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Editorial

Placing intelligence into an evolutionary framework or how *g* fits into the *r–K* matrix of life-history traits including longevity

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Abstract

First, I describe why intelligence (Spearman's *g*) can only be fully understood through *r–K* theory, which places it into an evolutionary framework along with brain size, longevity, maturation speed, and several other life-history traits. The *r–K* formulation explains why IQ predicts longevity and also why the gap in mortality rates between rich and poor has *increased* with greater access to health care. Next, I illustrate the power of this approach by analyzing a large data set of life-history variables on 234 mammalian species and find that brain size correlates $r=.70$ with longevity (.59, after controlling for body weight and body length). A principal component analysis reveals a single *r–K* life-history factor with loadings such as: brain weight (.85), longevity (.91), gestation time (.86), birth weight (.62), litter size ($-.54$), age at first mating (.73), duration of lactation (.67), body weight (.61), and body length (.63). The factor loadings remain high when body weight and length are covaried. Finally, I demonstrate the theoretical importance of this approach in restoring the concept of "progress" to its proper place in evolutionary biology showing why, over the last 575 million years of evolutionary competition of finding and filling new niches, there has always been (and likely always will be) "room at the top."
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1. Introduction

In both vertebrates and invertebrates, the increments in neural complexity and brain size over the last 575 million years of evolutionary history (Fig. 1) are related not only to increasing behavioral

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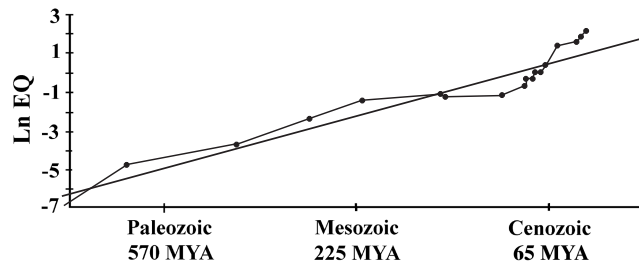*E-mail address:* rushton@uwo.ca.

Fig. 1. Average EQ (natural log), a measure of neural tissue corrected by body size, plotted against elapsed geologic time in millions of years (after Russell, 1983).

complexity (i.e., intelligence) but also to a matrix of life-history traits. For example, across 21 primate species, Smith (1989) found that brain size correlates .80 to .90 with life span, length of gestation, age of weaning, age of eruption of first molar, age at complete dentition, age at sexual maturity, interbirth interval, and body weight. As large brains evolved, they required more prolonged and complex life histories to sustain them. Large brains are also metabolically expensive, representing 2% of body mass but consuming 5% of basal metabolic rate in rats, cats, and dogs, 10% in rhesus monkeys and other primates, and 20% in humans.

   Are these merely disparate facts or do they reflect some unifying principle? The answer from evolutionary biology is that brain size and intelligence evolved as part of a "life history"—a genetically organized suite of traits that evolved together to allocate developmental resources to the goals of survival, growth, and reproduction. Traditionally, life-history theory compares the reproductive strategies of different species: *r*-selected species (e.g., fish) have many offspring and invest little or no parental care in any one whereas *K*-selected species (e.g., elephants) have fewer offspring and invest heavily with parental care and other resources in each. Most of the offspring of *r*-strategists die young, but because there are so many of them, enough reach maturity to assure their parents' genetic survival. Although *K*-strategists produce fewer offspring, they have a larger proportion surviving.

   The value of placing *g* within the *r–K* matrix is illustrated by its ability to explain puzzling questions, such as the one posed by Gottfredson and Deary (2004): "Intelligence predicts health and longevity, but why?" It also explains the paradox raised by Gottfredson (2004) of why, in spite of increased access to health care (especially in countries with socialized medicine, such as the UK), the gap in mortality rate between rich and poor is *increasing* rather than decreasing (see below). Moreover, placing *g* within the *r–K* matrix provides a theoretical, not just empirical basis for the Aristotelian restoration, returning the concept of "progress" to its rightful place in evolutionary biology.

2. The *r–K* matrix of life-history traits

   For over 20 years, I have been applying Harvard University biologist E. O. Wilson's *r–K* Life History Theory to human individual and group differences (Rushton, 1985, 2000; Wilson, 1975). The terms *r* and *K* come from the equation for population growth:

$$\mathrm{d}N/\mathrm{d}t = rN[(K - N/K)]/K$$

where N is the population size, K is the carrying capacity of the environment, and r is the rate of population growth. Individuals and populations able to produce high rates of growth (r-selected) reliably differ on a wide range of traits from K-selected individuals and populations. When population growth occurs, individuals capable of rapid reproduction increase in frequency. When the population size stabilizes, K-selected individuals come to predominate because under steady state conditions, they are more competitively successful at raising young and organizing the more complex societies that sustain them. The suite of r–K traits holds both within and between species.

The more K-selected an individual or population, the longer the gestation time, the slower the rate of maturation, the bigger the brain, the greater the intelligence, the better the health, and the longer the life. With humans, r–K theory explains social class and other group differences in speed of maturity, life span, number of offspring, the time between births, amount of parental care, infant mortality, even social organization, altruism, and sexuality, which all fit together like pieces of a puzzle (Rushton, 2000). All humans are K-selected relative to other species but some are more K than others. I dubbed the application of r–K theory to humans, "Differential K Theory" and speculated that both brain size and testosterone may be controller variables that establish the set point on the r–K continuum, which environmental variables can subsequently fine tune.

The first vertebrate species to evolve (fish and reptiles) were (relatively) r-strategists, whereas later species (mammals, especially primates) were K-strategists. For example, a cod produces thousands of eggs a year, but a female ape produces only one infant every 5 years. Those animal species that adopt the K-strategy, especially monkeys, apes, and humans, have large brains, are more intelligent, and live longer than r-strategists. K-strategists give their offspring a lot of care. They work together in getting food and shelter, help their kin, and have complex social systems. That is why the K-strategists also need a more complex nervous system and a bigger brain.

3. Brain size and longevity in mammals

One powerful way to demonstrate the validity of the r–K theory is to examine, across a reasonably large number of species, the variables hypothesized to covary. If the positions occupied by various species in multidimensional trait-space lie fairly close to a single line, the theory is supported. As a test, I examined the relation between brain size and longevity and other life-history variables over a wider range of species than done by Smith (1989).

I began by collating some of the cross-species data compiled by Eisenberg (1981) on longevity (n=170 species); gestation times (n=386); birth weight (n=305); litter size (n=386); duration of lactation (n=190); age at first mating (n=94); adult body weight (n=94); and adult body length (n=250). I added brain weight data for 94 of the species from a compilation by Sacher and Staffeldt (1974). I then used an Internet search engine on the animal names to increase the sample size using both field and zoo studies, choosing data from females where possible because material on reproductive variables was available there (n=182 to n=439). Sometimes, the data came from a single zoo specimen, and at other times, from a survey of a wild population. Because of the unsystematic nature of the compilation, the relationships to be reported occur *despite* measurement error.

The species selected vary physically and behaviorally. The small-sized animals included the Madagascar hedgehog (body length=185 mm; body mass=225 g; brain mass=2 g; and longevity=11 years) and the Senegal bush baby (body length=161.5 mm; body mass=229 g; brain mass=8 g; and

longevity=18 years). The large-sized animals included the giraffe (body length=4000 mm; body mass=1,017,000 g; brain mass=531 g; and longevity=36 years) and the African elephant (body length=5000 mm; body mass=2,766,000 g; brain mass=4480 g; and longevity=80 years). Intermediate in size were primates, such as the gorilla (body length=1335 mm; body mass=92,500 g; brain mass=406 g; and longevity=50 years) and the human (body mass=60,000 g; brain mass=1300 g; and longevity=75 years).

Brain weight correlated with longevity (.70), gestation time (.67), birth weight (.46), litter size (−.22), age at first mating (.50), duration of lactation (.54), body weight (.61), and body length (0.63). Remarkably, even after the effects of body weight and body length were controlled, brain weight still correlated with longevity (.59), gestation time (.66), birth weight (.16), litter size (−.18), age at first mating (.63), and duration of lactation (.61).

Further confirmation for the use of r–K theory comes from a principal component analysis. It showed that all the variables loaded on a single factor: brain weight (.85), longevity (.91), gestation time (.86), birth weight (.62), litter size (−.54), age at first mating (.73), duration of lactation (.67), body weight (.61), and body length (0.63). Nor did the loadings change much when the effects of body weight and body length were controlled: brain weight (.86), longevity (.89), gestation time (.17), birth weight (−.54), litter size (.78), age at first mating (.79), and duration of lactation (.80). Neither did the results vary if a principal axis factoring analysis was performed instead of a principal component factor analysis.

Can we extrapolate these findings on the relation of brain size, longevity, and other life-history variables *between* species to the much, much smaller variation *within* the human species? I think we can. As mentioned, the r–K continuum has been found to apply to differences within species as well as to those between species. This is really a mirror image of the "default hypothesis" that the factors that apply within groups also apply between groups (Jensen, 1998, p. 457). If intelligence test scores are used as a proxy for brain size, then the studies reported by Gottfredson (2004) and Gottfredson and Deary (2004) predicting longevity in 2309 Australians and 2230 Scots fall directly into place. Other studies have shown more directly that a larger brain protects against dementia. The Nun Study is a longitudinal study of 678 Catholic sisters whose IQ scores were estimated from samples of their writing at age 25 and who have entered the study from age 75 to 102 years, who are evaluated yearly, and who have agreed to brain donation at the time of death. Those with better writing ability, or who completed 16 or more years of formal education, or whose head circumference was in the upper two thirds, were four times less likely to be demented than those both with smaller head circumferences and lower education (Mortimer, Snowdon, & Markesbery, 2003). Having a larger brain did not decrease the chances of Alzheimer's brain disorder, but did allow the brain to function at a higher level despite the presence of abnormality.

Like most human traits, brain size and intelligence are moderately to highly heritable (50–90%; Thompson et al., 2001). So are health and longevity (Scriver, 1984). Consequently, as environmental conditions become equalized, the remaining variance must become increasingly genetic. Just as increasing equality of educational opportunity can lead to a 30% increase in the heritability of educational attainment within a single generation and concomitant decrease in family environmental factors (e.g., in Norway, pre- and post-1940; Heath et al., 1985), removing environmental barriers to health increases the variance accounted for by genetic factors.

The increasing heritability of longevity by the removal of deleterious environmental conditions explains some otherwise paradoxical findings about social class and health. One comprehensive review of class and health surveyed mortality rates in Britain from 1921 to 1971 (Black, 1980; Townsend &

Davidson, 1982). Everyone was living longer, but the professional classes gained more years than semiskilled and unskilled workers. In 1930, people in the lowest social class had a 23% higher chance of dying at every age than people in the highest social class. By 1970, this excess risk had grown to 61%. A decade later, it had jumped to 150%. In Britain, a National Health Service has long existed to minimize inequalities in access to medical care. The *increasing* correlation of health and social class makes sense when one realizes that removing environmental impediments makes individual-difference variables more dependent on innate characteristics.

The underlying explanation is that longevity is a coevolved adaptation with brain size and intelligence, and it is intelligence that underlies social stratification. As harmful environmental factors are removed and so no longer account for as much variance, that which remains must be increasingly due to genes. Because larger brains are more costly to build and maintain than smaller brains, they need to be housed in stronger, longer lived bodies (see also Miller, 2000). Darwinian evolution is frugal, not prodigal.

4. Is evolution progressive?

The originator of *r–K* theory, E.O. Wilson (1975, p. 101) wrote, "In general, higher forms of social evolution should be favored by *K* selection." Johanson and Edey (1981, p. 326) summarized their analysis of 5 million years of hominoid evolution in the catch phrase: "More brains, fewer eggs, more '*K*.'" Long before *r–K* theory, however, Aristotle (384-322 BCE) suggested the organizing principle that all organisms can be hierarchically ordered in a series of continuous minute steps from the inanimate, through plants, to the animals, and on up to human beings. Aristotle's observations on the trade-off between seed output and parental care and intelligence are astonishingly modern (Dunbar, 1993). In his *History of Animals*, he wrote:

> Now some simply like plants accomplish their own reproduction according to the seasons; others take trouble as well to complete the nourishing of their young, but once accomplished they separate from them and have no further association; but those that have more understanding and possess some memory continue the association, and have a more social relationship with their offspring.

Many historians and philosophers have considered Aristotle's Great Chain of Being to be one of the most important ideas in Western thought, especially when it is generalized to social organizations (Lovejoy, 1936; Ruse, 1996). With the advent of Christianity, Aristotle's organizing principle was theologized to place humans "a little lower than the angels," with God at the top. Charles Darwin (1859, 1871) returned the Great Chain of Being to its naturalistic foundation with his evolutionary theory of a movement from simpler to more complex forms. He frequently referred to evolutionary progress to refute concepts of a static world, as well as to counter a new school that denied any difference in adaptation between the simplest and the most complex organisms, because it would be an implicit denial of improvement through natural selection. The cliché that Darwin had once cautioned never to use the terms "lower" and "higher," was in reality only an aside in an early notebook, and one he routinely ignored.

Over evolutionary time, encephalization quotients (EQs), a measure of actual brain size to expected brain size for an animal of that body weight have increased among both invertebrates and vertebrates

[Fig. 1; following Jerison, 1973; EQ=cranial capacity $(cm^3)/(0.12)$(body weight in grams)$^{0.67}$]. Russell (1983) calculated that the mean EQ was only about 0.30 for mammals living 65 million years ago compared to the average of 1.00 today. EQs for living molluscs varied between 0.043 and 0.31, and for living insects, between 0.008 and 0.045, with the less encephalized living species resembling forms that appeared early in the geologic record and the more encephalized species resembling those that appeared later. Russell (1989) also demonstrated how, over 140 million years, dinosaurs showed increasing encephalization before going extinct 65 millions years ago (probably because of an asteroid impact or other catastrophic event). Russell extrapolated the data to suggest that if dinosaurs had continued on, they would have progressed to a large-brained, bipedal descendant.

Following World War II, the concept of biological progress fell into disrepute. Political correctness, based on an ideology of social equality, considered it anathema to describe any product of evolution as more "advanced" than any other. Stephen Jay Gould was especially zealous in arguing that the idea of evolutionary progress had directly contributed to the rise of Nazism. "Progress," he declared, "is a noxious, culturally embedded, untestable, nonoperational, intractable idea that must be replaced if we wish to understand the patterns of history" (Gould, 1988, p. 319).

Some evolutionary biologists, however, rejected the Gould type of wholesale rejection of progress. Richard Dawkins termed it "ludicrous," while E.O Wilson characterized it as, "part of the dull postmodernist cast that has seized some of our popular science writers" (see Miele, 2002, pp. 37 and 81, respectively). Wilson (1975) gave the progress idea renewed respectability when he outlined four pinnacles in the history of life on Earth. First, the beginning of life itself in the form of primitive prokaryotes (single cellular organisms with no nucleus); second, the origin of eukaryotes (cells with nucleus and mitochondria); third, large, multicellular organisms, which could evolve complex, specialized organs, such as eyes and brains; and fourth, the beginning of the human mind. He also described many vertical grades of independently evolving lines "which ascend from less advanced to more advanced states." Aristotle's organizing principle proved too powerful to be banished from biology.

Bonner (1980, 1988) has shown that the later an animal species had emerged in geological time, the larger was its brain, *and the more complex was its culture*. He followed paleontologists who used the word "lower" to refer to fossils when they simultaneously (a) are found in lower strata, (b) belong to a fauna or flora of earlier times, and (c) are typically more primitive in structure as well as because they are found in lower strata. Bonner noted that while it is almost always acceptable to refer to "lower" and "higher" *plants* in this way (e.g., slime molds versus angiosperms), it is often, but misleadingly, deemed a sin to classify a worm as a "lower" animal and a vertebrate as a "higher" one, although their fossils too are found in lower and higher strata.

The main empirical reasons given for denigrating the idea of progress in the evolution of brain size and intelligence, and examining their links to other life-history traits, such as longevity, is that few biological characters emerge in a simple linear order. Some comparative psychologists (e.g., Hodos & Campbell, 1969) have argued that studying animal intelligence using a general intelligence model or using general brain indices presented a danger of obscuring phylogenetic differences among species with similar learning abilities. However, the existence of multifactorial abilities in animals should not preclude us from also looking at total capacity. Restricting attention to the functioning of the parts without concern for the whole, as is currently fashionable among evolutionary psychologists with their modular ("Swiss Army knife") model of the mind (Cosmides & Tooby, 2002) is as unproductive as a concern for the whole without considering the parts. In the competition to find and fill new niches, there has always been (and likely always will be) "room at the top."

5. Conclusion

Most researchers have focused on one or two adaptations taken at the same time in specific organisms rather than on a suite of correlated characteristics coevolving over 4 billion years in many organisms, or even the full 5 million years of human evolution. However, because the life-history variables associated with brain size—such as longevity and social organization—correlate both across species and within humans, they call for a general theory to explain them (Rushton, 1985, 2000). Because, in the upward spiral of life, regulator genes have been identified in brain development, particularly in the ape lineage leading from mammals to humans (Evans, Anderson, Vallender, Choi, & Lahn, 2004), these might be relevant for understanding not just g, but the whole suite of traits that make up the r–K dimension. The once traditional view that man is the most "advanced" of species gains novel support from the perspective of an r–K dimension. If man can no longer boast of being "created in the image and likeness of God," he may, at least, take pride in having evolved to be the most K species on earth.

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