

RUSHTON'S RACIAL COMPARISONS: AN ECOLOGICAL CRITIQUE OF THEORY AND METHOD

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Many scientists have criticized Rushton's application of a hypothesis about r- and K-selection to putative human racial differences (e.g., Cain & Vanderwolf, 1990; Lynn, 1989a, 1989b; Silverman, 1990; Weizmann, Wiener, Wiesenthal, & Ziegler, 1990; Zuckerman & Brody, 1988). The criticisms of Rushton's theoretical approach by Weizmann et al. are certainly appropriate, but they were not sufficiently forceful in asserting the fact that Rushton's approach misses the point of r- and K-selection: It ignores ecological processes and assumptions that are central to the concept. The r/K model is a valid context for interpreting human life history characteristics only if the investigator is prepared to study these ecological processes and assumptions in well-defined human populations. As an ecologist by training, I hope to show in this commentary what the r/K model implies ecologically, what would be necessary to apply it properly to human populations, and how Rushton's investigations are incompatible with appropriate use of the r/K model.

I do not imagine that psychologists will share my degree of concern over the inappropriate use of ecological theory in this context. It would seem at first glance that my criticism of Rushton's research could be satisfied if he simply removed all attempts at evolutionary explanation from his racial comparisons. However, I will demonstrate an additional point that should still trouble psychologists: Even if this research were reworked without the claims to evolutionary legitimacy, its empirical flaws would remain unremedied. Basic methodological considerations apply to these racial comparisons irrespective of their context, whether is it biology, anthropology, psychology, or sociology.

What are r-selection, K-selection, (and alpha-selection), and how are they appropriately studied?

The ecological model of "r-selection" and "K-selection" (MacArthur, 1962, 1972;

MacArthur & Wilson, 1967) has been both fruitful and badly misused in the history of ecology (Boyce, 1984). The model's basic tenet, that the dynamics of a population may influence the evolution of life history characteristics, is still far from proven (Ricklefs, 1990, p. 578) despite 20 years of research. It is difficult for a scientist outside the field to appreciate all the variations and extrapolations that have been drawn from the model. Unfortunately Rushton has attempted to apply to human races a variation (Pianka, 1970), which has been widely published but is overgeneralized, poorly supported empirically, and depends on doubtful implicit assumptions (Boyce, 1984). The resulting publications (e.g., Rushton 1988a, 1988b, 1989; Rushton & Bogaert, 1987, 1988) have given the misleading impression to non-ecologists that Rushton's racial comparisons are legitimized by evolutionary ecological theory; in fact, they are not.

The r/K model is properly used to describe how natural selection might act on life history characteristics when the agent of selection is classified as acting in either a *density-dependent* or *density-independent* fashion (Boyce, 1984). Ecologists describe an agent of natural selection or population regulation as acting in a "density-dependent" fashion when its effects increase as population density increases. Food supply, endemic infectious disease, and predation often act in a density-dependent fashion. "Density-dependent" is used to describe natural selection when its effects are independent of population density. Temperature extremes, drought, or flooding often act in a density-independent fashion.

The r/K model was based originally (MacArthur, 1962, 1972; MacArthur & Wilson, 1967) on the relationship between two parameters of the *logistic* model of population dynamics — a model in which population growth over time is described by an S-shaped curve because the population eventually encounters some factor that limits it. The concepts of density dependence and independence are inextricably linked to the parameters of the logistic model, "r" and "K".

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The parameter “*r*” represents the rate of population growth in a given environment, when there are no density-dependent limitations on population growth. “*K*” refers to the “carrying capacity” of the environment for that population — the population density beyond which it does not grow because it is limited by some factor or factors that act in a density-dependent fashion.

“*K*-selection” is a process of natural selection in which the agent of selection acts in a density-dependent way. “*r*-selection” is a process of natural selection in which the agent of selection acts in a density-independent way. *K*-selection is expected to favour genotypes that can persist and increase at high density (thus increasing *K*), while *r*-selection is expected to favour genotypes that increase most quickly at low densities (thus increasing *r*).

There is a third important class of natural selection associated with population parameters, “alpha-selection”, which is selection for competitive ability (e.g., territoriality, aggression) (Boyce, 1984; Krebs, 1978). Like *K*-selection, alpha-selection also increases in intensity at high densities, but it can also operate at low densities. Instead of favouring genotypes that persist and increase at high density, it favours genotypes that, owing to their negative effects on others, often reduce the growth rate and the maximum population size. (See Table 1 for a summary of these three types of natural selection.)

Implications for Rushton’s racial comparisons

Little in any of Rushton’s publications on *r/K* theory and racial differences bears any relationship to these well-defined processes of natural selection. In fact, the central concepts of *r*- and *K*-selection (population dynamics, and degree of density dependence of natural selection) are conspicuous by their absence from Rushton’s work. This is a critical oversight because these concepts dictate many aspects of research design. The examples below demonstrate how Rushton’s failure to attend to the central concepts has led to circularity in hypothesis testing, internal contradictions in theoretical approach, and methodological inadequacy.

1. *Methods for studying r- and K-selection.* To generate valid predictions from the *r/K* model the following steps are required. (Stearns, 1977 and Boyce, 1984 discuss further the requirements for sound methodology in studies of *r*- and *K*-selection.)

- a. Specify a well-defined local population.
- b. Understand its population dynamics in the habitat in which the natural selection is hypothesized to have occurred.
- c. Identify agents of natural selection and determine whether they act in a density dependent (*K*-selecting) or density independent (*r*-selecting) fashion. Alpha-selection (frequency dependent selection for competitive ability) must also be considered.
- d. Test predictions about the effects of these agents of natural selection on particular life history characteristics.

Rushton has done none of these things in any of his publications on racial differences and the *r/K* model.

2. *Unit of analysis:* The population is the only appropriate unit of analysis for the *r/K* model, by definition, because *r*, *K*, and density dependence are *undefined* outside the context of a population. A population (“race population” or “local race”) is “a breeding population adapted to local selection pressures and maintained by either natural or social barriers to gene interchange” (Nelson & Jurmain, 1985, p. 193). Mayr (1963) labels these groups “local populations” or “demes”. This is clearly the unit to which demographic analysis can be applied.

In contrast, human races (“geographical races”, Nelson & Jurmain, 1985, p. 193) are made up of many separate local populations (Nelson & Jurmain, 1985, p. 193), each of which has occupied a specific habitat and ecological niche and therefore has experienced its own selection pressures.

Entire races of humans are not local populations or demes; therefore the *r/K* model makes no predictions about entire current human races.

The *r/K* model *has* been applied to larger groups than populations in other species (Boyce, 1984; Stearns, 1977), but this is appropriate only when we can assume that all populations of the larger grouping experience the same density-dependent or -independent selection pressures on life history traits. For many species, this may be a reasonable assumption, but for humans it is not. Human populations occupy many different ecological niches, and populations must be considered separately until it is shown that they are similar with respect to agents of selection on life history traits.

Rushton himself has made another strong argument against the analysis of racial groups, in

TABLE 1

Summary of three classes of natural selection that are related to population parameters and are thought to influence life history and behavioural characteristics.

| Type of selection | Defining characteristic; Independent variable | Typical agents of selection | Auxiliary independent variables | Dependent variables |
|-------------------|---|--|--|---|
| r-selection | Density independent: Intensity of selection is independent of population density. Predominates at low population density. | Temperature extremes, drought, natural disasters | Newly invaded habitat, unpredictable environment, variable environment | Individual characteristics that increase survival and reproduction at low population densities; result in increased r (rate of population increase) |
| K-selection | Density dependent: Intensity of selection increases as population density increases. Predominates at high population density. | Limited food supply, endemic infectious disease, predation | Long-established local population, predictable environment, stable environment | Individual characteristics that increase survival and reproduction at high population densities; result in increased K (maximum population size) |
| alpha-selection | Frequency dependent: Intensity of selection increases with frequency of individuals displaying behaviour that excludes others from resources. Can occur at either high or low population density. | Limiting resources that can be collected or guarded, such as shelter or some types of food | Similar to K-selection | Individual characteristics that improve ability to limit access of others to resources (e.g., territoriality); result in decreased r and/or K |

arguing for high heritabilities for the life history traits he measures (e.g., Rushton & Bogaert, 1988). Given the fact that all racial groups include numerous distinct populations that have colonized a variety of new environments in the last 20,000 years, non-zero heritabilities imply that each subgroup would have the potential to move away from the ancestral average as it occupied new environments with new selection pressures.

To get an idea of the kind of within-racial group divergence we might expect in only 10,000 years (500 generations), we apply the formula for response to selection differentials

$$R = h^2 * S$$

where R is the response to selection of the population mean in SD units, h^2 is the heritability of the trait, and S is the difference between the mean of the population and the mean of the reproducing parents, also in SD units (Falconer, 1960). If h^2 of the trait is 0.3 (Mousseau & Roff, 1987) and S is 0.01 (a moderate selection pressure), the population mean can be expected to have changed by 1.5 SD units at the end of 500 generations, or 10,000 years. Therefore, on the basis of Rushton's own suggestions about heritability, we must assume that populations within races have been substantially free to adapt to their particular ecological circumstances. The mean of any population is more likely to reflect its history of the last 10,000 years than to preserve the more distant ancestral conditions of that racial group.

3. *Generalizing to races.* Because local populations are the only appropriate units of analysis for r- or K-selection by definition, any generalizations to entire races must involve proper sampling of the populations assigned to a racial group. The requirements for unbiased sampling are the same here as in any other scientific study — all units must be equally likely to be sampled, the units must be independent of one another, and sampling must be either random or systematic. If there were a good reason for studying racial groups rather than populations, an investigator would have to do the following to generate valid generalizations:

a. Make a list of all distinct local populations of each racial group (Nelson & Jurmain, 1985, p. 193), or use a standardized list of distinct societies such as the Standard Cross Cultural Sample (Murdock & White, 1980).

b. Sample randomly or systematically from the list (Murdock & White, 1980, suggest

several methods for doing so). No local population is to be sampled more than once.

c. In a statistical analysis, each sampled population provides one datum (i.e., the mean of the population for the trait in question). The sample size is then the number of distinct local populations that have been studied.

d. In analyzing these data, it would be important to distinguish among several factors that might influence life history traits. This might be done with a 2-way analysis of covariance: The covariates would be population means for life history traits and density dependence of the natural selection, while grouping variables would be race and some measure of ecological niche.

4. *Importance of original habitat.* Populations studied in an analysis of r- or K-selection should be living in the habitat in which the selection is hypothesized to have operated. Therefore, data from the following types of populations are often misleading: those that have recently migrated to new habitat (e.g., all North Americans except Amerindians), those whose habitat has recently been radically altered (e.g., most Amerindians), and those who have experienced strong "unnatural" selection in the process of being exploited by other populations (e.g., Afro-Americans). Data from these populations should not be included in the analysis. There are two reasons for this. First, it is impossible to know what selection pressures operated historically on their life history traits, and whether their action was density-dependent or density-independent, without detailed knowledge of the population's dynamics in its ancestral habitat. Second, data on life history traits measured in new or recently altered environments are often inappropriate for understanding the adaptive role of the traits in their original environment, because of genotype-environment interactions.

Most of Rushton's racial comparisons have been given as verbal summaries or heavily abridged tables from other sources, rather than a more rigorous meta-analysis. He provides no evidence that he or the studies cited have sampled the populations of the races in an unbiased way (Point 3 above), or that the populations were studied in the habitat in which the hypothesized natural selection took place (Point 4 above). Readers should keep in mind, whenever Rushton suggests that there is a difference between races in some trait hypothesized to result from

differential r- or K-selection, that his sample size for that comparison should be the number of ecologically distinct populations studied.

5. *Specific selection pressures.* It is impossible to predict what life history traits will be favoured by any kind of selection unless you know what particular ecological factors influence life history traits in the specific population under consideration and have a model of how they function (Boyce, 1984). Different agents of r-selection will produce different selection pressures, as will different agents of K-selection.

This is a crucial point, especially because, for controversial traits like intelligence and rule-following, Rushton does not have even the guidance of Pianka (1970) for placing them on the assumed continuum; they are absent from Pianka's table. In fact, in the absence of detailed information about the ancestral ecology of the populations he is comparing, Rushton has no basis whatsoever for making predictions about these traits. The following example shows how different agents of r- or K-selection might influence intelligence:

a. Suppose population A is regulated by endemic infectious disease. Endemic infectious disease imposes density-dependent mortality, so it is generally an agent of K selection. Individuals with high intelligence would tend to be favoured under such a regime because of their understanding of hygiene and ability to discover and use medicinal herbs.

b. Suppose the members of population B experience high mortality during severe winter storms. Severe winter storms would be agents of r selection because they impose density-independent mortality. Individuals with high intelligence would tend to be favoured under such a regime because of their ability to design and build good shelters and use fire.

Thus, both r- and K-selecting agents can favour high intelligence.

With respect to social rule-following, Rushton's predictions in the absence of ecological information are equally unjustified. First, note that agents of r-selection are unlikely to influence social rule-following at all, because they act independently of the density of the population. In contrast, we do expect agents of K-selection to influence rule-following, but rule-following will be favoured only in situations

where there is no advantage to cheating. Consider the following two populations:

c. Suppose population C is also regulated by endemic infectious disease. Endemic infectious disease imposes density-dependent mortality, so it is generally an agent of K selection. In this case, individuals who violate rules of hygiene will be harmed, and rule-following behaviour will be favoured.

d. Suppose population D is regulated by limited food, which imposes density-dependent mortality and therefore is generally an agent of K selection, too. However, individuals can gain an advantage by violating rules of food-sharing, eating tabooed foods, or refusing to offer prescribed sacrifices of food to the gods, so this is a case in which K-selection would favour rule-breaking.

Thus, in the absence of information about specific agents of natural selection, general predictions about the resulting traits, such as Rushton's, are unjustified.

6. *Alpha-selection.* Inclusion of alpha-selection (selection for competitive ability) in a model of selection pressures on life history and behavioural traits casts additional doubt on any attempt to force the processes onto a one-dimensional continuum (Boyce, 1984). Given the extraordinary ability of some human populations to extinguish other human populations and other species, it seems reasonable to assume that alpha-selection has been important in human evolution. If Rushton ignores alpha-selection in his interpretation of the evolutionary origin of human traits, he must provide some empirical justification for doing so.

7. *Assumption of a unidimensional continuum.* K-selection and r-selection do not operate on a one-dimensional continuum (MacArthur, 1972, p. 228), as assumed by Rushton. The possibility of additional classes of natural selection such as alpha-selection (Point 6 above) alone is sufficient cause to question the r/K model's "prediction" of an "ordering" of individuals or groups. In addition, the influence of agents of r- or K-selection on life history traits is not necessarily opposite, as assumed by Rushton (Boyce, 1984; MacArthur, 1972, p. 229).

8. *Independent variables.* Like many hypotheses, Rushton's involves the relationship between two sets of variables (Table 1): The *independent variables* are direct indicators of

r- or K-selection (e.g., the degree of density dependence of the selection processes in each population studied). The *dependent variables* are the life history, behavioural, and personality characteristics of the populations. To test a hypothesis of this kind, scientists usually measure both the independent and dependent variables across a range of values and then assess their relationship by statistical methods. Rushton's approach, to test predictions about patterns among the dependent variables while ignoring the independent variables, borders on circularity and at best provides weak support for the hypothesis, because there are many other factors besides r- or K-selection that could be responsible for the patterns (Boyce, 1984; Pianka, 1970, p. 596; Stearns, 1977). In view of the lack of evidence for the hypothesized relationship between independent and dependent variables (Boyce, 1984; Ricklefs, 1990) after 20 years of investigation by ecologists, we should view Rushton's approach with considerable skepticism. In addition, as we shall see below, the predictions that follow from the little ecological information Rushton has about ancestral populations of the racial groups actually are contradicted by his data.

Readers should bear in mind that, when Rushton labels patterns of life history characteristics as "r-selected" or "K-selected", he does so with no information about the independent variables (direct measures of the processes of r-selection or K-selection); he is assuming Pianka's hypothesis about r- and K-selection, instead of testing it.

Rushton's defense of his theoretical approach

How is it possible that Rushton's attempt to study r- and K-selection in humans is so far removed from the central concepts of those processes? This is an important question, because Rushton uses the context of theoretical ecology to lend an air of legitimacy to his racial comparisons. Readers of the psychological journals in which this work is published, who might otherwise be skeptical, might feel that they are in no position to question research that claims to be an application of evolutionary ecology. In the "Reply to Weizmann," Rushton discusses his theoretical approach. This discussion alone indicates a lack of familiarity with ecological thinking and scientific method in general, which is inconsistent with the extremely difficult ecological problem Rushton has chosen to investigate.

Even though the admission is fundamentally damaging to his uncritical assumption of Pianka's continuum, Rushton (this issue) acknowledges that ecologists do not agree on Pianka's formulation of the r/K model and that there are (many) other hypothesized selection pressures on life history and personality traits. These other types of natural selection on life history and other traits include some that are also related to population parameters (e.g., alpha-selection) and must be considered if one is to get a complete picture of evolutionary processes associated with population dynamics (Krebs, 1978). If theoretical ecologists do not find the concepts of r- and K-selection straightforward, we might wonder whether this is the best area of ecology for psychologists to try to apply to human populations.

Further doubt is cast on Rushton's approach to evolutionary theory by his contention that "theories are not 'correct' or 'incorrect'". While it is true that we can never ultimately "prove" the truth of a theory or hypothesis, we can certainly show that one is incorrect by a number of means — (1) showing that it contains internal contradictions, (2) showing that one or more of its important assumptions is false, (3) showing that it is inconsistent with well-established theory, or (4) falsifying it with an empirical critical test. Pianka's (1970) continuum is immediately questionable on the issue of assumptions (Boyce, 1984) and internal consistency (Point 5 under "Implications...").

The fact that a theory or hypothesis can be intrinsically unsound implies that the choice of theoretical approach *is* important and that its choice is more than just a matter of taste, convenience, or "different perspectives". The problem becomes even more critical when the investigator is working outside his own field, for he is unlikely to appreciate the subtle ways in which hypotheses and models may differ. Rushton states that he chose Pianka's continuum on the basis of two apparently reasonable criteria. However, these two criteria have served him poorly. The first is a bad criterion for ecology in particular; the second actually provides grounds for rejection of the hypothesis Rushton has chosen, once we understand the processes r- and K-selection.

Rushton's first criterion: Simplicity of model

Rushton prefers "simple" models. Ironically, in ecology, the simpler the model appears, the

more ecological sophistication is required to understand and apply it. Here is the reason: Ecological systems are never simple. They always involve a number of biological and physical processes that interact in complex ways. The only difference between a complex ecological model and a simple one is that the "complex" model makes explicit, and hence clear to everyone, the relationships and processes of the real system that are hypothesized to be relevant, while the "simple" one renders them invisible by making "simplifying" assumptions about them. Simple models will be successful only if their simplifying assumptions either match reality or are unimportant.

There is nothing intrinsically wrong with using a simple model as long as one is aware of the underlying ecological processes and simplifying assumptions that have been made, and checks their validity in every application of the simple model. However, in the case of "simple" hypotheses about r- and K-selection, even ecologists have been lax about keeping the processes and assumptions in mind (Boyce, 1984).

Hypotheses about r- and K-selection have undergone several types of "simplification". First, theoreticians proposed a set of auxiliary independent variables (remember that the true independent variable is the degree of density dependence associated with the natural selection). These auxiliary independent variables included potentially quantifiable descriptors of environments, such as "predictability", and were assumed to be correlated with r- or K-selection. Often, additional assumptions were then made about the "predictability", say, of particular environments, such as mountaintops or the tropics. These layered assumptions, once made, often have been subsequently ignored by many ecologists, leading to confusion when the data do not fit the predictions of such "simple" hypotheses. The study of Zammuto and Millar (1986), cited by Rushton, is a perfect example of such confusion. These authors, trying to rationalize why many predictions from "simplified" hypotheses about r- and K-selection were inconsistent with their data, discovered several incorrect assumptions that had gone untested for 20 years! (Zammuto & Millar, 1986, pp. 1790, 1791).

Pianka (1970) introduced another type of "simplification" to the world of hypotheses about r- and K-selection, one that was especially popular because it was proposed at a time when ecologists were anxious to achieve status as a

"harder" science and so were particularly drawn to theoretical ideas that were elegant, simple, and general. As we have seen, in ecology these adjectives are usually synonymous with "requiring many assumptions".

Pianka assumed (1) that r- and K-selection would favour opposite traits (an assumption not made by the original model) and (2) that populations could respond to r-selection only through increased reproductive effort (an assumption especially unsuitable for humans). He composed a list of many life history and other characteristics that he predicted would be influenced in opposite directions under regimes of r- or K-selection. He thus hypothesized a unidimensional spectrum that ordered life history and other traits (excluding, notably, intelligence and rule-following).

In addition, by the time he had reached the end of his article, Pianka (1970, p. 596) had begun the unfortunate tradition of labeling sets of life history characteristics as "r-selected" or "K-selected" solely on the basis of where he had placed them on his hypothetical continuum, without any evidence that the processes of r-selection or K-selection had actually produced them. This tradition has permeated the ecological literature as well as Rushton's articles on racial comparisons, degenerating even to the point of using "r" and "K" as adjectives (e.g., "The more K the family...". Rushton & Bogaert, 1987, p. 533). It is careless usage and nearly always reflects a failure on the part of the author to remember that the relationship between population dynamics and organismal traits is one of several yet-unproven hypotheses, not a fact (Ricklefs, 1990).

To understand how damaging this tradition has been to clear thinking in ecology, imagine the following analogous situation in psychology: Suppose that a hypothesis suggested that the type of school a person attended as a child would determine certain personality characteristics. Suppose that psychologists like the hypothesis, and without waiting for definitive empirical evidence, began labeling suites of personality characteristics as "public school educated" or "private school educated". Thus, rebellious people (say) would be labeled "public school educated" and ambitious people (say) would be labeled "private school educated" in psychological journals, without determining whether they really had gone to those types of schools. A researcher from outside the field, unfamiliar with the history of

this usage, might conclude in good faith that public schooling produces rebellious behaviour when in fact the relationship between school type and personality was still only a hypothesis.

Not surprisingly, Pianka's formulation proved difficult to test rigorously because of its many implicit assumptions (Boyce, 1984), and years of attempts to test it in the field revealed little empirical support for it in any case, especially within species (Stearns, 1977). As Ricklefs (1990, p. 578) states: "Although the theory is plausible, a direct relationship between population growth rate or population fluctuations and life history characteristics has not been established". In summary, while ecologists are still interested in describing agents of natural selection as "r- or K-selecting", it is now recognized that these are only two of many dimensions that could be used to classify selective processes. They are far from being the all-encompassing explanation for variation in life histories, as Rushton assumes them to be.

Rushton's uncritical statement that vole population cycles result from dichotomous r- and K-selection leads us to a good example of the evolution of thinking among ecologists about natural selection on life history traits over the past 20 years. The paper cited, Krebs et al. (1973), dates from the period when it was popular to try to interpret many variations in life history in terms of Pianka's unidimensional continuum. Further thinking and study of the complexity of selection on behavioural characteristics has caused Krebs to conclude that a population that declines rapidly in numbers, as vole populations do periodically, cannot by definition be K-selected. If it is useful to categorize the mode of selection in declining vole populations at all, it is more likely to be alpha-selection (C. Krebs, pers. comm., September 1990). Once again, we are left with the conclusion that a unidimensional continuum is a poor representation of multidimensional ecological processes.

Given the pitfalls of trying to use simple models that represent complex realities, the wisest choice for a non-ecologist trying to study humans is surely a model that requires relatively few assumptions and instead lays out the relevant ecological processes and relationships in quantifiable terms, as a reminder to the investigator of what he should be measuring.

Rushton's Second Criterion: Consistency with Data

Rushton's second criterion for choice of model is that the theory should fit the data. This criterion

is reasonable, but in fact Rushton's data contradict the predictions that proceed from his own description of the ecological history of the races, in the key paragraphs in the "Reply to Weizmann et al.": "But why would Mongoloids have ended up the most K-selected?...". These paragraphs represent Rushton's only attempt to describe in ecological terms any process of r- or K-selection in humans. I will discuss them in some detail (1) because Rushton's assertions about the ancestral ecology of the races are almost completely undocumented, (2) because nearly every statement would be questioned by ecologists, (3) because the paragraphs' own internal contradictions demonstrate a fundamental failure to understand the processes of r-selection and K-selection, and (4) because Rushton's own descriptions of the ecology of ancestral populations imply that he has got the predictions exactly backward, if any generalizations could be made about current human races (which they cannot, see Point 3 under "Implications...").

First, a meaningful answer to the question "But why would Mongoloids have ended up the most K-selected?..." must describe a process of K-selection. The answer should include the identification of an agent of natural selection and some indication of the density dependence of its action (its relationship to the parameter K). Rushton never mentions density-dependence, population dynamics, or environmental carrying capacity (K) in his answer to this question. Instead, he states that "Predictable environments are an ecological precondition for K-selection". This is incorrect, the citation of Weizmann et al. notwithstanding. The ecological *sine qua non* for K-selection is a history of some specific mode of density-dependent natural selection, which will occur when the population is at or close to environmental carrying capacity (K) (Boyce, 1984; MacArthur, 1962, 1972; MacArthur & Wilson, 1967; Pianka, 1970). In fact, Pianka (1970), the source of Rushton's continuum, clearly includes "predictability" in his table not among the independent variables (which are the processes of r- and K-selection), but among the hypothesized correlates to be investigated! Environmental variability and predictability may well be correlated with r-, K-, or alpha-selection, or they may independently influence life history characteristics (e.g., Goodman, 1979; Hastings & Caswell, 1979; Murphy, 1968; Schaffer, 1974) but models of environmental predictability, like the r/K

model, are yet to be thoroughly tested (Ricklefs, 1990).

Second, Rushton apparently does not realize the complexity of the topic of environmental predictability. Zammuto and Millar (1985), for example, list 18 different measures of predictability. The dozens of empirical and theoretical ecologists who have struggled for decades with the problems of defining, measuring, and theorizing about environmental variability and predictability would be astonished to find Pleistocene environments so easily characterized as “highly predictably harsh” (Asia), or “less predictable” (Africa) with no references or indication of how these concepts were defined or measured by Rushton.

Third, Rushton describes tropical savannahs (without references) as being characterized by “viral, bacterial, and parasitic diseases”. Since endemic infectious diseases usually impose density-dependent mortality, they are generally agents of K-selection. Thus, Rushton’s own suggested agents of natural selection on African populations imply that African populations have had a strong history of K-selection, as well as the r-selection implied by “droughts” (also undocumented). An ecologist would also want to compare quantitatively the degree of r-selection imposed on Negroid populations by Pleistocene African droughts, with the degree of r-selection imposed on Pleistocene Asian Mongoloid populations by bouts of unusually severe winter weather, or with the degree of r-selection imposed historically on Central American Mongoloid populations by devastating earthquakes and volcanic eruptions.

Fourth, Rushton describes how Mongoloid populations “moved north”. Indeed, Mongoloid populations have spent long periods of time invading new habitats — first Asia, then the Americas (Nelson & Jurmain, 1985). Given that populations entering new habitats are freed for a time from density-dependent controls, they experience r-selection (Boyce, 1984; MacArthur, 1972; MacArthur & Wilson, 1967; Pianka, 1970; Ricklefs, 1990). Therefore, the r/K model predicts that Mongoloid populations should have experienced strong r-selection in general, especially compared with African populations, which have been in the same place for at least 140,000 years. As Rushton’s own arguments imply, African populations have had much more opportunity to approach their environmental carrying capacity and to experience K-selecting

agents of natural selection, such as endemic infectious disease. In addition, Rushton lists many traits of Mongoloid peoples that are thought to represent adaptation to cold. Cold weather acts in a density-independent fashion (adaptations to cold improve survival in cold weather regardless of population density); cold weather is normally an agent of r-selection.

Thus, Rushton’s claim about the empirical ordering of life history and behavioural traits in the racial groups exactly contradicts general predictions that follow from his own claims about their ancestral ecology and the r/K model (Boyce, 1984; MacArthur, 1972; MacArthur & Wilson, 1967; Pianka, 1970; Ricklefs, 1990, p. 577). (Specific predictions from the model could be made only about individual populations after careful study in their historical habitat, as I have pointed out above).

The only ecological study cited by Rushton in these paragraphs is his statement that Zammuto and Millar (1985) demonstrated that many organisms “become more K-selected with increasing elevations and latitude” (Rushton, this issue). Zammuto and Millar actually found little support for predictions from several “simplified” hypotheses about r- and K-selection, and did not actually measure the process of K-selection at all. Once again, careless usage of the phrase “K-selected” to describe suites of organismal characteristics, rather than a process of density-dependent natural selection, indicates circular reasoning rather than support for Rushton’s hypothesis.

Standards of investigation

Rushton complains of a “double standard” being applied to judgments of the quality of his research. If there is a double standard, it reflects common sense and careful science. There are several reasons why a research program like Rushton’s requires unusually high standards of investigation. First, Rushton has undertaken to use an ecological model that demands considerable ecological sophistication for its proper application. Second, he has attempted to generalize his findings to large, widespread groups of humans. These characteristics render his research program articularly ambitious, and it demands correspondingly sophisticated research methods. The procedures suggested in Points 1 and 3 under “Implications for Rushton’s research” are, in fact, minimal standards for the problem that

Rushton has chosen. The design of his research does not meet these standards.

Rushton's choice of research demands high standards of investigation for a third reason as well. When research has the potential to be misused or to cause harm to people, it is perfectly appropriate to apply more stringent standards to its publication, as we do routinely in setting standards for drug testing or food preparation, depending on whether the product is to be used by humans or animals. Rushton himself does not deny that racial comparisons have in the past been abused. Contrary to Rushton's contention, however, it is generalizations about characteristics of visibly different or subordinate groups that lead to institutionalized violence and exploitation, not environmental or genetic arguments.

With these grave considerations in mind, investigators, reviewers, and editors have a special responsibility when dealing with research of this sort, to make sure that it is published only when it is of the highest quality. The job is all the harder when the research in question crosses disciplinary lines.

References

- Boyce, M.S. (1984). Restitution of r- and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics*, 15, 427-447.
- Cain, D.P., & Vanderwolf, C.H. (in press). A critique of Rushton of race, brain size, and intelligence. *Personality and Individual Differences*.
- Falconer, D.S. (1960). *Introduction to quantitative genetics*. New York: Ronald Press.
- Goodman, D. (1979). Regulating reproductive effort in a changing environment. *American Naturalist*, 113, 735-748.
- Hastings, A., & Caswell, H. (1979). Role of environmental variability in the evolution of life history strategies. *Proceedings, National Academy of Sciences*, 76, 4700-4703.
- Krebs, C.J. (1978). *Ecology: The experimental analysis of distribution and abundance*. New York: Harper and Row.
- Krebs, C.J., Gaines, M.S., Keller, B.L., Myers, J.H., Tamarin, R.H. (1973). Population cycles in small rodents. *Science*, 179, 35-41.
- Lynn, M. (1989a). Race differences in sexual behavior: A critique of Rushton and Bogaert's evolutionary hypothesis. *Journal of Research in Personality*, 23, 1-6.
- Lynn, M. (1989b). Criticisms of an evolutionary hypothesis about race differences: A rebuttal to Rushton's reply. *Journal of Research in Personality*, 23, 21-24.
- MacArthur, R.H. (1962). Some generalized theorems of natural selection. *Proceedings of the National Academy of Science, USA*, 48, 1893-1897.
- MacArthur, R.H. (1972). *Geographical ecology*. New York: Harper & Row.
- MacArthur, R.H., & Wilson, E.O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Mousseau, T.A. & Roff, D.A. (1987). Natural selection and the heritability of fitness components. *Heredity*, 59, 181-197.
- Murdock, G.P., & White, D.R. (1980). Standard cross-cultural sample. In H. Barry, & A. Schlegel (Eds.), *Cross-cultural samples and codes*. (pp. 3-44). Pittsburgh: University of Pittsburgh Press.
- Nelson, H., & Jurmain, R. (1985). *Introduction to physical anthropology*. St. Paul: West.
- Pianka, E.R. (1970). On r- and K-selection. *American Naturalist*, 104, 592-597.
- Ricklefs, R.E. (1990). *Ecology*. New York: Freeman.
- Rushton, J.P. (1988a). Race differences in behaviour: A review and evolutionary analysis. *Personality and Individual Differences*, 9, 1009-1024.
- Rushton, J.P. (1988b). The reality of racial differences: A rejoinder with new evidence. *Personality and Individual Differences*, 9, 1035-1040.
- Rushton, J.P. (1989). Race differences in sexuality and their correlates: Another look, and physiological models. *Journal of Research in Personality*, 23: 35-54.
- Rushton, J.P. (1990). Do r-K strategies underlie human race differences? A reply to Weizmann et al. *Canadian Psychology*, 32:1.
- Rushton, J.P. & Bogaert, A.F. (1987). Race differences in sexual behavior: Testing an evolutionary hypothesis. *Journal of Research in Personality*, 21, 529-551.
- Rushton, J.P. & Bogaert, A.F. (1988). Race versus social class differences in sexual behavior: A follow-up test of the r/K dimension. *Journal of Research in Personality*, 22, 259-272.
- Schaffer, W.M. (1974). Optimal reproductive effort in fluctuating environments. *American Naturalist*, 108, 783-790.
- Silverman, I. (1990). The r/K theory of human individual differences: Scientific and social issues. *Ethology and Sociobiology*, 11, 1-10.
- Stearns, S.C. (1977). The evolution of life history traits: A critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*, 8, 145-171.
- Weizmann, F., Wiener, N.L., Wiesenthal, D.L. & Ziegler, M. (1990). Differential K theory and racial hierarchies. *Canadian Psychology*, 31, 1-14.
- Zammuto, R.M. & Millar, J.S. (1985). Environmental predictability, variability, and *Spermophilus columbianus* life history over an elevational gradient. *Ecology*, 66, 1784-1794.
- Zuckerman, M., & Brody, N. (1988). Oysters, rabbits, and people: A critique of "Race differences in behaviour" by J.P. Rushton. *Personality and Individual Differences*, 9, 1025-1033.

TROIS POINTS DE VUE CONCERNANT LES DIFFÉRENCES RACIALES

RÉSUMÉ

Les trois articles précédents traitent tous des points de vue controversés de J. Philippe Rushton concernant les différences raciales parmi les êtres humains. Dans le premier article, Rushton répond à une attaque antérieure de sa théorie de la part de Weizmann et ses collègues. Les deux autres articles sont des réponses à Rushton.

Selon Rushton, les idéaux démocratiques sont compatibles avec la théorie de l'évolution de Darwin, mais ces idéaux ne nous forcent pas à croire à l'uniformité biologique. Il présente des données qui suggèrent l'existence de différences raciales en ce qui concerne la grandeur du cerveau, l'intelligence, le délai de maturation, la retenue sexuelle, le tempérament, et l'organisation sociale. Rushton divise son argument en deux sections principales: (1) données et (2) théorie.

En ce qui concerne les données, Rushton n'a recours qu'à son compte rendu d'études déjà publiées, qui comprennent des données venant de l'Afrique, de l'Asie, de l'Europe et de l'Amérique du Nord. Ces données, selon Rushton, indiquent que pour un grand nombre de variables il existe une configuration précise où l'on trouve les "Mongoloids" et les "Negroids" aux bouts opposés de la gamme et où l'on trouve les "Caucasoids" à une position intermédiaire. Il fait remarquer qu'il existe une variation considérable à l'intérieur de chaque groupe. Rushton admet qu'il y a plusieurs sources d'erreur dans les données qu'il présente, mais il maintient qu'il n'a trouvé aucune étude qui signale des résultats opposés à la configuration qu'il présente. Il suggère que cette configuration est tellement stable qu'il est très peu probable qu'elle puisse s'expliquer par des erreurs de mesure. Même si des analyses subséquentes révélaient des sous-groupes qui ne se conformaient pas à la configuration générale, Rushton maintient qu'il ne serait pas logique de permettre à des cas isolés d'éclipser le général.

Rushton accuse les critiques tels que Weizmann et ses collègues de ne pas prendre en considération les différences raciales en ce qui concerne le comportement sexuel. De telles différences ont des conséquences graves selon Rushton qui constate que la prédominance mondiale des maladies transmises sexuellement telles que la syphilis

et le SIDA se conforme à la configuration à laquelle il fait souvent référence. En ce qui concerne le SIDA, Rushton dit que cette configuration se manifeste à la fois entre et à l'intérieur des pays. En plus du comportement sexuel, Rushton discute la configuration raciale qu'il propose en ce qui concerne le crime, la fertilité humaine, la grandeur du cerveau et l'intelligence.

Se tournant vers la théorie, Rushton donne une explication de sa théorie r/K (r représente le taux d'augmentation maximum d'une population auquel contribue la reproduction prolifique; K représente le plus grand nombre d'organismes d'une espèce qui peuvent se maintenir indéfiniment dans une partie donnée de l'environnement). Les symboles r et K désignent des différences entre la procréation et les soins des parents. Les huitres, qui produisent 500 million d'œufs par an mais qui ne s'occupent aucunement de leur progéniture, servent d'exemple de la stratégie r ; les grands singes, qui ne produisent un enfant que tous les cinq ou six ans mais qui s'occupent beaucoup de leur progéniture, servent d'exemple de la stratégie K . Les êtres humains sont des stratèges K mais, selon Rushton, il existe des différences r/K entre les espèces, y compris entre les êtres humains. En ce qui concerne la stratégie K , il maintient que les "mongoloids" sont plus K que les "caucasoids" qui sont plus K que les "negroids". La théorie r/K prédit les différences d'espacement entre les naissances, le nombre d'enfants, le taux de mortalité des enfants, la stabilité de la famille, la quantité de soins données par les parents, le poids à la naissance, la durée de la vie, l'intelligence, l'altruisme, et d'autres variables.

Rushton dit que son explication du comportement social est basée sur l'influence génétique, pas sur le déterminisme génétique. La disposition génétique et l'environnement agissent l'une sur l'autre. Néanmoins, il est important d'étudier les influences biologiques aussi bien que celles de l'environnement, même au risque d'offenser la sensibilité politique.

En réponse, Weizmann et ses collègues mettent en question la façon dont Rushton se sert de sa théorie r/K . Ils ne contestent pas l'emploi de cette théorie en tant qu'heuristique, mais ils critiquent les versions de la théorie qui relie la

sélection naturelle aux traits génotypiques spécifiques. Ils maintiennent que la manière dont Rushton aborde la théorie r/K mène à des prédictions arbitraires et nécessite une attribution idiosyncratique du statut r/K à des traits différents, tels que la criminalité et l'altruisme. Ils mettent également en question la manière dont Rushton se sert du concept de race dans sa division des êtres humains en "Mongoloids", "Caucasoids" et "Negroids". Ils citent certaines données qui indiquent que la variation entre les races s'élève à moins d'un septième de la variation à l'intérieur des groupes. Il y a, par exemple, plus de variation génétique à l'intérieur de la population africaine du sud du Sahara qu'il n'y a à l'intérieur de toute autre population humaine. Ainsi, si on fait des classements selon la race, on devrait considérer les Africains comme un groupe de races plutôt qu'un seul groupe racial. Pour ceci et d'autres raisons, ils considèrent le concept de race inepte du point de vue biologique. Ils sont également en désaccord avec les présomptions de Rushton concernant l'endroit et l'époque où ces prétendues races ont évolué sur la terre. Ces présomptions sont essentielles à l'assertion que les noirs sont plus r que les blancs ou les orientaux.

La deuxième réponse à l'article de Rushton est écrite d'un point de vue écologique. Anderson donne une explication détaillée du modèle r/K ,

et désigne quatre étapes qui seraient nécessaires à la génération de prédictions valables:

(1) spécifier une population locale bien définie;
 (2) comprendre la dynamique de sa population dans le cadre de l'habitat où l'on pense que la sélection naturelle a eu lieu;

(3) identifier les agents de la sélection naturelle et les relier de manière précise au modèle de la sélection r/K ;

(4) mettre à l'épreuve les prédictions concernant les effets de ces agents de sélection naturelle sur des caractéristiques particulières de l'histoire d'une vie.

Anderson prétend que Rushton n'a suivi aucune de ces étapes dans aucun de ses articles sur les différences raciales et le modèle r/K .

Finalement, elle tente de démontrer que même si Rushton abandonnait toute prétention à la légitimité évolutionnaire, les défauts empiriques de sa position resteraient. Elle maintient qu'un programme de recherche tel que celui de Rushton nécessite des exigences d'enquête anormalement élevées pour deux raisons: afin que le modèle écologique dont Rushton se sert soit convenablement appliqué il faut une sophistication écologique considérable et Rushton a tenté de généraliser ses résultats à des groupes humains très grands et très étendus. Elle trouve que le dessein de ses recherches n'est pas à la hauteur des exigences requises.