

Postadaptations

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Synonyms

Evolutionary baggage (Appenzeller, 1999)

Definition

Postadaptations are traits that were once adaptations to specific environmental conditions but have lost their adaptive value due to changing conditions, making them less relevant or even maladaptive in current environments.

1. The Evolutionary Fate of Traits: From Adaptation to Postadaptation

Traits that were once adaptive, and sometimes crucial for survival and reproduction in specific environments, may lose their functional significance or even become maladaptive as conditions shift over time. To fully comprehend the potential role and evolutionary history of any biological trait, it's essential to consider its function and significance not just in present environments, but also in past contexts shaped by selective pressures and environmental necessities. This principle holds particularly true for the human species, which has undergone substantial environmental and lifestyle changes throughout its evolutionary journey, especially in recent cultural history. However, this also extends to domesticated species and other organisms living in environments reshaped by agriculture or urbanization. As an increasing number of species inhabit such rapidly transforming environments, this principle has gained even more relevance.

Even within the current habitat of a species across its entire range, there can be considerable heterogeneity. In certain parts of a species' range, a specific trait might be adaptive, while in others, it may hold no adaptive value. Consequently, the same trait should be classified as an adaptation in some parts of the range and a postadaptation in other parts of the range.

2. The Challenge of Determining Adaptiveness in a Changing Environment

Determining the relevant conditions when assessing the adaptiveness of a trait can be challenging. For example, the lifestyle of modern humans has undergone considerable changes in the past century due to technological advancements and the eradication of infectious diseases. This process has led to the loss of adaptiveness for numerous traits and behavioral patterns once deemed adaptive. Thus, these can now be classified as postadaptations. On the other hand, some traits that are currently adaptive were not so in the past, and can, therefore, be classified as exaptations.

Establishing the appropriate time frame to determine what constitutes an adaptation can prove difficult. Traits viewed as adaptive today may not have been perceived so in the past, and vice versa. Typically, it is simpler to identify when a trait starts being adaptive,

while recognizing when a trait loses its adaptive value can be more complex.

For instance, abilities like texting on a cell phone or driving a car could be considered adaptive following the advent of mobile phones and cars, respectively. However, these skills cannot be categorized as biological adaptations, as they haven't existed long enough for corresponding alleles to proliferate through natural selection. Nevertheless, the structures responsible for these skills can and should be classified as exaptations. It is both entirely valid and potentially insightful to investigate their original biological functions.

On the other hand, some adaptive traits have had sufficient time to evolve through slow evolutionary mechanisms, such as the accumulation of necessary mutations via selection. For instance, the ability to digest lactose in adulthood (Gerbault et al., 2011), may have developed due to favorable alleles that were selected after the inception of pastoralism. Others may have evolved following the advent of agriculture or urbanization. However, pinpointing these historical events can be challenging, as they unfolded gradually, with differing timings and rates in various parts of the world.

2.1 Agriculture and Urbanization's Impact on Adaptations

Agriculture and urbanization have significantly impacted the environment of our species, fostering new physiological and behavioral adaptations while causing many former biological adaptations to lose their adaptive value. The emergence of urban lifestyles, for instance, has led to the proliferation of alleles coding for physiological resistance to infectious diseases, as well as the dispersion of alleles responsible for behavioral immunity - those coding for behavioral patterns capable of reducing infection risks.

In numerous cases, behavioral immunity proves more vital than physiological immunity, as associated behavioral patterns can swiftly disseminate through a population due to a combination of imitation and the Baldwin effect (Baldwin, 1896). In densely populated urban environments, alleles for behavioral patterns like social phobia, xenophobia, or obsessive-compulsive disorder can prove beneficial in safeguarding individuals and populations against infectious diseases.

However, as the environment continues to evolve, with the advent of higher hygienic standards and advances in medical sciences, even such traits may start to lose their selective advantages. They may forfeit their functional significance, transitioning into postadaptations. In today's world, traits such as obsessive-compulsive behavior or social phobia may even become maladaptive for individuals, and traits such as xenophobia could become maladaptive for society. Thus, it is crucial (though frequently challenging) to consider the temporal environmental contexts when seeking to understand the emergence and loss of adaptive (and maladaptive) traits.

2.2 A Brief History of Rh Factor Polymorphism

Although not definitively proven, the evolutionary history of Rh negativity's origin provides a captivating and complex illustration of adaptive trait evolution. Strikingly, roughly 16% of Europeans exhibit the Rh-negative blood type, suggesting they carry mutated alleles of the RHD gene, characterized by a significant deletion (Wagner & Flegr, 2000). This polymorphism, however, poses an evolutionary conundrum, as carriers of the less frequent allele - Rh-negative women in predominantly Rh-positive populations, and Rh-positive

men in predominantly Rh-negative populations - were consistently penalized by natural selection. In the era before the advent of modern prophylactic methods, Rh-positive newborns of Rh-negative mothers often perished from hemolytic disease (Bowman, 1997; Filbey, Hanson, & Westrom, 1995). Under these circumstances, the RHD polymorphism should have been unstable, resulting in only one type of RHD gene (one allele) persisting in a population.

The evolutionary puzzle of RHD polymorphism in human populations has sparked debate for many years (Feldman, Nabholz, & Bodmer, 1969; Fisher, Race, & Taylor, 1944; Haldane, 1922). Still, several recent studies support the theory that heterozygote advantage maintains this polymorphism (Flegr & Escudero, 2016; Flegr, Hoffmann, & Dammann, 2015; Flegr, Kuba, & Kopecký, 2020; Flegr, Toman, Hula, & Kankova, 2020; Kaňková, Flegr, Toman, & Calda, 2019). Researchers have found that heterozygotes boast better health than both Rh-negative and Rh-positive homozygotes. The substantial impact of Rh phenotype on physical and mental health was only recently identified, having eluded researchers' notice for nearly a century. This oversight often arises because, in many respects, Rh-positive homozygotes have even poorer health outcomes than Rh-negative homozygotes and the serological techniques commonly used for Rh assessment do not distinguish between Rh-positive homozygotes and heterozygotes (Flegr, Toman, et al., 2020).

The prevalence of Rh-negative individuals varies significantly across different countries, with a notably higher frequency observed in Europe and among individuals of European descent in other parts of the world (16%) compared to Africa (5%) and Asia (1%) (Mourant, 1954). The high frequency of Rh-negative subjects in some regions of Europe, such as the approximately 27% found in Basques, has traditionally been attributed to the founder effect and drift. However, recent studies suggest that natural selection may have also played a role in the Rh-negative allele's dispersion.

Indeed, certain hypotheses strongly supported by empirical data propose that pathogenic selection pressure might have propelled the dispersion of Rh-negative alleles. For instance, Europe's lower prevalence of the parasitic infection toxoplasmosis compared to other global regions may have facilitated the Rh-negative alleles' spread (Novotná et al., 2008). Given that cats are the definitive hosts of the *Toxoplasma gondii* parasite and domestic cats have been a recent addition to Europe (Torrey & Yolken, 1995), it's plausible that toxoplasmosis's lower prevalence in Europe 2000 years ago contributed to the Rh-negative alleles' emergence and spread. Europe's toxoplasmosis prevalence is currently around 30%, but most countries report an approximate 1% per year decrease. This reduction likely results from recent hygiene standard improvements and eating habit shifts, such as preparing meat from cooled or frozen sources (Tenter, Heckeroth, & Weiss, 2000).

Studies indicate that Rh-positive individuals, especially heterozygotes, may be shielded from latent toxoplasmosis's negative impacts. For instance, simple reaction time tests have shown that *Toxoplasma*-free, Rh-negative individuals have the swiftest reaction times. However, Rh-negative individuals' psychomotor performance significantly declines upon *Toxoplasma* infection, whereas Rh-positive individuals' performance remains unaltered. Infected Rh-negative individuals demonstrate the longest reaction times, while Rh-positive infected heterozygotes have the shortest. Intriguingly,

Toxoplasma-positive heterozygotes' reaction times outperform those of non-infected heterozygotes (Flegr, Novotná, Lindová, & Havlíček, 2008; Novotná et al., 2008). This positive impact of toxoplasmosis, along with recent research suggesting *Toxoplasma*-infected heterozygotes have better health than *Toxoplasma*-free individuals (Flegr 2020b) indicates that humans may have adapted to being *Toxoplasma*-infected, which was likely our ancestors' natural state in Africa.

Hence, the Rh polymorphism's evolutionary history offers a captivating and complex narrative. In Africa, home to a variety of small and large cat species, *Toxoplasma* infection was almost universal until recently. This made being an Rh-positive heterozygote highly adaptive. However, as our ancestors migrated to Europe, where cats were rare, Rh-negativity became advantageous, triggering the Rh-negativity allele's spread. The arrival of domestic cats in Europe several centuries ago led to an uptick in toxoplasmosis prevalence, reinstating the Rh-positive heterozygote as the most adaptive trait. Nonetheless, the mean fitness of different Rh genotypes' oscillation was moderated by selection favoring heterozygotes and affected by systematic negative selection against the rarer allele due to hemolytic disease in newborns.

2.3 Health Hypothesis of Demographic Transition: The Impact of Fast and Slow Life-History Strategies on Population Dynamics

The potential for adaptations and exaptations to transform into postadaptations due to environmental changes can significantly impact the outcomes of scientific studies. This factor should be taken into account when interpreting results. For instance, consider studies that test the hypothesis attributing demographic transition to improvements in public health. Demographic transition is a demographic phenomenon commonly observed in countries experiencing a marked increase in living standards. This transition is characterized by a sharp decline in population growth rate. Multiple alternative explanations have been proposed for this phenomenon. However, most have been disproven by empirical data, as the associated socio-economic or cultural changes often occurred either much earlier or much later than demographic transitions, i.e., the rapid decrease in fertility rates.

One hypothesis that has consistently withstood attempts at falsification is the health hypothesis of demographic transition. According to this perspective, the significant improvement in the health of residents, primarily in wealthy countries with widespread access to healthcare, is the main cause of the demographic transition. Following the advent of agriculture, our species began consuming food that we were not biologically adapted to. This dietary shift led to a decline in our health condition (Armélagos, Goodman, & Jacobs, 1991; Eaton, Eaton, & Konner, 1997). The spread of infectious diseases was facilitated by increasing urbanization, which exacerbated this declining trend in health. The implications of this health decline included a reduced life expectancy and smaller physical stature of our ancestors compared to pre-agriculture and urbanization populations (Eaton et al., 1997).

A significant yet less obvious consequence of declining health was the shift towards a fast life-history strategy (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Reznick, Bryga, & Endler, 1990). Individuals in worse health instinctively try to reproduce as soon as possible and as quickly as possible, even before reaching the optimal

age for reproduction (as many of them never reach optimal age due to poor health). As a result, they produce a large number of offspring, but only a small proportion of them reach reproductive age. This leads to a positive feedback mechanism, further worsening the health of the population and an even more pronounced transition to a fast life-history strategy. As rudimentary but increasingly beneficial medical methods were introduced during the 19th century, combined with improvements in hygiene and food provision, child mortality rates started to decline rapidly, resulting in exponential population growth in numerous regions.

In wealthy countries, future advances in medicine and hygiene over the past 150 years have gradually improved the health of a large proportion of the population. For instance, a recent study demonstrated that the average body temperature has steadily dropped from 37°C to 36.4°C over this period, indicating a likely decrease in chronic inflammation rate among the population (Protsiv, Ley, Lankester, Hastie, & Parsonnet, 2020). Additionally, an increase in average body height further attests to the improving health of individuals in developed countries. As a result, an increasing number of people are reverting to a slow life-history strategy, characterized by a reduced reproductive rate and delayed onset of reproduction.

The health hypothesis of demographic transition was recently examined in a large online study conducted in the Czech Republic with a sample size of 33,000 individuals (Sýkorová & Flegr, 2021). The researchers aimed to verify the fundamental premise of the health hypothesis—that individuals in poorer health tend to reproduce faster and start reproducing earlier. They also tested several sub-hypotheses related to the assumed shift between fast and slow life-history strategies. The study affirmed the basic hypothesis, revealing that individuals with poorer health or a genetic predisposition for future health deterioration exhibited signs of a fast life-history strategy. Specifically, the researchers found that these individuals had a lower age of menarche in women, higher sexual desire, earlier reproduction, and a lower number of children for both genders. Women in poorer health also began their sexual lives earlier than healthier women. However, the study failed to confirm some preregistered hypotheses. For instance, the hypothesis that individuals in poorer health would have more children at a young age but fewer children overall compared to healthier individuals was not supported. Instead, it was found that individuals with poorer health had slightly more children overall.

The most plausible explanation is that individuals with poorer health tend to reproduce earlier in anticipation of a future decline in fertility and vitality. However, due to advancements in modern medicine, this decline is less pronounced than our genes have prepared us for. The transition to a fast life-history strategy may be considered a post-adaptation—it may be beneficial for individual fitness in the current context, but it may not contribute to personal well-being. This shift could be detrimental to the population and species as a whole, as individuals with poorer health are now contributing more genetic material to future generations than healthier individuals. As medical science progresses, this trend is likely to become more pronounced. While ethically we can't counter this trend by disadvantaging individuals with health issues, it may be necessary to reassess our current negative stance on interventions into the germ line cells' genome to ensure the long-term health of our species.

3. The Search for Our Ancestral Home: Reconsidering the Environment of Evolutionary Adaptedness for *Homo Sapiens*

The environment that shaped our phenotype, including our minds, throughout the course of human evolution is a topic of extensive discussion in cultural anthropology. It is a common belief that humans lived as hunter-gatherers in small groups on the African savannas for hundreds of thousands of years (Heerwagen & Orians, 1993). Consequently, many anthropologists consider the African savanna and mixed woodland habitats as our *environment of evolutionary adaptedness* (Tooby & Cosmides, 1990). This context is typically used to evaluate the adaptedness of specific human traits.

However, this view might be challenged for at least two reasons. Firstly, the savanna may simply be the habitat where human remains are most likely preserved as fossils, particularly in comparison to the African tropical forests (Roberts, Boivin, Lee-Thorp, Petraglia, & Stock, 2016). It is conceivable, therefore, that our ancestors spent the majority of our species' history in tropical rainforests or coastal regions.

The second reason questioning this perspective is rather intriguing. The adaptations of sexually reproducing species are more likely to occur in the environment in which they live immediately after their divergence from their ancestral species, rather than in the environment they inhabited for most of their evolutionary history. Some genetic theories propose that sexually reproducing species remain evolutionarily adaptable only for a brief period (10-20 thousand years) following their origination through a specific type of speciation (typically peripatric speciation). After this period, they become macro-evolutionarily frozen and micro-evolutionarily frozen or elastic, and cease to effectively respond to selection pressures. Species in this state of macro-evolutionary freeze are relegated to a passive existence, waiting either for environmental changes that could drive them to extinction or for another speciation event that could revive their evolutionary plasticity, facilitating adaptation to a new environment. Our closest relatives, the chimpanzees and gorillas, inhabit tropical forests. This suggests that humans may have evolved in, and are possibly adapted to, such a biome. Therefore, any adaptations to life on the savanna might be exaptations, leaving us with numerous post-adaptations, which are traits not beneficial in the habitats where most current cultures have existed or continue to exist.

3.1. From Punctuated Equilibrium to Species Obsolescence

Eldredge and Gould proposed an alternative to the gradualistic approach of the modern evolutionary synthesis (Eldredge & Gould, 1972). They posited that the evolution of multicellular organisms is punctuated, characterized by brief periods of swift phenotypical change, typically untraceable in the paleontological record. These episodes are followed by extended periods of evolutionary stasis during which the species' phenotype remains stable, comprising 98-99% of a species' existence.

This punctuated nature of evolution has been a contentious subject over the past 50 years, with several explanations proposed, including four specific genetic mechanisms (for review, see (Flegr, 2010)). Eldredge and Gould's initial hypothesis was grounded on E. Mayr's theory of genetic revolution (Mayr, 1954, 1963). According to this theory, a random shift in gene pool composition, driven by the sampling effect after a small population breaks off during *peripatric*

speciation, could be a critical factor. The founder-flush model (Carson, 1968) suggests that population expansion into an open ecological niche relaxes all forms of selection, allowing recombinants and mutants with suboptimal phenotypes to survive (crossing valleys in the adaptive landscape). The genetic transience model (Templeton, 2008) attributes the increase in selection responsiveness mainly to an increase in selectable genetic variability. This is achieved through the transformation of non-additive (and therefore non-selectable) genetic variability into additive genetic variability in the emerging species.

The theory of frozen plasticity, proposed by Flegr (Flegr, 1998, 2010, 2013) suggests that evolvability increases transiently when alleles with frequency-dependent effects on fitness are eliminated by genetic drift and the sampling effect in small, isolated populations during peripatric speciation. As small populations are unable to respond to selection, their evolution is guided by genetic drift. However, when the small population expands, it surpasses the influence of drift and maintains its evolutionary plasticity due to the absence of frequency-stabilized polymorphism. This allows for an easy response to selection and adaptation to the current environment. Over subsequent generations, rare mutations with frequency-dependent effects on fitness accumulate in the gene pool of the new species through the process of stability-based sorting (Toman & Flegr, 2017). The existence of these alleles leads to the microevolutionary elasticity and macroevolutionary freezing of the species, causing it to lose its capacity to respond to selection resulting from environmental changes. Consequently, the species gradually becomes obsolete and can only passively await extinction for the rest of its existence.

All four of these theories address the punctuated pattern of macroevolution, but their ability to explain other evolutionary and ecological phenomena varies. Moreover, they can elucidate why most species are burdened with postadaptations, making them obsolete in many aspects. Residing in evolutionary stasis for the majority of their existence, sexual species are typically adapted to the past conditions at the time of their last significant anagenetic change, rather than the current conditions.

4. Postadaptations: The Journey Toward Rudiments and Atavisms

Throughout the evolutionary process, postadaptations often lead to the emergence of rudiments and atavisms. These diminished structures or behavioral patterns no longer serve their original function due to their regression, yet they still emerge during ontogeny and can be observed in some form in adult individuals. While rudiments are present in every individual of a species in some form, such as the human appendix, atavisms emerge in a minor fraction of individuals due to specific combinations of 'obsolete' alleles - ones that once coded for beneficial traits but have become rare due to changes in environmental conditions or evolutionary pressures, and thus are scarce in the given time period. An example of an atavism is the occasional development of a tail in humans.

Typically, a postadaptation loses its function and adaptive value due to environmental changes. Should the original conditions return, the postadaptation might potentially regain its adaptive value. However, rudiments or atavisms lose their adaptive value not only because of environmental shifts, but also due to alterations in their own structure. This means that they cannot recover their function if

the original conditions return, except through the slow accumulation of new mutations guided by selection. The typical sequence of events begins with an adaptation or exaptation losing its adaptive value due to environmental changes, thereby becoming a postadaptation. Subsequently, mutations accumulate in the genes controlling its ontogeny, leading to its diminution. The structure then morphs into a rudiment, which eventually transforms into an atavism that appears with decreasing frequency across generations until it ceases to appear entirely.

The diminishing occurrence of an atavism over time is driven by the decreasing frequency of alleles in multiple loci responsible for programming the ontogeny of the atavistic trait. As the frequency of these alleles declines, the rare combinations that enable the emergence of the atavism become increasingly infrequent, eventually vanishing altogether. However, some relevant alleles may persist at low frequencies in the species' gene pool, permitting the reemergence of the adaptive trait under suitable selective pressure. This can prompt the parallel evolution of the trait, in which the common ancestor lacks the feature, but it appears to arise independently in descendant species under similar conditions and selective pressures (Whiting, Bradler, & Maxwell, 2003). Notably, the final structure and mechanism of ontogeny, as well as the genetic architecture of the same trait, often vary in descendant species because the probability of repeating the same evolutionary pathway is very low for complex traits. This principle, which is fundamentally statistical in nature, underlies the contemporary understanding of Dollo's Law (Dawkins, 1996). Originally introduced to paleontology by Louis Dollo in 1893, the law generalized the ubiquitous observation that an organ that once disappeared in evolution never reappears in the same form in descendant species (Dollo, 1893; Gould, 1970). However, Dollo's Law is now recognized to have many exceptions, particularly for less complex traits with simple gene architecture.

The reduction of an organ is not solely a passive process resulting from random mutation accumulation; in some cases, the reduction can be actively driven by selection. This takes place when the reduction of a redundant structure allows the resources initially dedicated to its creation to be reassigned to other structures. This reallocation of resources can occur either during embryonic development or following the completion of an individual's development, as preserving a nonfunctional structure can also impose demands on valuable resources (Wilkins, 2010).

The evolution of a rudiment does not necessarily conclude with its transformation into an atavism and subsequent disappearance. In many instances, the structure is never completely reduced. This typically happens when the developing organ serves a purpose during the organism's embryogenesis, or when the reduced structure retains one of its multiple, often unrelated, functions in the adult organism. For instance, the long appendix of herbivores plays a vital role in digesting plant food. The human appendix cannot perform this function, but it does contribute to maintaining the ecological balance of intestinal microflora, promoting the rapid recolonization of the intestine by symbiotic microorganisms following severe diarrheal disease or the application of broad-spectrum antibiotics.

Another potential fate for a postadaptation is for the corresponding rudiment to become a preadaptation for an entirely new

function, unrelated to the function that the structure served in its unreduced form. This pathway is likely quite common, given evolution's known ability to ingeniously improvise and effectively repurpose seemingly useless structures to create useful ones.

Conclusion

Postadaptations represent an intriguing and often overlooked facet of evolutionary biology, as they illuminate the dynamic interplay between traits and their ever-changing environmental contexts. Studying postadaptations can deepen our understanding of how evolution crafts, repurposes, or even discards traits based on their adaptive or maladaptive value in current and past environments.

When adaptations lose their adaptive value due to environmental changes, they transition into postadaptations. This process may sometimes lead to the emergence of rudiments or atavisms, providing visible evidence of these transformations. Despite the lessened or lost functionality, rudiments may still serve important roles in embryogenesis or fulfill secondary functions in the organism. They can also potentially transform into preadaptations for novel functions, illustrating evolution's impressive capacity for creative reuse. Atavisms, or rather the alleles responsible for their emergence, may persist in low frequencies within a population, permitting the reemergence of lost traits under suitable conditions.

In some instances, changes in the environment or lifestyle, such as the advent of agriculture, urbanization, or technology, can expedite the synchronous transition of many traits from adaptations to postadaptations. This dynamic becomes especially relevant for our species in our modern world, which is characterized by rapid and profound changes in living conditions for many species, including humans.

The conditions and challenges we face today are radically different from those our ancestors encountered. Traits that were once beneficial in past environments might no longer serve us or might even prove detrimental in our current societies. An awareness of this evolutionary narrative helps us understand the causes of many negative phenomena we encounter, whether they relate to physical and mental health (e.g. obesity) or societal functioning (e.g. xenophobia).

In conclusion, the study of postadaptations expands our understanding of evolution beyond the confines of immediate adaptiveness, introducing a temporal dimension that acknowledges the shifting contexts in which traits function. While the issue of preadaptation is a popular and frequently discussed topic in evolutionary biology, questions concerning postadaptations are often overlooked. This may be a mistake, as our understanding of the concept of postadaptations can provide insights into a number of important questions about evolutionary dynamics.

Cross-References

Preadaptations, Spandrels, Adaptation, Baldwin Effect, *Toxoplasma* Infection, Life-History Strategy, Environment of Evolutionary Adaptedness, Rudiments, Atavisms.

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