mortality. Better off are the offspring of K selected parents. Their children are still benefiting from parental support.

Then there is Washburn and Lancaster's argument (1968, p. 297), that "an advantage of slow maturation is that learning covers a series of years," and that more rapid maturation would reduce "the chances that any member of the group will know the appropriate behavior for rare events." Thus, it would seem that in an environment such as the Savanna, with occasional famines, long lives might be selected for.

Consider intelligence. In good times when resources are readily available, there may be no reproductive advantage to intelligence, and perhaps a disadvantage to the large brain and other resources needed to support it. Indeed, if the primary determinant of gestation time is the time needed for the brain to grow to its optimal size at birth (as Sacher & Staffeldt, 1974 suggest), large brains are inconsistent with the r short gestation strategy. However, when conditions turn adverse, the intelligent may survive better. Thus, Rushton's K characteristic of intelligence may be better suited for survival in adverse times.

What about self restraint, anxiety etc? These K traits would seem to contribute to survival in adversity by encouraging preparation (such as food storage) during good times. They may also encourage the maintaining of good relationships with neighbors who may be able to help during adversity. Anxiety may also discourage moving into variable areas.

Why does the above argument disagree with the biologists' general conclusion that environmental variability selects for r characteristics? One reason is that the biological arguments were developed with colonizing species in mind. As pointed out, the African Savanna does not represent the type of environmental variety which constantly is creating new environments to be colonized. Humans, regardless of race, do not use the colonizing strategy as their primary response to environmental variability. Instead, they try to survive the adversity through intelligence, cooperation, and other means.

DISEASE RESISTANCE VERSUS COMPETITION FOR FOOD

How strongly fluctuating environmental conditions select for K characteristics partially depends on the nature of the conditions. Where the adverse environmental conditions merely kill adults or offspring at rates that are independent of the genotype of the adults or offspring, the environmental problem clearly leads to selection for maximizing r, and for r characteristics (high birth rates, more twinning, and short generations). Many adverse environmental conditions appear to be like this. Seeds fall on infertile ground, or in already occupied areas. Fluctuating tides strand offspring. Many deaths by predators are essentially independent of genotype. If the offspring are where the predators are feeding, they are eaten. This type of environmental problem selects for r characteristics, and appears to be the type of environmental variability envisaged by biologists.

Other causes of death are most common when population density is high ("density dependent mortality"). Examples would include death from seeds being shaded by other plants, inadequate opportunity of the young to find food due to competition from conspecifics, etc. A population in a stable environment normally rises to the carrying capacity of that environment (referred to as K in population biology). Then both adults and offspring deaths rise. These are the direct and indirect effects of competition from other individuals. In such stable environments, genotypes best suited for competition with other individuals of the same type survive better. Then there is selection for a set of characteristics referred to as (surprise), K characteristics.

In humans, many diseases probably should select for r characteristics in that they kill apparently a random (or at least in a way uncorrelated with K characteristics), and greater parental investment

doesn't greatly affect normal (non-famine) mortality. The best defense against such disease is to have many offspring, thus swamping the losses from mortality. Thus, diseases can select for the r characteristic of fast reproduction, although this is not part of standard r vs K theory.

If the effect of disease is to keep the population well below carrying capacity, food will be sufficiently abundant that efficiency at food gathering will not be selected for. Many characteristics Rushton calls K are those that assist in food gathering. Consider intelligence. Suppose intelligence makes an individual twice as successful as another at food gathering. Imagine food is sufficiently common that the high intelligence hunter meets the needs of his family in 4 hr, and the less intelligent in 8 hr. The offspring of both individuals will be well fed, and there will not be strong selection for intelligence. Such conditions might exist in an area where disease kept the population density low, and per capita food supplies were high.

Now suppose that less disease increased the population density, lowering the food available for foraging, and reducing the foraging yield (in calories per hour) to a third of what it had been. Now the less intelligent require 24 hr (3×8) to obtain enough food for themselves and their family, and the more intelligent only 12 hr (3×4). Since there are much less than 24 hr of daylight available for foraging, the less intelligent will have inadequately fed families, while the more intelligent will still have well fed families. Such an environment would select for intelligence. This mechanism could produce an inverse correlation between disease risk and intelligence.

The above theory might be generalized to an r vs K selection theory. K characteristics are those that assist in competing with other individuals of the same species, especially for food. Thus it might be argued that areas of high disease rates would select for r characteristics, while areas with less disease would select for K characteristics.

This might explain the apparent difference in certain r vs K characteristics between races. Africa is today an area of higher incidence of infectious diseases than Europe or Asia. Many of the African diseases are tropical diseases, (malaria, yellow fever, etc.) that are rare further north. If such differences in continental disease patterns have prevailed for thousands of years, it could explain some of the differences. Since many of the tropical diseases depend on tropical organisms to transmit them (mosquitos, certain snails, etc.), the tropics may have had different and higher disease rates than northern areas for thousands of years.

The chief objection to the above theory is that most scholars question whether any hunter–gatherer populations originally had high levels of most communicable diseases (Dunn, 1968). Current, isolated hunter–gatherer populations appear relatively free of communicable diseases. A small band cannot sustain most infectious disease because all members of the band become immune and the disease dies out. In large, high density agricultural populations disease can persist because there are always new individuals who have not developed immunity. If, as it appears, tropical hunter–gatherers were relatively free of communicable diseases prior to agriculture, theories that depend on differences in disease rates to explain differences in other characteristics will fail.

A disease model also appears to make one other incorrect prediction. Populations evolving in the disease prone areas would be expected to be selected for disease resistance as well as for high population growth, r characteristics. Populations in other areas would be selected for the K characteristics needed for survival, but not for disease resistance. Disease resistance (and a strong immune system) contribute to long life. Thus, if population differences in r and K characteristics were a result of regional differences in disease, it would be the r selected populations that would be more disease resistant, and which would have the longer lives in modern circumstances where the communicable diseases have been suppressed.

This conflicts with Rushton's finding that Negroids (who evolved in high disease rate tropical regions) had the shortest life span, with Caucasians next, and then Mongoloids. Biologists have classified a short life span as an r characteristic. Thus, differential disease rates between areas could account for some of the r vs K differences Rushton found. However, there is evidence against this being the explanation.

If differences in disease rates do prove to be part of the explanation, the theory would not be an r vs K selection theory, because resistance to disease and a long life span are considered K characteristics, rather than r characteristics.

CONCLUSIONS: r SELECTION VERSUS r CHARACTERISTICS

The reader would be tempted to conclude from the above that Rushton is wrong in stating that Negroids appear to be r selected relative to other races. However, this does not follow. Actually, Rushton, by assembling much data, has made a strong case that they display many characteristics that biologists would describe as r characteristics, and which in many species have resulted from r selection. The above argument has merely questioned whether the mechanism that produced them is really r selection.

If a biologist from another planet was given a description of the environment the Negroid race is believed to have evolved in, he would probably conclude that Negroids should be the most K selected, not the most r selected. Thus, it is suggested that Negroid characteristics should not be regarded as the product of r selection.

What is the benefit of Rushton having pointed out that Negroids have more r characteristics than other races? Do we just have a new mnemonic for remembering the rank order of the races on certain characteristics (useful only to the few biologists for whom the phrase r selected calls a list of traits to mind, and who care about racial characteristics)? One possibility is that Negroids are indeed r selected, we just don't know the mechanism yet. This seems to be Rushton's original position.

An alternative, preferred by the writer is that Rushton has indeed called attention to some interesting empirical regularities, which clearly need explanation. However, the explanation is probably not r selection, but something else.

ALTERNATIVE THEORIES

One possibility for that something else is differences in testosterone levels. Lynn (1990) and Ellis and Nyborg (1992) have proposed that many of the observed racial differences could be explained by differences in the levels of testosterone among the races, and Ellis and Nyborg (1992) have documented that U.S. Negroid veterans have higher levels of testosterone than Caucasian ones, although the adult differences appear too small to explain much of the observed differences in behavior.

Lynn further observes that the severity of the winters was greatest in Northeast Asia, moderate in Europe, and least in the tropics, a ranking which corresponds to the rankings of testosterone levels. He suggests that in the coldest climates "children would have needed considerable attention. Optimal fitness would have been secured by having few of them and giving them more care, that is by shifting to a higher K reproduction strategy." Lower levels of testosterone could have done this.

Lynn (1991) later proposed that differences in climate may have led to racial differences in intelligence, because cold winters required higher intelligence. The author (Miller, 1991) in commenting on this, pointed out that food storage was a strategy frequently used to survive cold winters, and intelligence and foresight was required to implement this strategy.

Part of the persuasive power of Rushton's argument arises from the large numbers of traits for which Rushton found the races could be ranked Negroids, Caucasians, Orientals. This is the precise ordering predicted by Rushton's theory (granting him his assignment of characteristics as r or K). This is less impressive when it is realized that any theory that predicts a variation with the severity of the winter, or with latitude, would produce this ranking.

The author has an alternative explanation (which admittedly was influenced by Lynn's comments on the severity of the winters) for the empirical regularities Rushton called attention to. It is proposed that in humans, as in animals, males occupy different positions on a paternal investment (with provisioning as the most important form) versus mating effort continuum. In warm climates females can typically gather enough food to support themselves and their children. In cold climates, hunting is required, and females typically do not hunt. Thus, males in cold climates were selected to devote more of their efforts to provisioning, and less to seeking matings. In warm climates, such male provisioning was not essential, even if desirable. Thus, during the hunter–gatherer period of human evolution the optimal combination of mating effort and parental investment varied with the severity of the winters.

Mating success is promoted by such characteristics as a strong sex drive, aggression, dominance seeking, impulsivity, low anxiety, sociability, extraversion, and a morphology and muscle enzymes suitable for fighting. Provisioning is assisted by altruism, empathy, behavior restraint, a long life. The resulting differences help explain differences in testosterone levels, monoamine oxidase levels, muscle structure, body build, strength of sex drives, genital size, age of first sexual activity, life span, criminality, and possibly twinning rates. The areas where gathering had been most important and pair bonds weak developed high rates of polygyny. Once agriculture emerged, the tropical areas emerged as areas where women could grow enough food to support themselves and their families. Males maximized the number of surviving offspring by using their resources to obtain additional wives, rather than to feed the offspring of existing marriages.

The r/K theory of Rushton and Lynn focuses on whether a given amount of energy should be devoted to producing a few offspring with much investment in each, or many with little investment per offspring. The possibility that an individual male might leave more surviving offspring if he reduced his total level of parental investment, and devoted the resources saved to obtaining more opportunities for mating is not discussed. In contrast, my theory places the emphasis on the male's tradeoff between devoting energy to seeking more opportunities to mate, or devoting energy to parental investment.

However, developing this theory in detail and contrasting its implications with that of Rushton's would take considerable space and is the subject of another paper (Miller, 1993).

SUMMARY

Many r selected animals are found in variable environments. However, their strategy for surviving the inevitable adverse periods is often to form resting eggs or pupae (Pianka, 1970) or seeds in the case of plants.

Humans, of course, do not have an alternative state to survive adversity in, and the benefits they would derive from an r strategy during good conditions are offset by the disadvantages in the adverse parts of a cycle. It is not clear that over a complete cycle, variability favors r selection for humans. The impact of variability on humans is often to change the birth rate, and the survival of the young, rather than adult survival. Biologists have argued that when variability primarily affects the young, variability selects for K characteristics rather than r characteristics. Adversity that reduces the food supply (drought) produces essentially the same pressure of population on food supply as is produced by a population that has risen to equal the carrying capacity. In either case, there is selection for K characteristics. Traits such as intelligence, a long reproductive life, a high investment in each child facilitated by a long period between children, would help humans to survive the long droughts that characterize the African Savanna. Thus, the biologists' generalization that certain forms of variability selects for r characteristics may not predict the human's response to the types of variability found in the African Sahel.

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