

Is humanity undergoing a transition to reproductive specialization? Insights on the evolution of modern societies to superorganisms

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Abstract

A current discussion centers on whether human societies are undergoing a major evolutionary transition in individuality (METI) toward superorganisms. A METI typically involves a population composed of independent units evolving to form a new unit of a higher level of complexity, as for instance, the emergence of multicellular organisms from unicellular organisms, or the evolution of superorganisms, such as beehives. It has been proposed that for a METI to occur, certain key criteria must be met, including division of labor, exponential increase in size, inseparability, and reproductive specialization. All of these characteristics have been documented in human populations over the past 12,000 years, except for reproductive specialization. This involves that only a fraction of the population carries out reproductive functions, while the rest performs maintenance tasks. Recently, human populations are experiencing the so-called “demographic transition,” characterized by a decrease in infant mortality, followed by a decrease in birth rates. The causes of this transition are mainly sociocultural, leading to diminished reproductive competition, which, in turn, could lead to biological infertility. This begins a positive feedback loop of declining fertility, potentially leading to a demographic winter and the risk of extinction of modern societies. To prevent such an outcome, governments will probably implement rescue measures that could lead to reproductive specialization. The study of transitions has medical importance because they may cause shifts in health-disease landscapes.

Keywords: Complexity. Evolution. Extinction. Infertility. Reproduction. Transitions.

Introduction

In recent years, abundant literature has emerged analyzing the evolution of life toward progressively more complex forms. In addition, it has been assessed that most of the characteristics present in biological evolution are also present in the sociocultural evolution of human populations¹. It is known that biological complexity does not always evolve in a linear, monotonic manner, but sometimes increase in leaps toward higher hierarchical levels. Such leaps have been termed “major evolutionary transitions in individuality,” or (METI)².

During the evolutionary period of time that comprises METI, highly independent, autonomous, free-living individuals, lose most of their independence to become part of a new whole. Evolutionary transitions within biological evolution can be divided into two categories: (1) an egalitarian transition implies that two organisms of different species come together in symbiosis or endosymbiosis to form a more complex unit. The classical example is the emergence of eukaryotic cells from an endosymbiotic process between two species of prokaryotes. (2) a fraternal transition occurs when

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individuals of the same kind progressively become more cohesive and interdependent, such that the population gradually transforms into an individual of a higher hierarchical level. The two main examples of fraternal transitions are the emergence of multicellular organisms and the origin of superorganisms (complex colonies) in some eusocial species of ants and bees.

Recent efforts to operationalize the parameters involved in METIs have resulted in the identification of at least four common features: (1) increasing interdependence between individuals, resulting in inseparability from the group; (2) labor specialization or division of labor; (3) a drastic increase in size, and (4) reproductive specialization, i.e., reproductive function is limited to a few individuals in the community such as germ cells and stem cells in multicellular organisms, or queens and drones in a beehive^{3,4}. Additional factors involved in the evolution toward greater complexity are progressive enhancements in communications systems, such as the evolution of endocrine and paracrine signaling systems in multicellular organisms, or complex chemical signaling in ants-and the emergence of more abundant and efficient energy sources⁵.

It has been noted that the sociocultural and technological evolution of human beings in the past 12,000 years exhibits most of the characteristics of a METI. Therefore, it has been suggested that human societies may be experiencing a fraternal METI toward human superorganisms^{3,6}. However, unlike previous METIs, the evolution of human superorganisms would be triggered by sociocultural and technological factors, rather than exclusively by biological ones.

The sole remaining factor to affirm that human societies are evolving into superorganisms is reproductive specialization, which in multicellular organisms and superorganisms is evidenced by a strong reproductive skew among group members⁶. Moreover, humans exhibit less reproductive skew than other mammalian species⁷. However, the possibility that human societies may be experiencing the beginning of a transition toward reproductive specialization has not been examined so far. Thus, finding signals that indicate that humanity is experiencing such a transition is important for assessing a METI driven by sociocultural and technological factors. This may have profound implications for future healthcare, medicine, and epidemiology. As an example from the recent past demographic and economic transitions have changed health-disease landscapes worldwide, increasing the incidence of cardiovascular and metabolic diseases⁸. As I will argue, the decay in fertility rates in modern human societies

may be an early sign of a transition to reproductive specialization. This paper is not intended to be an exhaustive review of the causes of human infertility, but rather to assess the likelihood of reproductive specialization emerging within economically and technologically advanced human societies in the coming decades, in the larger framework of a human METI.

Reproductive specialization in multicellular organisms and superorganisms

I will examine reproductive specialization in multicellular organisms, specifically humans, at two levels of biological complexity: cellular reproduction (division) and the reproduction of entire multicellular organisms. At the most basic level, cells must divide to (1) give rise to an adult multicellular individual with a multiplicity of cellular specializations, and (2) to replace old, specialized cells that are continually dying. Most multicellular organisms begin their lives as a totipotent unicellular organism, the zygote, which passes this totipotency to the first generations. From a technical point of view, these first generations are pluripotent, capable of generating cells belonging to the three embryonic germ layers. During human embryogenesis, cells, induced by epigenetic modifications, progressively lose this capacity. Throughout the rest of a human's life, tissues regenerate from a pool of multipotent stem cells (MSC) that continue to divide. These MSCs are capable of generating all types of specialized cells, but each type is restricted to a specific organ or system^{9,10}.

MSCs from different tissues and their committed direct descendants have a high reproductive capacity and are responsible for maintaining the cell population in the organ. Unlike these, specialized cells have a limited reproductive capacity. The path from totipotency to specialization is mostly irreversible *in vivo*, although the reprogramming of specialized cells to pluripotent cells *in vitro* is possible by inducing the expression of Yamanaka transcription factors, a procedure with enormous therapeutic potential¹¹. The natural pathway leading from multipotentiality to a specialized cell is determined by signals from the extracellular matrix, as well as by intercellular and mitochondrial signaling¹²⁻¹⁴. These signals induce epigenetic changes, the most important of which is gene silencing through DNA methylation and histone modification^{15,16}. In the process of cellular replacement during the lifetime of an individual, reproductive specialization entails that the task of

generating new specialized cells is limited to MSCs in each organ.

At the next level of biological complexity, a multicellular organism with sexual reproduction reproduces by generating new multicellular individuals. Here, the task of generating new individuals falls exclusively on the gametes, for which there is, during early embryogenesis, an early sequestration of an immortal germline: the germplasm¹⁷. Similarly, once the gametes give rise to a zygote and therefore to a new organism, their somatic descendants lose that capacity. Reproductive specialization means that only cells of the germline are responsible for the generation of new multicellular individuals.

Finally, at the highest level of biological complexity, in some eusocial species of bees and ants, the tasks of generating new individuals for the colony and establishing new colonies are handled by a few individuals, such as queens and drones in honeybees. In these species, the workers play the role of the “somatic line”, while the reproductive individuals assume the role of a “germline”¹⁸. The mechanisms that give rise to reproductive specialization and sexual dimorphism vary widely among different species of eusocial insects and range from phenotypic plasticity influenced by the environment (epigenetic determination) to being fully determined by the genotype^{19,20}, which is evidence of convergent evolutionary pathways, and though, of an underlying biological advantage offered by these traits.

Biological advantages of reproductive specialization

In both sexually reproducing organisms and superorganisms, non-reproductive individuals specialize in tasks that contribute to the maintenance and survival of the group, i.e., somatic specialized cells in the multicellular organism or workers in honeycombs. Their main role is to be an interface with the environment to ensure the survival of the germplasm. Since there is no reproductive competition among these non-reproductive individuals, the characteristics of each sex are not necessary for them. For instance, in eusocial insects, the workers are usually asexual, unlike drones and queens, which exhibit notable differences between them, i.e. sexual dimorphism. The loss of sexual characteristics in non-reproductive individuals represents a form of evolutionary phenotypic simplification (simplification of individuals coupled to an increase in group complexity as an evolutionary mechanism can be reviewed in references^{3,21,22}).

An accepted explanation for the evolution of reproductive specialization is that to avoid subversion within the group, individuals must be genetically similar, and this similarity is achieved through a genetic bottleneck, marking a new beginning for each organism or superorganism. Genetic homogeneity is attained because all cells descend from a single cell (the zygote) in the case of organisms, or from a single queen, in the case of eusocial insects. However, an alternative (or perhaps complementary) explanation for the evolution of reproductive specialization is the division of labor, which results in the maximization of energetic efficiency for the group. That is, cooperative communities where individuals specialize in a specific task, including reproduction, are economically more efficient than those in which “everyone does everything,” providing the group with a competitive advantage. Therefore, reproductive specialization could be part of a broader division of labor. Division of labor and other features seen in the transition from complex populations to organisms and superorganisms, primarily evolve as traits related to the survival of the group rather than the survival of the individual (for a review on multilevel selection see reference²³). Reproductive specialization allows the energy of a few individuals to be focused on the task of reproduction.

Sexual dimorphism in humans

Sexual dimorphism can be defined as the physical or behavioral characteristics that differentiate males from females of the same species²⁴. I will extend the usual definition to include all the differences present at various levels of biological complexity between both sexes. **Table 1** shows the most prominent dimorphic features at the different levels.

At a molecular level, men are differentiated from women by the presence of a Y chromosome, and specifically, by the presence of the SRY gene. The expression of this small gene –which encodes a transcription factor– at the 6th week of gestation in the bipotent gonad, determines sex through the activation of a gene cascade that leads to the formation of testes²⁵. In women, the absence of the SRY gene determines a different activation pathway led by WNT-4. In addition to SRY, the Y chromosome harbors important genes for spermiogenesis.

Once the testis is differentiated, Leydig cells actively secrete testosterone. In general terms, testosterone and its derivative hormone, dihydrotestosterone, establish the virilization of the external genitalia, giving rise to the penis and scrotum. In the absence of testosterone, the genitals develop into vulvar structures and the

Table 1. Sexual dimorphism in humans at different levels of biological complexity. Unfolding of the male and female phenotypes and successful procreation requires integrity in the sequential activation of complex genetic networks

Level of biological complexity	Males	Females
Molecular	Presence of a Y chromosome	Absence of a Y chromosome
	Presence of a SRY gene	Absence of a SRY Gene
Gondal	Presence of testis, testosterone secretion	Presence of ovary, estradiol, and progesterone secretion
Genital	Presence of the scrotum and penis, the development of Wolf conducts derivatives	External genitalia: Vulvar structures, clitoris, lower 2/3 of vagina. Internal genitalia: Uterus and fallopian tubes
Secondary sexual characteristics	Larger lean mass, stronger complexion, presence of facial hair, android distribution of pubic hair	Larger cosmetic adipose tissue in breasts and hips, gynecoid distribution of pubic hair
Sexual identity	Male brain	Female brain
Sexual orientation	Attracted by females	Attracted by males

lower two-thirds of the vagina. Similarly, the secretion of testosterone in the fetus and the early post-partum period produces cerebral virilization, probably being the main determinant of male sexual identity and orientation²⁶. In addition, the Sertoli cells of the embryonic testicle secrete the anti-Müllerian hormone, which prevents the formation of fallopian tubes and the uterus. Testosterone secretion is interrupted during childhood but resumes in adolescence with the secretion of pituitary gonadotropic hormones, leading to the development of male secondary sexual characteristics. In the absence of testosterone, female secondary sexual characteristics, conditioned by estrogens and progesterone, predominate (a comprehensive review of human sexual development can be found in Rey et al.²⁷).

Evolutionarily speaking, sexual dimorphism at all levels –from the presence or absence of a sexual chromosome to the generation of testes or ovaries, the emergence of secondary sexual characteristics, and behavior that leads to the search for a sexual partner and subsequently to successful sexual intercourse and pregnancy– aims to increase the fertility of the individual. They constitute fine clockwork mechanisms with multiple activation cascades that involve many genes. Disruption of these genes can lead to disorders of sex development, conditions associated with reproductive development, intersex, and variations in sex characteristics, all of which may have a negative impact on fertility.

The evolutionary mechanisms of sexual dimorphism arise from a type of selection different from natural selection, coined by Charles Darwin as “sexual

selection.” Traits related to sexual selection do not contribute to the survival of the individual, but only to its ability to reproduce. For these traits to emerge and be maintained in populations, strong reproductive competition between individuals of the same sex is required²⁸. Consequently, the loss of reproductive competition could lead to a process of progressive simplification of sexual dimorphism and a drop in fertility rates.

Demographic transition triggers sociocultural infertility

In the past two centuries, humanity has experienced enormous advances in public health and therapeutics, which, along with alimentary transitions, have resulted in a drastic drop in infant mortality rates. The decline in mortality rates has been followed by a decline in fertility rates. The changes in the demographic composition of countries due to these two phenomena have been coined “the demographic transition”²⁹. Typically, pre-transition population pyramids, as their name indicates, are triangle-shaped, with a wide base that represents a growing population with high natality rates and high mortality across all age groups. During the demographic transition, as both birth and death rates decrease, the base of the pyramid becomes narrower and this narrowness ascends, gradually reversing the shape of the pyramid, with a large aging population in the upper segments, and a narrow base that represents the youngest segment (an example of population pyramids from some Latin-American countries can be found in reference 8).

The demographic transition began in Europe in the 18th century and gradually spread to the rest of the world. During recent decades, the fertility rate in high-income and some middle-income countries has fallen below the population replacement rate of 2.1 children per woman, which is a component of the so-called “second demographic transition”³⁰.

The sociocultural causes of demographic transitions are varied, all resulting in a psychosocial shift toward a decline in reproductive drive. Most probably, the main triggering factor of the current decline in birth rates in modern societies is the economic transition, i.e., when society changes from a state of deprivation to an abundance of food and other resources. As a society prospers and therefore the basic needs of its inhabitants are met, the energy consumption per capita increases, which in turn raises the costs of childrearing; consequently, there is a tradeoff from quantity to quality in procreation³¹. In addition, sociocultural changes in gender equality have allowed women to obtain better education and enter the workforce. As a result, women’s productive activity competes with the procreative function, such that parenthood is postponed and the number of children per woman decreases. Thus, in modern advanced human societies a tradeoff between reproduction and production occurs³⁰. Finally, the decline in reproductive activity in humans and other species could be influenced by endocrine and behavioral changes induced by increased population density^{32,33}. In addition, sociocultural changes could barely reduce fertility rates without technological advances in contraceptive methods.

For practical purposes, I will divide the decline in fertility among modern human groups into two types: (1) sociocultural infertility, which is voluntary and motivated by the sociocultural factors listed above, and (2) environmental/biological infertility, determined by those factors that decrease the probability of pregnancy despite the attempts to achieve it. Table 2 summarizes the main causes of the declining fertility rates and their possible impact in fertility parameters. Most likely, the increase in sociocultural infertility in modern human populations predates the increase in environmental/biological infertility. Sociocultural infertility and reduction in child mortality rates may lead to a progressive increase in environmental/biological infertility due to loss of reproductive competition^{22,34}. Under a regime of poor reproductive competition due to sociocultural factors, fertile individuals have the same probability of reproducing as less fertile ones, not only because many of the biologically fertile individuals voluntarily

Table 2. Possible causes and outcomes of fertility decline in post-transition societies

Causes of sociocultural/technological infertility
Raise in costs of childrearing
Better education and work opportunities for women
Effective contraceptive methods
Causes of biological/environmental infertility
Loss of reproductive competition
Endocrine disruptors
Psychological response to stress and population density
Possible negative outcomes in fertility
Drop in testosterone levels in men
Drop in sperm counts
Raise in the prevalence of Polycystic Ovary Syndrome
Raise in the proportion of non-heterosexual individuals
Loss of sexual dimorphism

postpone or avoid parenting, but also because the less fertile are now able to reproduce due to improvements in assisted reproduction technologies.

What might be the biological repercussions of the loss of long-term reproductive competition? First, mutations that decrease sexual dimorphism and fertility can easily survive and increase in frequency in the population through individuals with low fertility who reproduce using assisted reproduction technologies. Consequently, there will be a loss of negative (purifying) selection on genes that maintain sexual dimorphism and fertility. Second, there may be a loss of positive (directional) selection, obliterating adaptation to environmental insults to fertility. The most outstanding example of environmental noxa detrimental to fertility is endocrine disruptors³⁵.

Evidence of increasing biological/ environmental infertility

A progressive decline in the biological fertility of human populations is evidenced by several parameters linked to fertility. In men, a gradual decline in mean sperm counts has been observed³⁶, as well as in mean testosterone levels³⁷. In Western women, consultations for polycystic ovary syndrome have increased in recent years³⁸.

On the other hand, there is a growing social acceptance of individuals who self-identify as non-binary or do not conform to the traditional classification of two genders, with the emergence of the so-called “gender ideology”³⁹. Although the genesis of variations in traditional sexual partner-seeking behavior is largely presumed to be cultural, the underlying influence of

biological/environmental factors cannot be ignored. In this context, a genome-wide association study found that the effect of multiple genetic variants accounted for between 8% and 25% of the variation in homosexual behavior⁴⁰. A possible decline in the proportion of heterosexual couples may be a contributing factor to decreasing birth rates.

The integrity of endocrine function is vital for finding a sexual partner and for procreation, and even small variations in hormonal levels can produce large systemic effects. Endocrine disruptors are natural or synthetic chemical substances that interfere with physiological endocrine systems either by blocking or mimicking hormones, with multiple consequences for human health. They can enter the body through different routes, such as inhalation, ingestion, or direct contact. Among the most abundant are plastics, such as bisphenol A and phthalates; some herbicides such as atrazine; and products widely used in manufacturing such as dioxins, perchlorates, polychlorinated biphenyls, polybrominated diphenyl ethers, and per/polyfluoroalkyls. Most endocrine disruptors have a negative impact on fertility^{35,41}. The increasing environmental accumulation of these substances could be responsible, at least in part, for the decreased biological fertility and variations in sexual behavior.

What should be the effect of increased exposure to endocrine disruptors in a population with a high reproduction drive? Although an initial drop in natality rates would be observed, positive selection for individuals harboring genetic variants that confer resistance to endocrine disruptors would rapidly occur. In this scenario of high reproductive competition, the population would become resistant in a few generations, without any further impact of the substances on fertility rates. Conversely, in a population with a low reproductive drive such as modern advanced human societies, the evolution of resistance to endocrine disruptors that are harmful for fertility should not be expected. A low reproductive drive results in low reproductive competition. Therefore, over time, biological parameters of fertility, as well as sexual dimorphism at all levels, should decrease. This, in turn, would lead to further drops in fertility, lower reproductive competition, further increments of infertility, and so on, in a positive feedback loop that could potentially lead to the extinction of humankind.

Possible future paths to human reproductive specialization

If the presence of environmental endocrine disruptors continues to grow, and the lack of reproductive

competition due to sociocultural infertility leads to an accumulation of deleterious mutations in fertility genes (sexual simplification), then the progressive decrease in birth rates worldwide must be an asymmetric, largely irreversible phenomenon. Therefore, a rebound of fertility in modern societies to past levels is unlikely. The consequence is an aging population, which would radically change the demographic, economic, and epidemiological landscapes of countries in the coming decades^{42,43}.

The evolution toward reproductive specialization must include two components: (1) decreased fertility in the majority of individuals and (2) increased fertility in the remaining individuals, sufficient for population replacement. Together, these two components would raise the reproductive skew. Although the former is now occurring in modern societies, there is still no evidence of the latter. Given the apparent inevitability of an aging population, in an effort to increase fertility rates, governments of countries that are in advanced stages of the demographic transition (like some countries from the European Union) usually offer economic incentives to boost fertility⁴⁴.

One scenario (although highly speculative) that could lead to sexual specialization is that, in an attempt to avoid demographic winter and its negative economic impact, governments could significantly increase monetary incentives for fertility. Then, a fertile fraction of the population might take advantage of these high economic revenues for reproduction, turning the task of procreation into an economic activity. To reverse depopulation, this fertile fraction must raise fertility rates needed for population replacement. However, if biological/environmental infertility continues to increase, this approach would not be feasible in the long run, and the reproductive fraction would need support from advanced assisted reproduction technologies.

If birth rates continue to drop and economic incentives fail to restore fertility rates, an extreme scenario could arise in which, facing an imminent extinction of human societies, governments might take complete control of the task of reproduction. This could be feasible, as ectogenesis technologies improve⁴⁵. Although this may seem a reminiscence of the dystopic novel by Aldous Huxley "Brave New World", the decimation of the most advanced human societies due to lack of reproduction is a real possibility³⁴, which may eventually require extreme measures. Both of the above scenarios could lead to reproductive specialization, with a fraction of the population (individuals or governments) assuming the task of reproduction (Fig. 1).

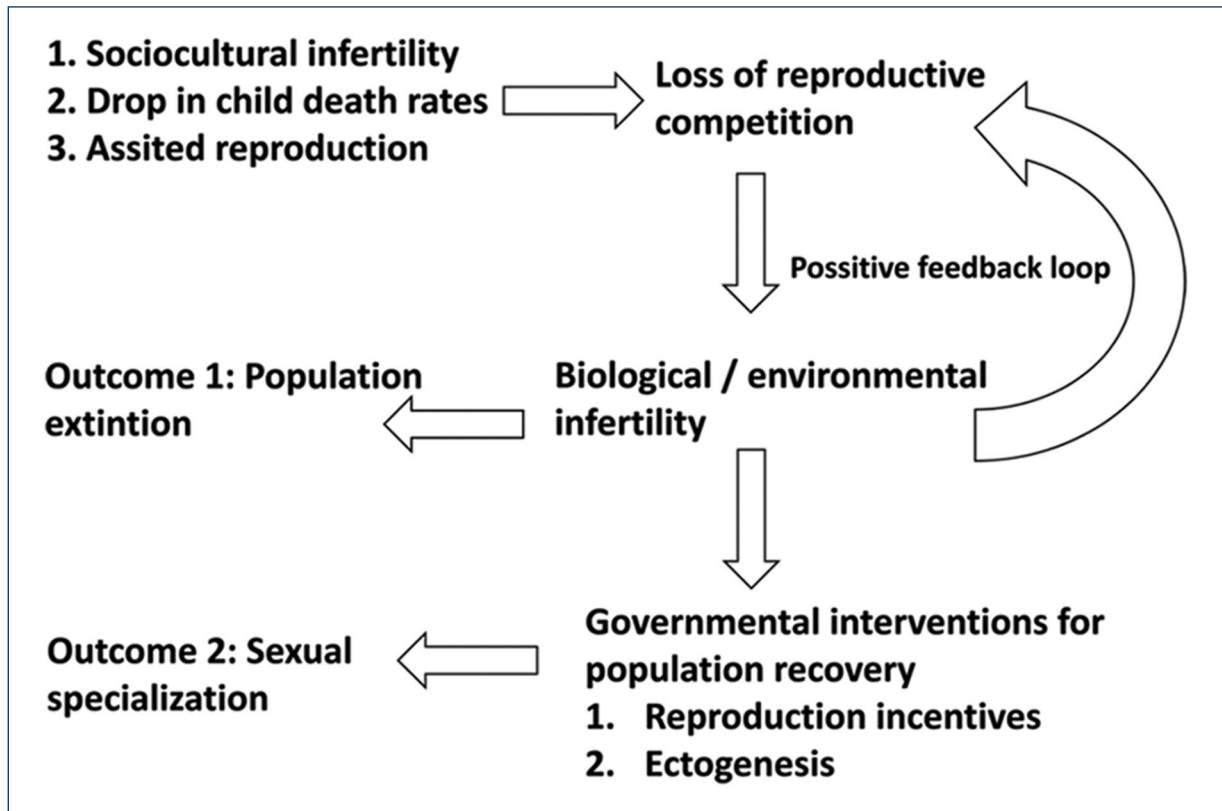


Figure 1. Possible outcomes of raising infertility in human populations. Loss of reproductive competition derives in a raise of biological/environmental infertility, further lowering reproductive competition in a positive feedback loop. Measures imposed by governments could derive in sexual specialization.

Conclusion

Currently, superorganisms (organisms composed of organisms) such as the beehive or the anthill, constitute the most advanced level of biological complexity on Earth. Whether or not human societies are completing a transition to human superorganisms guided by an interaction of sociocultural, technological, and biological factors is controversial, and one of the reasons is the absence of sexual specialization. However, recent economic and demographic transitions have been the genesis of an increasing decline in fertility rates in modern societies, due to a positive feedback cycle that could lead to sexual simplification and increased biological infertility. The potential rescue measures implemented by governments in response to the imminent demographic winter could limit the task of reproduction to a fraction of the population, or even to governments themselves, leading to reproductive specialization. As a byproduct, reproductive specialization may increase genetic homogeneity, a common characteristic of organisms and superorganisms. The emergence of a strong reproductive skew in advanced

human societies in the upcoming decades would be an unequivocal sign that we are in an ongoing METI toward human superorganisms. Finally, the impact of reproductive transitions on future human psychology, social interactions, political systems, and healthcare systems (among others) is uncertain. Governments, institutions, and the public must be aware that modern societies are thriving in an era of rapid changes which require high flexibility and adaptability.

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Ethical considerations

Protection of humans and animals. The author declares that no experiments involving humans or animals were conducted for this research.

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