



Acta Genet Med Gemellol 36:289-296(1987)
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Toward a Theory of Human Multiple Birthing: Sociobiology and r/K Reproductive Strategies

J. Philippe Rushton

Department of Psychology, University of Western Ontario, London, Ontario, Canada

Abstract. Using symbols from population biology, a continuum of reproductive strategies can be distinguished ranging from *r*, the production of large numbers of offspring provided with minimal care, to *K*, the production of few offspring nurtured intensively. While all humans are at the *K* end of the continuum, some are proposed to be more so than others. If multiple egg production is part of an *r*-reproductive strategy, certain facts may be ordered. Compared to mothers of singletons, for example, mothers of DZ twins have a lower age of menarche, a shorter menstrual cycle, a higher number of marriages, a higher rate of coitus, more illegitimate children, a closer spacing of births, a greater fecundity, more wasted pregnancies, a larger family, an earlier menopause, and an earlier mortality. Further, all twins have a shorter gestation period, a lower birth weight, and a greater incidence of infant mortality, with DZ twins having a greater frequency of health disorders, a higher mortality rate, and a lower rate of enrollment in volunteer registries. Multiple birthing also occurs more frequently in families of lower than of higher social status, and in those of African than of European and especially than of Oriental descent.

Key words: Altruism, Behavior genetics, Evolution, Fecundability, Life-history analysis, Sexual behavior, Twins

INTRODUCTION

The question of why different species have different numbers of offspring can be explained at both proximate and ultimate levels. Proximate levels emphasize the environmental and physiological mechanisms involved; ultimate explanations consider the evolutionary significance of phenomena in terms of reproductive fitness. Species have evolved numerous

strategies of genetic replication ranging from asexual reproduction (not entailing the fusion of gametes), through semelparity (reproducing once in a lifetime), to iteroparity (reproducing repeatedly over the life-cycle). Each of these strategies can be examined from both proximate and ultimate perspectives.

In his Presidential address to the Fourth International Congress, MacGillivray [21] touched on both proximate and ultimate types of explanation in his discussion of two historical hypotheses regarding human multiple birthing: “superfecundity” and “evolutionary atavism”. In this paper both these ideas will be organized within a sociobiological framework. Specifically, I suggest that human multiple egg production is an *r*, rather than a *K*, reproductive strategy and as such, is expected to underlie a variegated complex of characteristics concerning life histories, social behavior, and physiological functioning [35,42].

THE *r*/*K* CONTINUUM

The symbols *r* and *K* originate in the mathematics of population biology and refer to two ends of a continuum of reproductive strategies organisms can adopt, ranging from extreme *r*, involving maximum egg output and no parental care, to extreme *K*, emphasizing elaborate parental care in which the birthrate is reduced to a minimum [42]. As can be seen in Fig. 1, oysters, producing 500 million eggs a year exemplify the *r*-strategy, while the great apes, producing only one infant every 5 or 6 years, exemplify the *K*-strategy.

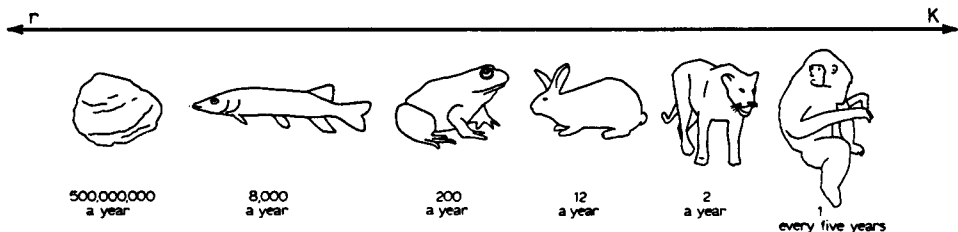


Fig. 1. The *r*/*K* continuum of reproductive strategies balancing egg output with parental care. (After Johanson & Edey [16]).

Evidence from both comparative studies and selective breeding experiments on species ranging from dandelions to fish, to mice, to men, indicate that reproductive strategies are correlated with other features of the organism's life history. Following Pianka [31], Wilson [42], and Barash [3], these are summarized in the Table. While each of the life cycle traits might independently contribute to fitness, the important point is that they are expected to covary along a single axis both between and within species. Despite some anomalies, many evolutionary biologists, having considered the literature, find the *r*/*K* continuum useful in organizing information on life histories [3,9,10,42].

From the Table, it can be seen that, in terms of family characteristics, *r* and *K* strategists differ in terms of litter size, birth spacing, total number of offspring, rate of infant mortality, and degree of parental care. In regard to individual characteristics, *r* and *K* strategists differ in rate of physical maturation, sexual precocity, life-span, body size,

Table. Some life history, social behavior, and physiological differences between r- and K-strategists (following Pianka, 1970)

r-Strategist	K-Strategist
<i>Family characteristics</i>	
Large litter size	Small litter size
Short spacing between births	Long spacing between births
Many offspring	Few offspring
High rate of infant mortality	Low rate of infant mortality
Low degree of parental care	High degree of parental care
<i>Individual characteristics</i>	
Rapid rate of maturation	Slow rate of maturation
Early sexual reproduction	Delayed sexual reproduction
Short life	Long life
High reproductive effort	Low reproductive effort
Productive energy utilization	Efficient energy utilization
Low intelligence	High intelligence
<i>Population characteristics</i>	
Opportunistic exploiters of environment	Consistent exploiters of environment
Dispersing colonizers	Stable occupiers of habitat
Variable population size	Stable population size
Competition variable, often lax	Competition keen
<i>Social system characteristics</i>	
Low degree of social organization	High degree of social organization
Low amounts of altruism	High amounts of altruism

reproductive effort, energy use, and intelligence. Finally, in terms of population and social system characteristics, they differ in their treatment of the environment, tendency to geographically disperse, population size stability, competitiveness, degree of social organization, and altruism.

Individuals and species are, of course, only relatively r and K. Thus rabbits are K-strategists compared to fish but r-strategists compared to humans. Primates are all relatively K-strategists, and humans are the most K of all. Indeed, as depicted in Fig. 2, the order primates displays a natural scale going from lemur to macaque to gibbon to chimp to humans, in which there is a consistent trend toward K with progressive prolongation of gestation period and life phases [19]. Note the proportionality of the four indicated phases. The postreproductive phase is restricted to humans. With each step in the natural scale, populations devote a greater proportion of their reproductive energy to subadult care, with increased investment in the survival of offspring.

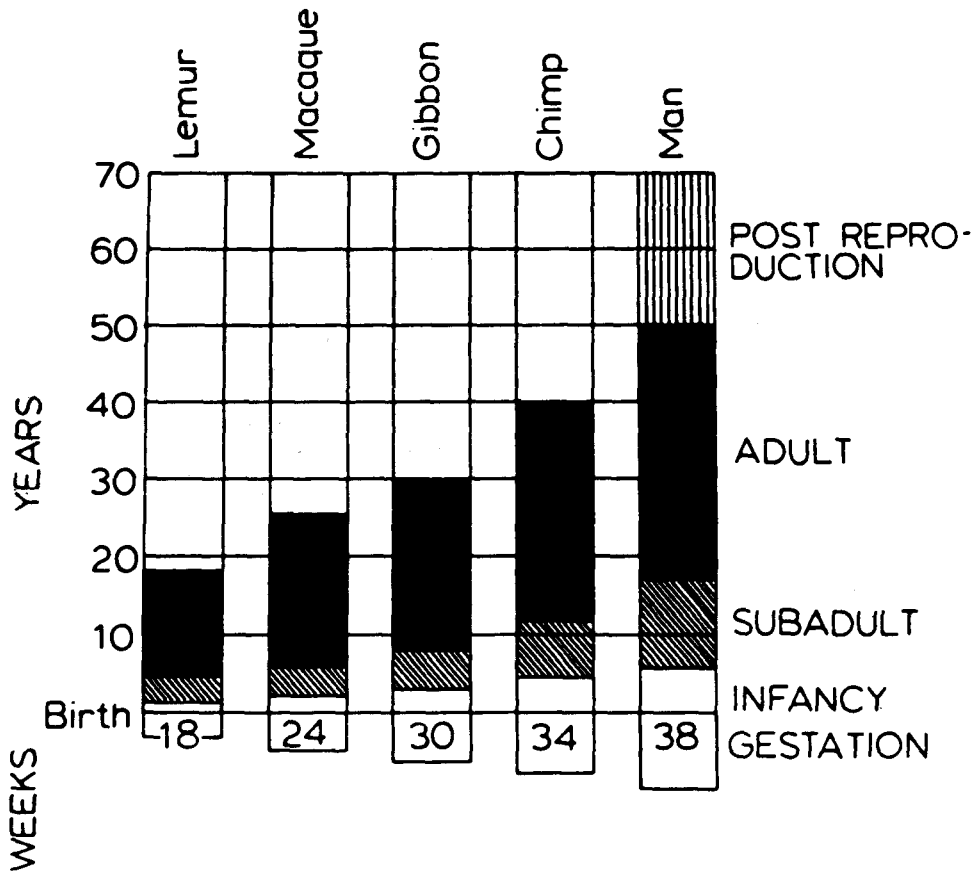


Fig. 2. Progressive prolongation of life phases and gestation in primates. Source: C.O. Lovejoy, 1981: *The origin of man*. Science, 211:341-350. Copyright 1981 by the American Association for the Advancement of Science. Reprinted by permission.

INDIVIDUAL DIFFERENCES IN K AMONG HUMANS

As a species, humans are at the K end of the continuum. What I am proposing, however, is that some people are genetically more K than others, and that K-behavior is associated with a constellation of personality attributes, all deeply embedded in evolutionary history [35]. Several falsifiable predictions derive from this analysis. The more K the family, the greater should be the spacing between births, the fewer should be the total number of offspring, the lower should be the rate of infant mortality, and the better developed should be the parental care. The more K the person, the longer should be the period of gestation, the higher the birthweight, the more delayed the onset of sexual activity, the older the age at first reproduction, the longer the life, the lower the sex drive, the higher the intelligence, the more efficient the use of energy, the lower the

dispersal tendency, the more social rule following the behavior, and the greater the altruism. Significant correlations are predicted to occur among all these indices of K.

Consideration of the available evidence offers a degree of support for the K perspective [35]. Many indices of K, for example, have been shown to be heritable, including family size and structure [7], the rate of growth from 3 months to 15 years in height and intelligence [43], the age of onset of puberty and menopause [4], the strength of the sex drive and its relation to age of first intercourse, intercourse frequency, and total number of partners [23], body mass [40], susceptibility to infectious diseases [12], the onset of degenerative diseases associated with ageing [28], longevity [8,14], and a wide range of relevant personality traits, including intelligence [4], social rule following [25], and altruism [38].

THE NATURE OF MULTIPLE BIRTHING

The more K the species, the smaller, on average, will be its litter size. Primates, including *Homo sapiens*, tend to have single offspring. However, all types of primates occasionally have multiple births. Multiple births are here considered to be indices of "litter size" and to represent an r-reproductive strategy. This directly follows in cases where multiple births result from the production of more than one egg at a time as occurs with DZ but not MZ twins. That DZ twins, more than MZs, are the result of an r-reproductive strategy, is suggested by evidence that their production is a) known to be genetically influenced and otherwise related to having large families [7, but see 30], b) increased by fertility drugs [41,45], and c) related to their mothers having higher levels of naturally occurring serum gonadotropin and estradiol [22]. Moreover, the tendency to produce DZ twins is related to several other r dimensions. Compared to mothers of singletons, mothers of DZ twins typically have a lower age of menarche, a shorter menstrual cycle, and a higher number of marriages [46], a higher rate of coitus [15], more illegitimate children [11,27], a closer spacing of births [1], a greater fecundity [2,6,29,32], more pregnancy wastage [46], a larger family [7], an earlier menopause [44], an earlier mortality measured by cancer of the pancreas (but not for other sites), by diabetes, other endocrine diseases, and allergies [47]. They do not, however, appear to have an earlier age at first live birth [46].

Twins themselves, of course, have shorter gestation periods, lower birth weights, and a greater incidence of infant mortality when compared with singletons [7]. In these respects, however, and possibly counter to predictions from K theory, MZ twins fare even worse than DZ twins, although this may be due to MZ twins more often being mono-chorial. Subsequently, DZ twins, compared with MZ twins, have a greater susceptibility to major health disorders such as schizophrenia, diabetes, hypertension, heart diseases, ulcers, and neuroses [18], and generally to have an earlier mortality [14].

Given that the production of DZ twins represents an r-strategy relative to the production of MZ twins or singletons, it would be informative to contrast the personalities and life histories of such twins. Usually, however, this is not feasible because of the under-representation of DZ twins in most studies and the possibly K nature of most DZ volunteers. Volunteering for research has often been considered a measure of altruism [33], a trait clearly related to K (see Table), and on which individual differences are partly heritable [38]. It is known that although MZ and DZ same sex twins co-occur in nearly equal

frequencies in Caucasian populations, DZ pairs volunteer about one-third less often for research than do MZ pairs [20]. Explanations for this range from difference in narcissistic motivation on the part of the twins [20], to the method of construction of twin registers by researchers [17,24]. K theory suggests an additional explanation: DZ twins, on average, are less altruistic, as well as more likely to be geographically dispersed (see Table) than MZs or singletons, and, therefore, less inclined to volunteer to help research. Moreover, this lack of altruism and tendency to disperse is postulated to be part of a syndrome of personality and life-cycle traits. Following the recommendations of Lykken et al [20] and others, therefore, it may be advisable to offer financial incentives to increase the representation of DZ twins. It would then be instructive to compare mean differences between MZs and DZs on life-history phenomena to test other predictions from K theory. Since males appear to be less altruistic, on average, than females [33,38], this disposition may also underlie the underrepresentation of males in volunteer twin studies.

GROUP DIFFERENCES IN MULTIPLE BIRTHING

Population differences exist in frequency of multiple birthing such that higher socioeconomic < lower socioeconomic, and Mongoloids < Caucasoids < Negroids. With respect to social class, studies have found the frequency to be greater among lower social class women in both European and African samples [13,27]. With respect to race, although MZ twinning is nearly constant at about three and a half per thousand in all groups, DZ twinning varies: the approximate rate per 1,000 births among Mongoloids is 3; among Caucasoids, 8; and among Negroids, < 16; with some African populations having twinning rates as high as 57 per 1,000 [7,26]. The incidence of non-MZ triplets and quadruplets shows comparable rank orders. For triplets, the rate per million among Mongoloids is 10; among Caucasoids, 100; and among Negroids 1700; and for quadruplets, per million, among Mongoloids, 0.000; among Caucasoids 1.0; and among Negroids, 60 [7,26]. Moreover, data from racially mixed matings suggests that the DZ twinning rate is largely determined by the race of the mother independently of the race of the father, as shown for Mongoloid-Caucasoid crossings in Hawaii, and Caucasoid-Negroid crosses in Brazil [7].

If the analysis of multiple birthing presented here is correct, then the differences observed between populations in other K related characteristics such as activity level, intelligence, longevity, rate of maturation sexual behavior, and social rule following [34-37], may take on deeper evolutionary significance. On many of these measures the rank order of whites is between that of blacks and Orientals, as it is in rate of multiple birthing, and gonadotropin levels [27,39]. The need for further research on these inter- and intra- population patterns is clearly warranted. A perspective from evolutionary biology may prove fruitful.

Acknowledgment. Supported in part by a grant from The Pioneer Fund, Inc.

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Correspondence: Dr. J.P. Rushton, Department of Psychology, The University of Western Ontario, London, Ontario N6A 5C2, Canada.