

From Quantity to Quality of Life: *r-K* selection and human development

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ABSTRACT: Evolutionary fitness is defined as the number of an organism's offspring likely to survive, apparently privileging quantity, rather than quality, of life. However, models of population growth distinguish between "*r*-selection", that occurs in unpredictable and risky environments, and "*K*-selection", characterizing stable environments. If offspring has a high probability to be killed by predators, disease, or other uncontrollable factors, the safest bet is to produce as many of them as quickly as possible (*r*). If offspring has plenty of chances to mature, but needs all its strength and intelligence to efficiently exploit scarce resources, it is wiser to aim for quality (*K*). The choice between the two strategies depends on early experience: people raised in a stressful environment exhibit typical *r*-traits, such as many and early sexual contacts, large families, risk-taking, and short life expectancy; in a safe environment, they will typically have lower fertility and higher life expectancy and invest in long-term benefits such as education. Socio-economic development with its accompanying demographic transition and drive to maximize QOL can be viewed as a shift from an *r* to a *K* strategy by humanity.

An evolutionary view of QOL

Quality of life (QOL) is becoming a very popular concept, being used in an ever growing number of contexts. Yet, while most people have an intuitive sense of what it means, it is difficult to find a good definition. Researchers have focused mostly on empirical methods for measuring QOL, using both subjective measures, such as life satisfaction, happiness or subjective well-being (SWB) scales, and objective ones, such as the Human Development Index [UNDP, 1999] or the Physical Quality of Life Index. While it has been shown that in practice the different methods mostly agree in distinguishing high QOL from low QOL [see e.g. Heylighen & Bernheim, 2000], they still lack a unified theoretical foundation.

The present paper proposes to seek such a foundation in the science of life itself. Biology is founded on the theory of evolution by natural selection. Living organisms exist because they have been selected for their capacity to survive and reproduce. This observation is summarized by the principle of "the survival of the fittest". In present-day

evolutionary theory, fitness is no longer defined as intrinsic robustness or adaptation to the environment, but as the average success rate of long term reproduction. More precisely, the fitness F of a type of organism can be defined as the expected number of individuals in the next generation divided by the present number. Therefore, $F > 1$ means that this type of organism is expected to become more common, $F=1$ that the population will remain constant, and $F < 1$ that it will decrease, and eventually become extinct. The logic of natural selection is simply that the variants with a lower fitness will lose the competition with the others, and eventually disappear. Thus, evolution constantly tries to maximize fitness. We might summarize this insight by noting that, according to Darwinian theory, *fitness is the true meaning of life*, i.e. the fundamental goal that all living organisms implicitly try to achieve, the property that characterizes them as living, and the original reason for which they have come into being.

At first sight, this statement appears like an instance of stark biological reductionism, replacing enlightened, humanistic values by a machiavellian struggle for life. Present-day commentators are much more likely to find the meaning of life in the striving for happiness or QOL for humanity as a whole. Yet, we wish to argue that these views can be reconciled, and that in our present, human context, fitness and QOL/SWB are actually two aspects of the same phenomenon.

This is most obvious for the subjective measures of QOL, since happiness can be defined as the sum of our accumulated feelings of pleasure and displeasure. Biologically, these feelings represent the degree to which our genetically inherited needs are satisfied [Heylighen & Bernheim, 2000]. Thus, pleasurable things, such as sex, food, and companionship, typically correspond to opportunities that are likely to enhance our fitness, whereas unpleasant experiences, such as hunger, thirst, and physical pain, represent dangerous situations that we better avoid if we want to maintain our fitness. Of course, the correspondence is imperfect, as evolution has not yet had the time to catch up with new circumstances. Thus, we may find pleasure in artificially sweetened soft drinks, heroin and tobacco that actually reduce our fitness. But such less-than-perfect result is only to be expected from the slow and haphazard process of trial-and-error that is biological evolution.

The more fundamental issue is how to reconcile the biological view of fitness with what we know about objective measures of QOL. Fitness is defined by the *quantity* of offspring to survive into the next generation, while QOL by definition focuses on *quality*. In our present society, survival of offspring is virtually guaranteed. Aiming for high numbers of offspring would only produce an unsustainable increase in population and the resources they consume. On a finite, resource-limited planet, such exponential growth must eventually lead to a collapse, characterized by the starvation, pollution and war that we have already witnessed in a number of quickly growing Third World populations, such as Rwanda. The quantity maximization that defines fitness therefore seems antithetical to quality of life as we understand it. To resolve this paradox, we need to take a better look at the mechanisms of population growth and natural selection.

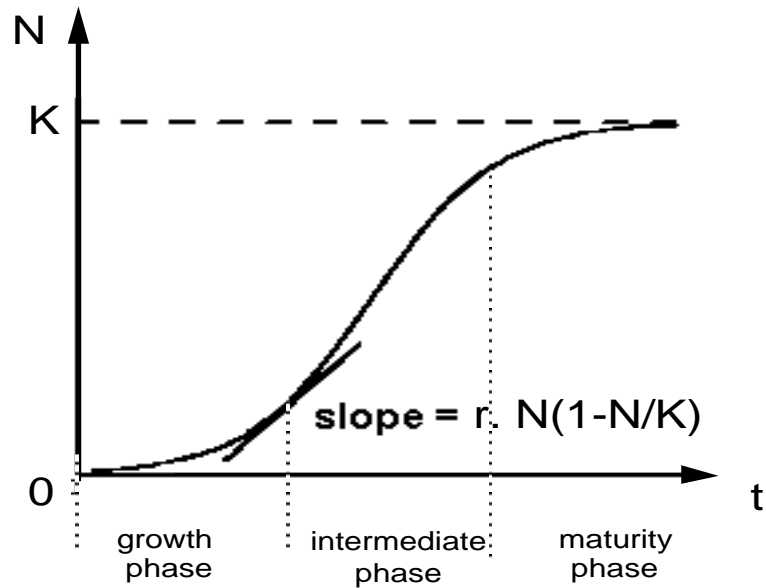


Fig. 1: the sigmoid curve depicting the growth of the population (N), as a function of time (t)

r - K models of population growth

In population dynamics, the increase in the number $N(t)$ of individuals at time t is traditionally represented by the following Verhulst equation:

$$\frac{dN}{dt} = r \cdot N \left(1 - \frac{N}{K}\right)$$

The equation expresses that fact that the growth in population (dN) is in first instance proportional to the population (N) that is already there—since more individuals have more offspring—, but eventually limited by the carrying capacity K of the environment, so that growth becomes zero when the population reaches this limit ($N = K$). The function $N(t)$ that is the solution to this differential equation is called the logistic function. It has a characteristic *sigmoid* (S-like) shape, as depicted in Fig. 1.

When we look at this curve we see initially (small t) an accelerating, exponential growth, as can be expected from a process where the increase is proportional to what is already there. The speed of this growth is represented by the parameter r : the larger r , the larger the increase as a proportion of the population, i.e. the larger the number of offspring produced per parent. However, this growth slows down and eventually reaches a ceiling, as the available resources are exhausted and the population approaches its maximum denoted by the parameter K .

We can distinguish three subsequent phases in the process: 1) a nearly exponential “growth” phase, dominated by the factor r ; 2) an intermediate phase where the speed of

growth switches from increasing to decreasing; 3) finally a “maturity” phase, where the growth slows down to zero, which is dominated by the fixed ceiling K (see Fig. 1). If we focus on the two extreme phases, we find two contrasting types of population dynamics, that in evolution correspond to what is called respectively *r-selection* and *K-selection* [Pianka, 1970; Wilson, 1975].

Let us start by discussing the mature, K -phase. In a stable environment with a fixed supply of resources, the population will stabilize around the K -value. In such environment, it does not make sense to produce a lot of offspring, since food is too scarce to keep them all alive. For the little food available, there will be a lot of competition, and therefore it pays to prepare the offspring well, making them as efficient, adapted and robust as possible. In other words, it is better to invest in quality than in quantity. Since the environment is predictable, it is worth aiming for the long term, allowing the offspring to grow, develop and learn for as long as possible, so as to gather maximum strength and competence. Thus, organisms will tend to have few, long-living offspring. Moreover, offspring are selected to be large, well-protected, energy efficient, and intelligent, so that they are likely to live long. Since they have much to lose and little to gain by getting into dangerous situations, they will tend to avoid risks.

However, such mature development pattern towards equilibrium is not possible when the environment is intrinsically dangerous and unstable. This may happen for example because there are large fluctuations in the availability of food, climate changes, parasite outbreaks, or predators. In such circumstances, the life of an individual is basically unpredictable, and parents have no control over which of their offspring will or will not survive. When life is a lottery, the only way to increase your chances of success is to increase the number of tickets you get. Thus, organisms are selected to produce as many offspring as quickly as possible (i.e. maximize r), in the hope that at least one of them would survive. Since most individuals are killed at an early stage, the population rarely reaches the carrying capacity of the environment, and therefore there often is a surplus of resources. Thus, it pays to be able to increase in numbers quickly to fully profit from this surplus. When the surplus is exhausted, the population will crash, but this would have happened anyway because of uncontrollable factors. Moreover, because the potential bounty is large, while there is little to lose in an intrinsically dangerous environment, it pays to take risks to get to these resources.

Such r -selection typifies species that have a lot of short-living offspring, such as bacteria, flies, mice, weeds, and rabbits. K -selection is typical for organisms whose offspring are few but long living, such as oak trees, elephants, parrots, and humans. We must add two qualifications to this simple distinction.

First, the choice between an r - and a K -strategy is a trade-off between *quantity* (speed of reproduction, number of offspring) and *quality* (competence for survival): the energy or effort invested in the one cannot be used for the other, and so species have to precisely allocate the amount they invest in each in order to maximize fitness. Since survival is necessary for reproduction, but no living system can survive indefinitely and therefore must eventually be replaced by its offspring, the ideal strategy is always a mixture of both. Therefore, the choice for a particular strategy is always *relative*: rabbits follow more of an

r-strategy relative to humans, but more of a *K*-strategy relative to fruit flies. Even within a species there is a margin of variation within the *r-K* continuum. For example, researchers discovered two varieties of the same opossum species, one living on the continent where they are threatened by predators, one on an island where their life is more safe. It turned out that even in captivity the island variety lived longer and had fewer offspring—i.e. followed more of a *K*-strategy—than its mainland cousin.

Second, *r-K* selection is merely the most elementary model within the more encompassing *life history theory* [Stearns, 1992], which examines how natural selection affects the different stages of an organism's life. For example, the dangers and opportunities are very different for a caterpillar and for a butterfly, although both are stages of the same organism. For some types of organisms, such as carps or trees, the juvenile stage is much more vulnerable and therefore *r*-like in its characteristics than the adult; for others, such as larvae of may-fly, it is the other way around. In such cases, the *r-K* continuum is too simple to capture the complexity of evolutionary strategies. However, the focus of our present research is on humans, where there are no clearly separate life stages, and therefore the *r-K* model seems most parsimonious to capture their behavior.

Table 1 summarizes the typical differences between organisms that follow either type of strategies [cf. Pianka, 1970; Wilson, 1975].

<i>r</i>-organisms	<i>K</i>-organisms
short-lived	long-lived
small	large
weak, vulnerable	robust, well-protected
fast maturation	slow maturation
prone to take risks	risk averse
opportunistic exploiters	consistent exploiters
less intelligent, experienced...	more intelligent, experienced...
strong sex drive	weak sex drive
reproduce at an early age	reproduce at a late age
large number of offspring	small number of offspring
small relative size at birth	large relative size at birth
little care for offspring	much care for offspring
variable population size	stable population size

Table 1: typical differences between organisms that follow *r*-strategies (e.g. rabbits, sparrows), respectively *K*-strategies (e.g. elephants, parrots)

***r-K* strategy and early experience**

The choice between an *r* and a *K* strategy does not need to be wholly fixed in the genes (*nature*). It can also be (epigenetically) shaped by early experience (*nurture*). Indeed, since the environment changes in carrying capacity and degree of risk or unpredictability over the generations, it is useful for an organism to be able to adapt its strategy to the current situation. This may apply in particular to humans, who excel in adaptability.

As proposed by Chisholm [1993, 1999], such epigenetic biological effects may be mediated by hormones, whose levels are dependent on experience. *r*-strategies are most appropriate in a dangerous, uncontrollable environment, where there is little guarantee of surviving into adulthood. Such an environment creates stress, which leads to the release of glucocorticoid hormones, such as cortisol [Sapolsky, 1996]. Therefore, we could expect that children who are subjected to chronically high levels of such stress hormones will be driven to develop into *r*-strategists, aiming for quick reproduction rather than long-term

maturation. Biologically, this can be achieved by increasing their levels of sex hormones: testosterone in men, estrogen in women. This leads to early sexual maturity, a strong sex drive, a tendency towards aggressivity and risk-taking in men, and high fertility in women. On the negative side, high levels of sex hormones are associated with a higher probability of heart diseases and cancer, and thus a shorter life expectancy.

While there is some evidence that such characteristics are indeed mediated by hormones, the focus of the present paper is not on the precise physiological mechanisms but on the functional hypothesis that stressful environments during childhood tend to lead to *r*-type behaviors throughout life. According to the well-known theory of Bowlby [1969], a primary cause of childhood stress is *insecure attachment* to the mother. This occurs when the child cannot rely on the mother for support when it needs it and/or is not allowed by the mother to explore the world on its own and thus develop autonomy. While such motherly neglect or overconcern is stressful in itself, it moreover is likely to indicate a dangerous external environment, which is either too demanding on the mother to have energy left to care for her child, or so risky that she cannot allow her child autonomy. Lack of attention to the child may also mean that the mother has too many other children to care for, which is itself a sign of an *r*-type situation. Thus, insecure attachment, through its stimulation of stress hormones [Gunnar, 1998], is a very strong indication for the child that it is growing up in an environment where an *r*-strategy is evolutionarily most appropriate [Belsky et al., 1991]. Less immediate causes of childhood stress may include sexual, physical or emotional abuse, malnutrition, diseases, living in true poverty, in a ghetto or war-zone. All of these can be seen as signals for the hormonal system to prepare the body and brain to invest their energy in short-term reproduction, neglecting long-term goals.

In contrast, a safe, caring, nurturing environment signals that it is worth investing in long-term development, building up the reserves of energy and experience that may lead to a long and healthy life, and that can be invested in turn in a few, well-cared for children. A possible mediator here is growth hormone, whose presence not only stimulates the development of muscles, bones and nerves, but protects against premature ageing. Conversely, it has been shown that high levels of stress hormones stunt the development of various tissues, and in particular the hippocampus region in the brain [Sapolsky, 1996], which is responsible for the consolidation of memories and thus the build-up of experience.

In summary, the location of the childhood environment on the *r*-*K* dimension appears to be translated into the level of stress hormones, which itself may affect the trade-off between sex hormones and growth hormones, and thus the pattern of development into adulthood. When we compare populations raised in stressful environments such as ghettos, war-torn or underdeveloped regions (e.g. Afghanistan, Congo, South Africa, Guatemala and the Gaza strip) with those in peaceful, affluent regions (e.g. the richer parts of Western Europe and North America), we indeed find the typical traits associated with the *r*-*K* trade-off (Table 1).

People raised in difficult circumstances typically have a lower life expectancy, are less tall, but more likely to become obese when they have sufficient food, and have a poor health. They tend to be considered as adults more quickly (e.g. child soldiers), to be less well-educated, have more and earlier sexual contacts, earlier pregnancies, and larger families.

Their newborns are more likely to be underweight, more prone to die, and more likely to be abandoned or to receive little attention. Moreover, adults are more likely to engage in risky, opportunistic activities that are attractive in the short-term but detrimental in the long-term, resulting in higher levels of criminality, militarism, violence, gangs, drug abuse, gambling, smoking, drinking, risky sexual behavior (e.g. promiscuity without AIDS protection), dangerous driving, and accidents at work. We find these same differences *within* societies when we consider lower social classes and ethnic minorities, such as Blacks or Hispanics in the USA, and Gypsies or Arab immigrants in Europe.

While many of these traits, such as lower life expectancy and higher childhood mortality, can be explained simply by the objective difficulties of the environment, other traits do not seem to make sense except in the light of the *r-K* hypothesis. When you live in a poor, dangerous environment where there is little medical, educational or social support, it would seem rational to have less rather than more children, and to wait with having children until you have saved sufficiently so that you are sure that you can take care of them. Moreover, in such an environment, you can less afford to take additional risks such as unprotected sex or drug use than in a society where there is a sophisticated infrastructure to help people who get in trouble. Yet, we see precisely the opposite: the more developed the society, the smaller the families, the later the age of first birth, and the more risk-averse people tend to be.

Another difference between the *r-K* model and a more traditional view is the time delay: stress during *childhood* is expected to produce *r*-type reproductive behavior during *adulthood*. This may explain the post-war baby boom, which lasted from about 1950 to 1965, i.e. one generation after the economic depression of the 1930's and the war ending in 1945. If the increased birth rate was due merely to improved economic conditions then it should have lasted at least into the 1970's. An alternative explanation is that the stress undergone by small children in the period 1930-1945 raised their fertility so as to prepare them to have large families by the time they became adult themselves. The next generation, raised in more comfortable, *K*-like surroundings, was less fertile, and this effect became only more pronounced as economic and social development continued.

Such on-going, hormone-regulated fertility reduction might even explain the observed decrease in sperm count in Western societies [Carlsen et al., 1992], which is usually attributed to pollution. An alternative, *r-K* model-based explanation may find support in the finding that at least in one study [Zheng et al., 1997] the decline correlated with the year of birth for men born in the period 1950-1970, i.e. the generation whose fertility fell most sharply.

If this general interpretation is correct, it suggests a testable prediction: after the fall of the Berlin wall in 1989 and the ensuing economic and political crisis, fertility sharply decreased in most post-communist countries, following the "rational" analysis that it is better to have less children in difficult circumstances. However, the *r-K* hypothesis suggests that this will be followed by a new baby boom starting about now, as the generation raised during those stressful years becomes adult, and this boom will last until a generation raised in more secure circumstances takes over.

Also note that the *r-K* hypothesis emphasizes uncertainty or risk as main factor rather than mere poverty. This means that *r*-behavior will be less pronounced in countries that have a low per capita GDP, but otherwise a predictable, safe society, such as the Indian state of Kerala or Eastern Europe before the fall of the wall. On the other hand, relatively wealthy but more unstable and violent communities, such as South Africa, certain Arab and Latin American countries and inner cities in the USA, will tend to exhibit more *r*-characteristics.

Indicators of QOL and *K*-selection

We now come back to the question in how far fitness can be equated with quality-of-life. *r*-selection clearly promotes quantity rather than quality. Many of the traits associated with *K*-selection (table 1), on the other hand, remind us of the criteria used to judge objective QOL or general development levels. Let us examine this correspondence in more detail, using the set of objective indicators which, according to the research of Veenhoven [1996], have a strong correlation with the average happiness, SWB or satisfaction in a country. Correlation may indicate a cause, an effect, or both. So let us examine, in Table 2, for each of the major correlates what kind of causal connection they may have to *K*-type behavior.

Indicator	Correlation with SWB	cause of <i>K</i> -strategy	effect of <i>K</i> -strategy
infant mortality	–	--	–
life expectancy	++	+	++
adequate nutrition	+	++	+?
lethal accidents	--	--	–
murder rate	–	–	–
war deaths	–	--	–
purchasing power	++	++	+
freedom	++	+	+?
equality	+	++	+?
corruption	--	–	–
education level	++	++	++
mental health	+	++	+

Table 2: Causal connections between SWB indicators (adapted from [Heylighen & Bernheim, 2000]) and *K*-traits. The marks specify the correlation between indicator and column header. "+" means positive, "–" negative correlation; a double mark means that the relation is especially strong, "?" that it is conjectured. The fact that for each indicator the signs in all three columns are the same (+ or –) indicates an unambiguous correspondence between SWB and *K*-strategy.

High life expectancy and low infant mortality are defining features of a *K*-pattern (table 1), but will indirectly contribute to the appearance of the pattern, as they indicate a more secure environment in which people—and children in particular—run less risk to die or to lose their parents or other family members. Lethal accidents, murders and war are all important risk factors, that negatively affect *K*-behavior. On the other hand, *K*-behavior will in turn reduce these factors, since it will promote less risk-taking behavior. Wealth, measured as average purchasing power, seems to be an important contributor to both SWB and *K*-behavior, but only up to a point [Veenhoven, 1996]: people should be wealthy enough to stave off the risks associated with inadequate nutrition, poor housing, lack of medical care, etc., but once these basic necessities are reliably available, further wealth seems to add little to quality-of-life. *K*-behavior in turn may increase wealth, by stimulating long-term investment.

As argued by Chisholm and Burbank [2001], inequality is a strong contributor to stress and uncertainty, and therefore negatively affects *K*-traits. Less obvious is the causal effect of *K*-strategies on equality, although they would seem to promote altruism as a type of behavior that only becomes beneficial in a term long enough to allow reciprocation. Freedom may also be a less obvious indicator, although its interpretation as personal control [Veenhoven, 1996] indicates a situation where people run less risk of being abused by dominant powers. Conversely, the more altruist and less aggressive *K*-strategists will be less inclined to bully others, and thus reduce their freedom. Corruption plays a similar role: in corrupt societies, there is less legal security. Conversely, *K*-strategists are less motivated to strive for the short-term advantages associated with corruption. Education is another strong correlate of *K*-behavior, since educated people know better how to avoid or deal with risky situations, while getting educated is a typical form of long-term development. Finally, mental health, defined as absence of emotional stress, anxiety and depression, is obviously correlated with the low cortisol levels that, as we suggested, trigger a *K*-behavior pattern. Conversely, a low-risk, long-term *K*-strategy is likely to reduce the incidence of stress, and thus improve mental health.

In summary, we find that every major indicator of SWB or QOL also seems to be a clear indicator of *K*-behavior, suggesting that QOL and *K*-behavior are different conceptualizations of the same phenomenon. However, this implies that every indicator of *K*-behavior must also be an indicator of QOL. The latter hypothesis entails a number of predictions about the existence of positive correlations between SWB and additional *K*-indicators, as listed in Table 1.

More specifically, we would expect the average happiness or life satisfaction of a group or country to be positively correlated with the average height, birth weight and the amount of care invested in children, and negatively correlated with the number of children per family, the age of first pregnancy, the sex drive, and the willingness to perform risky, opportunistic behavior. For several of these hypothesized relations, confirmatory statistical data seem to be available. For example, Chisholm [1999; Chisholm & Burbank, 2001] found a strong negative correlation ($r = -0.87$, $p < 0.001$) between the percentage of women giving birth before the age of 18 (indicating an *r*-strategy) and the Human Development Index of the country (which is positively correlated with SWB). Correlations of general development

level (and thus SWB) with height, birth weight and family size seem pretty obvious, and should be relatively easy to check. Since parental investment in child care, sex drive and risky behavior are not directly measurable, indirect indicators will have to be determined. Murder and accident rates have already been shown to be well-correlating indicators of *r*-strategies (Table 2), but these might be extended to smoking, drug use, crime in general, and rape in particular. Also the average number of sexual partners or the frequency of intercourse may provide a good indicator—insofar that reliable data exist.

Thus, the *r-K* model suggests a whole range of testable predictions that do not follow from a traditional QOL or SWB model. For example, intuitively we might expect SWB to be positively correlated with sexual activity, while the present model suggests a negative correlation. Of course, we will have to be careful to avoid confounds. For example, within a given population we may find that the most stressed people (e.g. outcasts, ill or depressed people, ...) have less access to sex, and therefore have a lower sexual activity. However, if we would compare two populations (say, two countries) in which the total access to sex is the same, we may find that the least developed one is also the one with the highest overall sexual activity.

Development as shift from *r* to *K*-strategy

The *r-K* model has important implications for our general understanding of social development. Most obviously, it provides a simple explanation for the *demographic transition*: the practically universal observation that as a population becomes socially and economically more developed, its fertility drops spectacularly—bringing down the average number of births per woman from 7 or 8 to less than 2. This has many practical implications.

First, it suggests that the best way to reduce unsustainable population growth in the long term is to increase the general level of physical, psychological, social and economic security in the population. It also explains why less developed minorities (e.g. Arabs in Israel, Gypsies in Eastern Europe, or Hispanics in the US) tend to increase in share of the population, threatening to overtake the majority. This often frightens the majority into becoming more controlling or oppressive, thus increasing the stress on the minority, pushing them into a stronger *r*-pattern of even faster population growth and more risky behavior (e.g. terrorism)—thus reinforcing the majority's reasons to be afraid. Ironically, if the majority wants to keep its position safe it would do best to make the life of the minority as comfortable as possible, helping them to develop economically, socially and intellectually, and thus reducing their birth rates and stress levels.

The *r-K* model also throws a new light on the problem of ageing populations in the most developed regions. While in most countries of Western Europe the birth rate seems to have become too small to sustain the population in the long term, this is compensated by a decrease in death rates, so that there is as yet no net decrease in population. According to *r-K* theory, the two phenomena necessarily go together, and therefore we can expect the increase in life expectancy to continue as people raised in more secure circumstances

become older. Life expectancy is defined as the average age at which people *presently* die. With a life expectancy of 75-80 years, these are basically the people born between the two world wars, when life was much more uncertain. The baby-boomers, who experienced more of a *K*-situation, can be expected to get much older on average. While it is at present impossible to tell whether the two phenomena will remain in balance, the *r-K* model gives us reason to assume that life expectancy is far from reaching a ceiling, and that death rates will continue to decline together with birth rates, keeping the population more or less constant. Theoretically, the only limit to this $r \rightarrow K$ shift is a completely stable population—in which no one dies and no one is born...

Another implication is that, as may be obvious from the bidirectional causal connections in table 2, *r*- and *K*-situations are largely *self-reinforcing*: a strategy built on short-term, risky behavior and quick reproduction creates a more uncertain environment in which children get less support, thus stimulating them to adopt the same kind of strategy. This may explain in part why the poorest countries, such as those of Sub-Saharan Africa, also tend to be the ones where long-term development is slowest. This means that strong, coordinated measures are needed to break out of such vicious cycle.

Happily, progress in QOL takes place on a very broad front [Heylighen & Bernheim, 2000], improving all the major conditions that determine risk and uncertainty, in most parts of the world. For example, advances in medical care and technology reduce the risks for disease, child mortality, children losing their parents, etc. Improving agricultural productivity and nutrition similarly reduce the risks of starvation and disease. Improvements in social organization and infrastructure reduce the risks for accidents, murder, wars and child abuse. Economic growth reduces the risks associated with poverty, loss of income, difficulty of getting the necessary medical support, etc. Finally, the globally increasing level of education makes people more aware of objective risks and opportunities for long-term investment, so that they get a better control over their lives.

The overall effect of such progress is reduced risk—especially in childhood—and therefore more pronounced *K*-traits in behavior. This reduces fertility, triggering a demographic transition. It makes people healthier, taller, and longer living, and decreases their motivation to engage in war, violence, drug abuse or other risky activities. It leads them to invest more in long-term development, though various forms of self-improvement, permanent education, health care, sustainable economic development, etc. Thus, the $r \rightarrow K$ transition may explain the Western world's growing focus on QOL, which is exemplified by the rise of non-material values, such as happiness, self-actualization and ecological awareness.

Conclusion

The biological view of fitness as the primary value guiding the evolution of life is not antithetical to the socio-political view of quality-of-life as the primary value guiding human development. If we assume that developed human populations are in a typical *K*-situation, characterized by low risk or danger, then selection for *fitness* is synonymous with selection

for *quality* of offspring. Quantity of offspring is only desirable in *r*-type circumstances, where life is risky and unpredictable, so that the only sure way to increase one's chances to leave offspring is to have as many of them as quickly as possible. What counts in natural selection is not the number of offspring *born*, but the number that will *survive long enough* to be able to produce offspring themselves. In a *K*-environment, where the supply of resources is limited but stable, this number can be increased only by maximally investing in individual offspring's chances for long-term development.

K-selection thus seems to promote all the characteristics that we associate with high QOL: high life-expectancy, health, education, safety, long term development, etc. Conversely, *r*-selection explains the traits we typically find in underdeveloped populations: short life expectancy, high (child) mortality, large families, risky behavior... Thus, the theory of *r-K* selection can help us to understand the dynamics of human development and its accompanying increase in QOL. In particular, it attracts our attention to a number of factors that have as yet received little attention in traditional QOL models: population growth, fertility, frequency of sex and risk-taking.

It allows us to better understand the medical, social and mental problems that are typically found in poor, suppressed and/or violent communities, such as heart disease, obesity, teenage pregnancies, fast spread of AIDS, crime and drug abuse. It may help us to tackle these traditionally recalcitrant problems by focusing our attention on what appears to be their underlying cause: uncertainty and stress during childhood. As such, the application of the *r-K* model to human society holds high promises for a more effective development strategy. But first the model will have to be more thoroughly tested, by comparing its predictions with the available statistical evidence.

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