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Human Evolution, Life History Theory, and the End of Biological Reproduction

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Abstract: Throughout primate history there have been three major life history transitions towards increasingly delayed sexual maturation and biological reproduction, as well as towards extended life expectancy. Monkeys reproduce later and live longer than do prosimians, apes reproduce later and live longer than do monkeys, and humans reproduce later and live longer than do apes. These life history transitions are connected to increased encephalization. During the last life history transition from apes to humans, increased encephalization co-evolved with increased dependence on cultural knowledge for energy acquisition. This led to a dramatic pressure for more energy investment in growth over current biological reproduction. Since the industrial revolution socioeconomic development has led to even more energy being devoted to growth over current biological reproduction. I propose that this is the beginning of an ongoing fourth major primate life history transition towards completely delayed biological reproduction and an extension of the evolved human life expectancy. I argue that the only fundamental difference between this primate life history transition and previous life history transitions is that this transition is being driven solely by cultural evolution, which may suggest some deeper evolutionary transition away from biological evolution is already in the process of occurring.

Keywords: Aging, biology, culture, evolution, future, human evolution, life history theory, primates.

INTRODUCTION

In this issue, we are attempting to provide a multidisciplinary perspective on the elimination of aging (from here referred to as "radical life extension"). The first thing that must be considered when discussing radical life extension (RLE) are the practical consequences such an achievement would have on human growth and reproduction. Popular and political opposition to RLE primarily stems from the belief that such a development would lead to catastrophic overpopulation issues.

In this paper I would like to specifically address how human growth and reproduction should be affected by the achievement of RLE. Such an understanding would help us properly prepare for the resulting demographic transformation, as well as restructure popular and political dialogue around real problems, as opposed to imagined problems.

In order to accomplish this I am proposing a straightforward methodology dependent on A) the evolution of human growth and reproduction, B) a situation of this evolution within the explanatory framework of Life History Theory (LHT), and C) an extrapolation of modern developed world sexual behaviour into the near-term future (~2040-2050). With such an approach we should be able to understand the evolved life history of humanity and how major technological breakthroughs related to RLE should affect our growth and reproduction patterns.

Hopefully such an analysis will give demographers, historians, anthropologists, biologists and futurists the framework they need to better understand the future of the human population.

HUMAN GROWTH AND REPRODUCTION

Every organism has an evolved life history pattern. A life history pattern is the way time and energy are allocated between growth, maintenance, and reproduction [1]. Throughout the evolutionary history of primates there have been three major life history transitions towards later sexual maturation and longer lifespan. These transitions occurred between [2]:

- Prosimians --> Monkeys
- Monkeys --> Apes
- Apes --> Humans

The life history characteristics of our closest relatives, the hominoids (*e.g*. chimpanzees, bonobos, gorillas) is particularly exaggerated towards later sexual maturity and longer life expectancy relative to the rest of the primate order [2]. That general pattern resulted in extreme degrees of parental care over long developmental periods [3]. However, humans have an even more extreme pattern. We dedicate more time and energy towards growth than any other primate species [4]. The life history consequences are dramatic, as more investment in growth pushes reproduction back further, and significantly lengthens our evolved maximum lifespan. Whereas orangutans, gorillas, and chimpanzees sexually mature between 8-10 and have an evolved lifespan between 40-50 [5], most humans reach full sexual maturity between 18-20 [6] and have an evolved average life expectancy ~80 (Table **1**) [2].

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Table 1. Great Ape and human life histories

Species	Sexual Maturity	Life expectancy
Orangutans (*Pongo*)	9-10	40
Gorillas (*Gorilla*)	8-9	40-45
Chimpanzees (*Pan*)	8-9	45
Human (*Homo*)	18-20	75-85

Our extreme drift towards later sexual maturation and longer lifespan led to two interesting emergent parenting traits unique among even our fellow hominoids: reproductive support by post-reproductive individuals and extensive male support of reproduction via provisioning of both females and offspring [4, 7]. Throughout human evolution it did not take a village to raise a child, but it literally required a band of close kin. Due to this organization, a few other novel traits emerged:

- Reproductive support by post-reproductive individuals (specifically post-reproductive females) likely led to the development of menopause [8, 9]. Menopause allows older females to shift time and energy away from their own reproduction and towards their close kin's reproduction [9].
- Maintenance of extensive male support of reproduction via provisioning of both female and offspring likely led to concealed ovulation and continuous, nonreproductive sexual activity [10, 11]. Both traits help maintain extended male-female relationships [3].

These "uniquely unique" features of human life history relate back to one central adaptation: the human brain, and more specifically the neocortex [12]. For a primate of our body and brain size, the human neocortex is 35-60% larger than expected [13]. And it is this physical adaptation that is responsible for all of our behavioural uniqueness, like a theory of mind [14], language [15], music, art, and high intelligence [11].

Since the human life history pattern has grown divergent from our fellow hominoids we must address when it evolved. Growing consensus suggests that our life history pattern started to co-evolve gradually with the emergence of the genus *Homo* approximately 2 million years ago. Techniques for understanding the evolutionary emergence of modern human life history is related to understanding the relationship between life expectancy and brain size in mammalian species [5, 16], as well as the relationship between lifespan and age-at-first reproduction [17, 18]. The paleoanthropological record provides us with both the cranial and the bone and dental evidence needed to piece together the evolution of human encephalization quotient (EQ) as well as average sexual maturation. As a result, we can estimate the evolution of long human lifespan and the evolution of modern human life history more generally [6].

From the contemporary fossil hominin record we see evidence for three or four major transitions in the emergence of modern human life history related to encephelization and sexual maturation (Table **2**) [9, 11].

Although this evidence suggests that longer lifespan emerged in punctuated equilibrium bursts [11], the bone and dental evidence suggests that the main push towards later sexual maturation came with the emergence of post-*Homo erectus* hominids [19, 20]. We know that the australopithecines had a life history pattern similar to extant great apes (*i.e.* "live fast and die young") [19]. Early *Homo* as well as *Homo erectus/ergaster* forms were unlike either extant hominoids or modern humans [21]. Both dental evidence and cranial size evidence suggests that they were exhibiting the early stages of what would eventually become the modern human life history, as they were aging slower, reproducing later, and living longer than their australopithecine predecessors [21, 22]. There are currently some difficulties understanding exactly when the modern life history pattern evolved post-*Homo erectus* but it is present in the Upper Paleolithic [6].

However, understanding *when* our life history evolved is not the same as understanding *how* our life history evolved. And for that we will need to explore Life History Theory (LHT).

Table 2. Major transitions in human life history

Species	Time (mya)	Cranial Capacity (cc)	Estimated: Sexual Maturity / Life Expectancy	
Australopithecines	6-4	450	10	50
Homo habilis	2	600	12-13	60
Homo erectus/ergaster	1.7-0.5	800	15-16	70
Archaic humans	0.3-0.1	1,300	18	80

LIFE HISTORY THEORY AND HUMAN EVOLUTION

The history of life can be conceptualized as the history of variant chemical structures harvesting energy to create ever more complex replicates of similar forms [23]. Life History Theory (LHT) attempts to explain the "trade-offs" that occur as a result of this process [24]. The three pertinent facets of life history to consider include how organisms spend energy on growth (*i.e.* traditionally investment in somatic cells), maintenance (*i.e.* avoidance of mortality), and reproduction [1, 12, 19]. By dedicating energy towards growth and maintenance, an organism can enhance future reproduction [2]. Growth and maintenance have traditionally been conceptualized as "somatic effort" (*i.e.* somatic cell diversification and replacement, see [24]). On the other hand, organisms can also dedicate energy towards reproduction. By dedicating energy towards reproduction, organisms must invariably reduce the amount of energy dedicated towards growth and maintenance, as well as reduce the chances of reproducing in the future [23].

Throughout this entire process, finite energy budgets fundamentally cause the aforementioned trade-offs. If energy were unlimited, organisms could in principle start reproducing soon after birth (*i.e.* no trade-off between growth and reproduction) and preserve themselves indefinitely (*i.e.* perfect maintenance) [23]. But throughout the entirety of biological evolution, energy has never been free and abundant, it has always been costly and scarce. Therefore, all organisms must spend it strategically, in a way that best maximizes fitness [1].

In sum, finite energy budgets can be used for the continued growth and maintenance of the organism (which increases chances of future reproduction), or finite energy budgets can be dedicated towards replication (which decreases the chances of future reproduction). As a result of this trade-off, an entire organisms existence is about finding a strategic balance between current and future reproduction.

For our purposes, this theory can help us explain the divergent reproduction and mortality patterns in humans [25]. So what evidence do we have to work with? Remember, there are four divergent human life history characteristics (as summarized above) [4]:

- Extended developmental period (*i.e.* childhood)
- Long life span
- Reproductive support from post-reproductive individuals
- Extensive reproductive support from males

We also know that these exaggerated and unique life history features evolved with larger brain size, specifically large neocortex size, which is also a unique feature among humans. The dominant LHT explaining this emergence is that our extreme intelligence, as produced through our enlarged neocortex, co-evolved in response to gradual dietary shifts to high calorie food sources [4]. Throughout the punctuated equilibrium-like bursts in brain size, we find evidence of substantial transitions to exploitation of increasingly diverse and meat-abundant diets [9, 26, 27]. Importantly, the exploitation of these diverse and meat-abundant diets were achieved via the construction of increasingly complex technology [28].

What does this all mean for our exaggerated shift in life history towards longer developmental periods and longer life spans? First and foremost, it meant that our ability to efficiently extract more energy from our environment was dependent on inherently cultural and technological processes. These processes are in turn facilitated by the acquisition of increasingly high levels of knowledge, skills, and social coordination, which require longer developmental periods dedicated to *learning* [4]. Due to the high levels of learning needed in order to maximize adult survival, our ancestors invested more energy in growth to maximize future reproduction [29]. An adult-sized, fully mature five-year old human could simply not compete with an adult-sized, fully mature twenty-year old human [12]. Therefore, childhood became an intellectual and social stage of development requiring increasingly large amounts of time and energy at the expense of current reproduction [12]. We have our fundamental life history trade-off.

MODERN WORLD

Throughout modern human (*i.e. Homo sapiens sapiens*) pre-historic and historic evolution our life history patterns have not diverged from the evolved pattern. In both hunter-gatherer and agricultural systems, we allocated time and energy towards growth and reproduction at roughly the same intervals. This may at first seem strange considering massive socio-sexual changes resulted from the emergence of defensible and heritable wealth in agricultural systems [12]. Examples include [30, 31, 32]:

- Higher emphasis on symbolically mediated long-term pair bonds (*i.e.* marriages)
- Patrilineal inheritance
- Exaggerated emphasis on division of labour

The reason these changes during the agricultural revolution did not significantly alter our life history pattern was because energy remained costly and scarce for the large majority of humans, which in turn resulted in similarly high fertility and mortality rates. If anything, fertility and mortality rates on average increased slightly in agricultural systems in comparison to hunter-gatherer systems [33]. Therefore, all human life before the modern world was characterized by 15-20 years of "pre-reproductive" life, a post-reproductive life-span that could last 30-40 years, and an organization including extensive reproductive support from adult males and post-reproductive females. This evolved life history strategy proved best for maximizing fitness.

Enter the Industrial age. Most historians agree that the Industrial Revolution started in England approximately 200-250 years ago and diffused quickly throughout Western Europe, the United States of America, and Britain's settler colonies (*e.g.* Canada, Australia, New Zealand, etc.) in the 19th century [34, 35]. This revolution released new energy into our system from fossil fuels and ushered in the era of very rapid technological progress [36]. This new Industrial system led to massive demographic changes as industrializing regions of Europe and North America experienced a sharp decline in both mortality and fertility [12]. For the first time in modern human history, some human populations had experienced a change in their life history pattern.

Overall the demographic transition is characterized by two main trends. The first trend is a reduction of fertility to replacement or below-replacement levels (~2.1). The second trend is a reduction of mortality that allows most individuals in society to reach an advanced post-reproductive age (~80). Both trends are universally associated with socioeconomic development (*i.e.* "modernization") and a transition from a pre-industrial to an industrialized economy [33]. Reduced fertility primarily results from the *further* extension of "childhood". However, it is probably more accurate to state that reduced fertility results from continually delayed biological reproduction post-sexual maturation. The continued trend towards delayed biological reproduction was again accompanied by a further intensification of parental investment, and parents choosing to invest time and energy in the "quality" of offspring as opposed to the "quantity" of offspring [33].

This transition to a new life history pattern is not the result of one specific culture or "Westernization". The demographic transition is directly the result of socioeconomic development and industrialization. In the beginning of the 21st century, the first regions of the world to industrialize have already completed the demographic transition (*e.g.* Europe, Northern America, Japan, Australia, New Zealand, etc.) [37]. Many newly developed countries in East Asia have also completed (or are nearing completion) of their demographic transition [38]. Furthermore, much of Asia, Latin America, and most recently, Africa, have experienced the beginnings and maturation of the demographic transition [37]. Many experts expect the full realization of the demographic transition to manifest globally by the year 2050, as long as current socioeconomic industrialization trends continue [37]. As far as the developed world is concerned, the two trends associated with the demographic transition are expected to continue accelerating (*i.e.* reduction of fertility and mortality) as improvements in socioeconomic conditions only serve to intensify these processes [39].

Evolutionary theorists have had a difficult time reconciling the demographic transition within an adaptive life history model [33]. Why does increased socioeconomic development result in a failure to increase reproductive success? A failure to identify an adaptive cause is a major problem since its universality suggests that these trends can only be explained in deeper evolutionary terms. Proposed explanations have included maladaptation to contraceptive technologies [40], fragmentation of kin networks [41], emerging roles of social prestige in labour market [42], and rising investment costs in producing socially and economically competitive offspring [33]. The best life history framework is definitely provided by the idea that industrialization makes it increasingly energetically costly to invest valuable time and energy in current reproduction. However, this framework cannot address the relatively new phenomenon of adults en masse opting *not* to reproduce. Arguably, delaying biological reproduction completely and effectively removing oneself from reproductive gene pool is a novel behavioural phenomenon for an individual organism with reproductive capability. This makes modern societies life history trajectory increasingly bizarre and difficult to explain when conceptualized within a traditional life history framework.

INTO THE FUTURE

I propose that our changing life history pattern is best explained as the fourth evolutionary exaggeration of the characteristic primate life history pattern towards later sexual maturity and longer life expectancy. This is fundamentally being driven by the same processes as previous primate life history transitions, namely selection for individuals with ever-greater levels of knowledge, skills, and social coordination, which require ever-longer developmental periods dedicated to learning. However, the major difference between this transition and previous transitions is that this transition's *dominant* evolutionary pathway is cultural, as opposed to biological. As a result, the reduction of biological fertility is adaptive for the continued acceleration of cultural reproduction. The on-going selection for cultural reproduction comes at the direct expense of biological reproduction. If true, this could suggest that cultural evolution is in the early stages of modelling and replacing the biological evolutionary process. Such a development would mark a new evolutionary period in the history of life as all of previous life history was driven by variant chemical structures harvesting energy to create more complex replicates of similar forms (as opposed to variant cultural structures).

Evolutionary scientists have long recognized that the cultural evolutionary process shares many non-arbitrary parallels with biological evolutionary processes [43], and that these cultural evolutionary processes are uniquely manifest in the human species [44, 45]. Experiments show that cumulative cultural evolution is not only unique but can also result in adaptive complexity in behaviour and can also produce convergence in behaviour [46, 47]. Before the emergence of humans biological evolution was the only way this type of adaptive complexity could emerge. With cultural evolution as a new mechanism for complexity construction the entire evolutionary process is more potent and can operate much more quickly [47]. Furthermore, cumulative cultural evolution consumes all of human individual and collective existence. The human life is one spent first learning the knowledge, inventions, and achievements of previous generations, and then secondly, building upon them (*i.e.* ratcheting "up" the complexity) [45]. In the modern world, all individual and collective economic success is dependent on our cultural and technological complexity, the mechanism for which is our ability to understand and make use of imparted knowledge and artifacts [46]. From this perspective it does not seem unreasonable to suggest that one evolutionary process (*i.e.* culture) is growing more dominant than another (i.e, biology). To envision these as evolutionary pathways, I would propose that one evolutionary pathway is "biochemical" and one is "technocultural".

Considerable evidence supports the assertion that cultural replication is now in the early stages of superseding biological replication as the dominant form of complexity construction. In the modern world we find ourselves in an ever-more challenging cultural environment that is accelerating pressures for the acquisition of ever-more cultural information. Of course, the pressure to learn ever-more cultural information has been a feature of our species since our emergence. This process has operated via the mechanism of the cultural ratchet (see: [45]), but I argue that the selection for this process is now superseding biological processes. The pressures to learn ever-more advanced cultural information are most notably manifesting in the pressure for ever-more people requiring ever-more advanced forms of education. We should expect this trend to continue, and in fact accelerate quite quickly throughout the 21st century along with the continued diffusion and exponential improvement in information and communication technologies (ICT). Specifically the emergence of ever-more advanced robotics and artificial intelligence systems should replace the need for humans to do low-skill, low-education jobs. The removal of low-skill, low-education jobs should increase individual opportunity to explore cultural reproduction-as-vocation (e.g., music, art, science, engineering, etc.). Artificial intelligence systems becoming embedded in operating systems and apps should also increase our ability to do ever more complex jobs that require ever-more advanced degrees. Finally, wearable computing, and in a decade or two brain-interface devices, should exert a strong pressure on people to acquire more and more cultural information to remain socially and economically competitive (for detailed information on a potential evolutionary pathway see: [48]).

Evidence that cultural replication is now superseding biological replication can also be found in two other phenomena emerging in their early stages: increasing life expectancy and increasing number of people in developed countries opting not to biologically reproduce at all. In our evolutionary past, increasing life expectancy co-evolved with increasing brain size [12]. In the modern world our absolute brain size is not expanding but the amount of information our brain is required to accumulate in order to compete is certainly increasing (again, see: [48]). Furthermore, as many computer scientists, philosophers, and futurists have pointed out, we are actually extending the information our neocortex collects into ever-more sophisticated computers. This type of "mind outsourcing" is an idea that works well with the extended mind hypothesis, which asserts that our species has always extended mind into external mediums since the emergence of verbal language (see: [49]). However, the digital substrate is something new. Many suspect that our exponential outsourcing of mind-to-computation will result in our eventually connecting our minds to the "cloud" and enhancing the processing power of our neocortex via this mechanism (see: [50, 51]).

Undoubtedly this process is a cultural evolutionary process leading to increased brain capacity, and not a biological evolutionary process. If the past is any indication we should expect our life expectancy to increase along with this type of brain expansion. The mechanisms to achieve this are already emergent and practical application of them should be near-term realities from the continued advance of biomedicine and genetics [52, 53]. Such advances are likely to include the practical application of replaceable stem cell organs, the complete prevention of degenerative diseases, and a fundamental understanding of reversible genetic causes of aging. Currently, stem cell organ replacement is likely to reach a practical application stage in 10-20 years, and fundamental reversible causes of aging have already been identified (see: [54, 55]). Therefore, it is reasonable to suggest that the beginnings of radical life extension have already started. If that thesis is not convincing, it is undoubtedly true that the cultural war on aging has already started, as many major biomedical companies, including a new biomedical branch of Google (*e.g.* [56], are investing heavily in research related to identifying the reversible causes of aging (for more see: [53]).

Finally, another sign that cultural reproduction is taking the place of biological reproduction is the simple fact that many individuals in the developed world are, for the first time, making the culturally informed decision to not reproduce biologically. This phenomenon is helping drive the trend towards a developed world that is already below replacement fertility level (*e.g.* [39, 57, 58]) (Table **3**). This means that we are currently at a crucial time period, as it appears we are reaching the "tipping point" where biological reproduction is becoming "too costly" to justify in the face of rising pressure for ever-greater cultural reproduction, as well as the increased opportunity for cultural reproduction-as-vocation. Most experts today do not factor in these pressures that will likely lead to ever further reduction of biological reproduction. However, leading reports still suspect that nearly half of the world's population is currently residing in countries at or below replacement level fertility [57]. Many other rapidly developing regions of the world should approach these fertility levels within mere decades [57] and the entire world should have completed the transition to below replacement level fertility by 2050 [37].

Surprisingly, these hypothesized trends (*i.e.* increased pressure to acquire ever-more cultural information, increasing life expectancy co-evolution with increased brain capacity, and increased autonomous individual decisions to avoid biological reproduction) are not at odds with Life History Theory (LHT). As stated above, traditional LHT conceptualized growth and maintenance in solely biological terms (*e.g.* somatic cell replacement and maintenance) (*e.g.* [24]). As a result traditional LHT presents a "sex versus soma" framework (*e.g.* [19]). However, for organisms like humans, growth and maintenance can also be achieved through cultural learning via the brain [23]. So within this LHT framework I am proposing that an emerging fourth primate life history transition is in the process of reducing energy dedicated to current biological reproduction indefinitely. This is occurring in favour of allocating energy towards ever-more advanced culturally mediated growth and maintenance through learning via our enlarged (and perhaps soon-to-be-dramatically enlarged) brains. The mechanisms to realize this transition, as described above, are already emergent. All selection for this process is undoubtedly being driven by cultural evolution as opposed to biological evolution, which may suggest that a new evolutionary process is soon to predominant the biological evolutionary process. Complexity would be directed by mind.

Table 3. Global Fertility Rate (2014 est.) [64]

Replacement Fertility Rate (2.1)	# of Countries	Examples
Countries > 2.1	108/224	Niger, Philippines, Belize, Yemen
Countries < 2.1	116/224	France, Norway, Australia, Canada
Countries < 1.5	32/224	Germany, Japan, Italy, South Korea
Countries < 1.0	2/224	Macau, Singapore

I predict that the full realization of this life history transition should occur before 2050, which suggests that this theory could be in some way connected to the hypothesized metasystem transition commonly referred to as *Global Brain* (see: [48, 59-61]). In order to take this 21st century future seriously we need only assume that the pressures of the modern developed world hold and accelerate globally. First and foremost, the pressures for the acquisition of more advanced cultural information must accelerate as a result of advanced ICT. This will continue to force an extension of a widespread postponement of biological reproduction. Secondly, continued advances in our understanding of aging and degenerative diseases must accelerate dramatically, allowing us to radically extend life expectancy and possibly usher us into a post-aging world. This will remove the evolutionary imperative to create complexity through biological reproduction, as delaying current reproduction would always be preferred in favour of dedication of energy towards culturally-mediated growth and maintenance.

In the future, further research into the specific causal mechanisms driving a potential complete end to biological reproduction is needed. At the moment the exact mechanisms are unknown. However, one possible causal mechanism explaining how culture, technology, and information can impact the biological change in reproduction has been discussed by Kyriazis in this issue.

However, although the extrapolation of current trends and framing these trends within well-tested evolutionary frameworks is a useful methodological tool for explaining our likely future, we cannot be 100% certain that this is our future. Fundamentally, this life history future is dependent on continued system-level socioeconomic development as supported by the current industrialized energy regime, as well as a smooth transition to a new post-industrial energy regime before 2050. In short, this life history future is fundamentally dependent on abundant energy globally. This is not an outrageous assumption (see: [62, 63]). However, if current trends are significantly ruptured by large socioeconomic processes related to a collapse of our current energy regime, and/or a failure to establish a post-industrial energy regime, we should not expect the life history trajectory outlined above.

CONCLUSION

Human life history throughout our species evolution can be thought of as one long trend towards delayed sexual maturation and biological reproduction (*i.e.* from "living fast and dying young" to "living slow and dying old").

Due to the evolution (and consequent complete dependence) on our large brains, human life history is organized around the acquisition of cultural information. This has always required inordinate amounts of time and energy dedicated to growth. Over the past 200-250 years, humans in the industrialized world have experienced a significant rupture to this pattern. This rupture is best explained as yet another primate extension of pre-reproductive years and extension of life span. Fundamentally, this transition is only different from previous transitions in that the dominant evolutionary processes driving this exaggerated life history is cultural. This explanation adequately addresses what previous demographic transition life history explanations fail to address, especially in regard to autonomous adult humans opting to not reproduce biologically at all.

In the case that my aforementioned assumptions prove incorrect, this analysis should prove useful for the important reason that you can make a fairly reliable prediction for biological reproduction given radical life extension (RLE). If RLE is not achieved before 2050, but instead at some later date, 100, 150, or 500 years from now, this will likely coincide with the indefinite postponement of current biological reproduction in favour of current cultural reproduction. Therefore, any popular or political opposition to the practical application of RLE breakthroughs on the basis that they would lead to catastrophic overpopulation issues, are almost definitely unfounded. Also, any scientists currently involved in research related to RLE should not fear that their breakthroughs will lead to major population problems that will need to be solved at some future period of time.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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PATIENT'S CONSENT

Declared None.

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