Runaway Sexual Selection Model

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Synonyms

Autoelexis; Coevolutionary elevator; Runaway process; Sexy sons hypothesis

Definition

An evolutionary mechanism characterized by the continuous enhancement or accentuation of a particular trait within a species, resulting from the mutual influence of female mate preferences and male trait displays, ultimately causing an exaggerated development of the trait.

Introduction

Runaway selection is an evolutionary mechanism proposed in the 1930s by statistician and evolutionary biologist R.A. Fisher in his book *The genetical theory of natural selection* (Fisher, *1958*) as an explanation for the emergence of the so-called exaggerated secondary sexual characteristics through sexual selection. According to Fisher, the origin of these often-conspicuous structures, which sometimes reduce their bearer's chances of survival in the wild, lies in sexual selection. Specifically, the emergence of these traits involves the existence of a characteristic that increases the fitness of its bearer, usually the male, and the existence of a preference for this characteristic among members of the opposite sex, typically females. Both the male trait and the female preference must exhibit variability and nonzero heritability. When these conditions are met, a coevolution of the male trait and female preference inevitably occurs, and according to Fisher, this coevolution has an accelerating character. The more the trait is present in the population, the more it pays for females to preferentially mate with bearers of this trait, and the more females exhibit a preference for the trait, the more it pays for males to bear it. Thanks to this positive feedback loop, the development of the trait has an accelerating character, with Fisher even suggesting that it initially involves an exponentially accelerating process. This process is particularly effective when the male trait is quantitative, such as tail feather length or human intelligence, and the female preferences are relative, meaning that females always choose males with the highest expression of the trait from the available options.

It is evident that the enlargement of a particular structure cannot continue indefinitely. Beyond a certain size, the structure begins to reduce the viability of its male bearer, either directly, such as by hindering movement mechanically, or indirectly, by requiring the allocation of excessive resources for its development. However, the process of increasing the expression of the male trait, such as enlarging its size, continues until the negative impact of the trait on natural selection outweighs its positive influence on sexual selection. According to Fisher, most of the exaggerated traits we currently observe in nature have arisen rapidly due to the aforementioned positive feedback loop, but they now persist in a stable state where the forces of natural and sexual selection are balanced.

The evolution of an exaggerated trait is largely unidirectional. Once a preference for a specific trait becomes widespread in a population, it is difficult to reverse the runaway process, even if the trait begins to harm its bearers. The reason for this can be explained by the **sexy son hypothesis**, which Fisher also initially formulated (Fisher, *1915*, *1958*). Imagine a population where a female, due to a mutation, starts to prefer males with a different phenotype, such as short tail feathers instead of long ones. If this trait – short tail feathers – were heritable, she would give birth to short-tailed sons who would have greater viability than males with long tail feathers and a higher percentage of them would reach adulthood. However, since most females in the population would still prefer males with long tail feathers, these highly viable males would not have the opportunity to reproduce. Consequently, the female with a preference for the new trait would pass on fewer genes to the next generation compared to females with the original preference for a trait disadvantageous in terms of natural selection. This principle, which ensures the irreversibility of female choice, is sometimes referred to as the *Fisherian process*. It is essential to emphasize that the Fisherian process and the *runaway process* address two distinct aspects of the sexual selection process driven by the female choice mechanism. The former explains the unidirectional nature of the process, while the latter highlights its accelerating character.

Sexy Males-Preferring Daughters Hypothesis

The sexy sons hypothesis is a well-known concept in evolutionary biology and evolutionary psychology. It demonstrates that reversing sexual selection based on the runaway process is challenging. If a female in a population where most other females prefer long-tailed males starts to favor short-tailed males, her sons will inherit their father's short tail. Consequently, they might have higher viability but will be less "sexy" – they will be penalized in sexual selection because the majority of females in the population prioritize long-tailed males. It is thus adaptive for females to suppress their preferences and prioritize the same males as most other females in the population. In many species, we indeed observe that females preferentially copulate with a male they have seen copulating with other females – a phenomenon called *mate-choice copying* (Kavaliers et al., *2017*).

Expanding on the sexy sons hypothesis, the *sexy males-preferring daughters hypothesis* can be introduced as a complementary idea. This new hypothesis proposes that males gain an advantage by reproducing with females who choose to copulate with the most preferred males, as opposed to those who prefer to copulate with them, i.e., by engaging in mate-choice copying, a behavior that has been demonstrated even in human males (Gouda-Vossos et al., *2018*). Otherwise, they risk fathering not only non-sexy sons (which they cannot avoid) but also daughters who prefer less-preferred males, who will, in turn, give birth to non-sexy sons in future generations. Therefore, the stability of the runaway process might be maintained not only by the factors underlying the sexy sons hypothesis but also by those related to its analogous counterpart – the sexy males-preferring daughters hypothesis.

Challenging Fisher's Runaway Selection: The Impact of Female Choice Costs and Mutational Bias on Trait Evolution

Although Fisher was a mathematician by training, he relied on verbal models in his book, causing him to overlook that his model could only work under specific conditions. Precise analysis of the relevant mathematical models revealed that Fisher's runaway selection model can function only when female choosiness comes at no cost. In such cases, across a wide range of initial conditions, an equilibrium in the representation of alleles for the preferred trait and alleles for the preference of the trait is established. Under these circumstances, the runaway process can lead to the development and long-term persistence of the exaggerated trait (Kirkpatrick, *1982*). However, if female choice entails a non-zero cost for the female, such as time or energy spent in selecting mates, the entire development process is unstable, and exaggerated traits cannot be sustained through this mechanism. In equilibrium, males with the specific trait have the same biological fitness as males without it, and females gain nothing by distinguishing between them. Since discrimination is not cost-free for females, the genes responsible for distinguishing between males will gradually disappear. Females will stop preferring males with the exaggerated trait, and it will eventually vanish from the population due to natural selection (Lande, *1980*).

A certain solution to this problem was proposed by Bulmer (Bulmer, *1989*). He demonstrated that the equilibrium in the representation of genes for preference and the preferred trait can stabilize if there is a mutational bias in the population, meaning that mutations leading to a decrease in the expression of a specific secondary sexual trait occur more frequently than those leading to its increase. This situation is quite common in complex traits. If a trait is formed during ontogenesis by the interaction of multiple genes, most mutations, i.e., random changes in these genes, lead to a disruption of cooperation between these genes and, therefore, a reduction in the expression of the trait. As a result of mutational bias, most males have a suboptimal phenotype at any given moment, i.e., suboptimal expression of the trait, and it is beneficial for females to discriminate between them.

In the 1990s, Maynard Smith focused on the issue of the runaway process in detail (Maynard Smith, *1991*). In his review article, he showed that the probability of the emergence of exaggerated traits due to runaway selection alone is relatively low, especially in animals living in monogamous partnerships. He argued that although mutational bias can stabilize the equilibrium state at which the runaway process can occur, it cannot explain the initiation of the process itself. If the initial frequencies of genes for the preferred trait and the gene for its preference are low, both gradually approach an equilibrium state with zero frequencies. He suggested that other mechanisms, specifically those described by the indicator hypothesis and the handicap hypothesis (see relevant chapters), are involved in initiating the runaway process leading to the development of exaggerated traits.

Redefining Runaway Selection: Intralocus Selection, Coevolutionary Elevator, and the Complexification of Ornaments

Fisher and most of his followers used the classical neo-Darwinian theory to explain the emergence of secondary sexual traits, particularly exaggerated traits. This theory assumes that the criterion for an organism's success is its biological fitness, i.e., simplistically, the number of offspring that reach reproductive age. However, modern post-neo-Darwinian theory based on intralocus selection between competing alleles shows that the criterion for the success of an allele/mutation is not how many offspring its carriers have, but how many copies of the allele itself are transmitted to the next generation (Dawkins, *1976*; Hamilton, *1964a*, *b*). This implies that some alleles can spread even if they reduce the biological fitness of their carriers. This very concept can be relevant in the context of runaway selection, and consequently, processes that appear to be in conflict with the findings of neo-Darwinian models can take place.

The interallelic selection theory gives rise to the model of **coevolutionary elevator (autoelexis)** (Flegr, *2005*, *2022*; Gardner & West, *2010*). This model also assumes that the reason for the emergence of exaggerated traits is the coevolution of genes for the male trait and the female preference for the specific male trait. The model assumes that there is constant variability in mating preferences among females in the population. Individual females have different tastes and therefore prefer males with different traits, even traits that are not currently present in the population. At the same time, individual males differ in their phenotype. When a trait appears in a male due to mutation and there is a female with a preference for this trait, a runaway process can be initiated. This process promotes the spread of both the male allele for the trait and the female allele for the preference of the trait. A genetic correlation between the two alleles quickly forms, even if they are located on different chromosomes and there is no gene linkage between them. Whenever a female mates with a male with the corresponding trait, for example, a male with a red dot on the head, she increases the chance of transmitting not only the allele responsible for the red dot on the male's head but also the allele for the preference for males with a red dot on the head to the next generation. If the male has a red dot, his father probably had one too. And his mother, who mated with a male with a red dot, probably also had an allele for the preference for males with a red dot. When a female with a preference for males with a red dot mates with a male with a red dot, she passes on not only a copy of her allele for the preference for males with a red dot but also a copy of such an allele present in the male's genome.

From the perspective of the allele for a particular preference, it is advantageous to mate with a male possessing the preferred trait, even if the trait is disadvantageous in terms of natural selection, and offspring carrying it have, on average, lower biological fitness than individuals without the trait. As the theory of intralocus selection emphasizes, each allele "plays for itself," meaning it spreads when it is passed on to the next generation in a greater number of copies than competing alleles, even if those competing alleles provide their carriers with higher viability and fecundity. In this regard, all alleles of all genes are selfish, with their carriers' overall biological fitness being of secondary concern to the alleles

themselves. The coevolutionary elevator model demonstrates that the runaway process can function under much broader conditions than models based on the neo-Darwinian theory of intraspecific selection.

After some time, the new trait spreads throughout the entire male population (fixes), and the runway process of spreading both alleles stops. However, before or after this occurs, a new allele of a gene may appear in the population, capable of expressing its presence externally, perhaps by creating a blue ring around the red dot. If there are females in the population with a preference for a blue-framed red dot at that moment, a new runaway process can be triggered, ultimately leading to the rapid spread of the new trait. This process can be repeated indefinitely. As a result, the originally simple surface ornamentation gradually becomes more complex and increasingly intricate.

The spread of a new secondary sexual trait may initially seem to contradict the sexy sons and sexy males-preferring daughters hypotheses. However, this contradiction is only apparent. These hypotheses address situations where the occurrence of a new trait (e.g., shorter tail feathers) is mutually exclusive with the trait that most females prefer (e.g., longer vs. shorter tail feathers). The coevolutionary elevator model posits that males exhibit the new trait alongside the original traits. Generally, there is no reason for females lacking the allele for preference for the new trait to specifically discriminate against carriers of the new trait. Males exhibiting the new trait (e.g., males with blue ringed red dot) typically possess the same set of secondary sexual traits as males without the new trait (males with red dot). Consequently, they experience the same level of favor or disfavor from the majority of females as other males in the population. However, they also enjoy the additional favor of females with a preference for the new trait.

Indeed, some traits can be mutually exclusive, like a red and yellow dot occupying the same spot on the body. However, alleles that generate new traits without excluding the current expression of the original trait – such as an additional blue ring around the red dot – have a much higher likelihood of initiating the runaway process and spreading via the coevolutionary elevator mechanism than alleles that replace the red dot with a yellow one. Consequently, the entire process is more geared toward the complexification of ornaments rather than their indefinite transformation.

From Beauty to Speciation: Exploring the Coevolutionary Elevator's Impact on Addressable Phenomena and Species Diversification

The coevolutionary elevator model accounts for a variety of previously observed phenomena. Among these is the fact that numerous organisms display remarkable beauty, possessing intricate patterns or structures on their surfaces or exhibiting similarly complex behavioral patterns. Internal organs, on the other hand, are not nearly as beautiful, and in transparent fish, the unsightly asymmetrical bundle of digestive organs is often hidden in a neat, opaque silver pouch. This set of phenomena related to *natural aesthetics* was described by Adolf Portmann and his followers (Komarek, *1997*; Neubauer, *1985*; Portmann, *1964*) as the manifestation of so-called *addressable* and *non-addressable phenomena* (the latter occurring in organisms lacking the capability of vision, such as some marine flatworms). They explained both classes of phenomena as a manifestation of the general tendency of living organisms to self-presentation. However, they did not offer

a specific mechanism or evolutionary significance for this tendency, so Portmann's biology is slowly fading into oblivion, even in its seemingly last stronghold, the Faculty of Science in Prague.

A large part and perhaps even all addressable phenomena can be relatively easily explained as a manifestation of the coevolutionary elevator. Once an allele appears in any gene of a male that can somehow manifest itself externally (self-present), there is a relatively high chance that in the same population, there will be a female who will prefer this particular trait in males. This can immediately trigger the runaway process of the evolutionary elevator, which begins to increase the frequency of alleles for the trait and alleles for its preference at an accelerating pace (in a Fisherian manner). This will happen even if the trait does not bring any other advantage to its bearer, and with sufficient intensity of sexual selection, an allele that harms its bearer will also spread.

In contrast, most newly formed alleles that cannot signal their presence in an individual's genome, and thus cannot utilize the coevolutionary elevator for their spread, have a much lower chance of significantly expanding or even becoming fixed in a population under normal conditions. This applies even to alleles that increase the biological fitness of their carriers and even to those that are dominant and therefore have a positive effect on biological fitness in heterozygotes. In most metazoan species, local populations are so small that the fate of advantageous mutations with a reasonably high selection coefficient is determined more by genetic drift (i.e., chance) than by natural selection. In a small population, a limited number of advantageous mutations and new alleles arise over a unit of time. If it is a species with a truly high effective population size, selection also determines the spread or loss of a mutation. However, in the early stages of spreading a new allele, chance again plays a role in whether the allele will expand enough for its selective advantage to become effectively utilized alongside the element of chance. Moreover, in a large population, the spreading of an allele is usually very slow, and only a small fraction of potentially useful alleles achieve fixation.

The coevolutionary elevator can simplify the fixation of any externally manifesting trait in two ways. The first is the classic runaway process occurring within the population. Due to the existence of positive feedback, alleles for the new trait and its preference spread exponentially within the population, following the principle described by Fisher in the 1930s. In the case of the coevolutionary elevator, the advantage of genetic linkage between the two alleles is also utilized, ensuring that the act of pairing with a suitable mate will support not only one's own genes for the given trait and preference but also copies of these genes found in the mate's genome. This allows for the rapid fixation of both alleles even if the population is truly vast.

The second way of accelerating the fixation of new alleles involves the possibility of a population of males carrying a specific trait and females preferring this trait undergoing speciation, due to their representatives having a preference for mating with one another. This creates a small population of a new species within the large population of the old species, in which both alleles can rapidly become fixed. Species with mating systems that allow for the smooth functioning of the coevolutionary elevator thus speciate more easily and frequently, giving rise to new species. This can provide them with a significant advantage in *species selection* (see also the chapter Evolution by non-individual selection pressures), i.e., competition between evolutionary lineages for the highest

speciation rates and the lowest extinction rates. These lineages (e.g., those with complex ornaments on the body surface) can eventually prevail even at a macroevolutionary scale.

Beyond Visual Traits: Exploring the Role of Acoustic and Olfactory Signals in Runaway Sexual Selection

Visual traits are not the only characteristics that can be the trigger and subject of runaway sexual selection. Acoustic traits, such as individual elements of bird song, can also play a role. This might be the reason why bird songs are so complex and temporally variable. And perhaps this is also why songbirds are such a species-rich group.

In mammals, it is likely that olfactory traits, such as unique body odors, may play a role in sexual selection. In mammals and other vertebrates, major histocompatibility complex (MHC) proteins seem to play a crucial role in determining an individual's body odor. These proteins transport a distinctive set of peptides to the cell surface for each individual. These peptides either originate from proteins synthesized within the cell (the peptides bound to class I MHC proteins, which are present on nearly all nucleated cells in the body) or from proteins absorbed through pinocytosis or phagocytosis from the surrounding environment (the peptides bound to class II MHC proteins, which are found only on certain immune system cells).

MHC antigens bind to peptides derived from both parasites and the body's own proteins. Both types of peptides are equally transported to the cell surface and presented to T cells for inspection. Each T cell contains a unique T cell receptor, with the gene for its synthesis arising during its development through the random combination of several DNA segments, each of which is present in the genome in multiple variants. This receptor, which naturally occurs in multiple copies on the T cell, is capable of recognizing a specific peptide bound to MHC proteins. Cytotoxic T cells recognize peptides bound to class I antigens, and helper T cells recognize peptides on class II antigens, as described below.

As a whole, T cells can recognize an immense number of both existing and non-existing peptides. However, only peptides derived from parasites can be recognized as foreign. During a specific stage of their development, T cells pass through the thymus (hence the name T cells), where those that recognize any peptide on MHC molecules undergo cellular suicide. T cells with a non-functional T receptor, incapable of binding to MHC molecules, also undergo suicide in the thymus. Mature T cells circulating in the body can only bind to MHC protein complexes with a peptide that did not occur in the thymus, such as a peptide derived from a virus. If it is a cytotoxic T cell, it kills the cell presenting the peptide from the virus, thus preventing viral replication. If it is a helper cell, it provides a growth factor to the cell capable of absorbing viral proteins from its surroundings, such as a B cell with a surface immunoglobulin capable of binding to a viral particle, allowing it to multiply.

In most populations of any vertebrate species, there is a tremendous polymorphism of MHC proteins. There are up to hundreds of alleles for each of the several MHC genes expressed in cells. This ensures that virtually every individual in the population has a unique combination of MHC alleles, and as a result, transports a completely unique pattern of peptides to the cell surface from the same sample of proteins (such as proteins from the same virus). Most biologists believe that the primary function of MHC protein polymorphism is to ensure that a parasite, such as a virus, cannot, through point mutations, eliminate the peptides that enable its host species recognize its presence in the cell. Due to each individual of the host species having a unique combination of MHC alleles from their several MHC genes, they transport a different set of peptides derived from the protein of the same virus to the surface of infected cells and present them for inspection by their T-cells. As a result, the virus cannot eliminate peptides recognized by the host's immunity, because which peptides will be targeted by T-cell recognition will differ from one individual to another.

Peptides bound to MHC antigens are relatively short. In the case of class I MHC antigens, which are present on all cells, they have fewer than ten amino acids. Therefore, they can evaporate after being released from MHC proteins and influence individual body odor. It is known that MHC proteins play an important role in sexual selection. Initially, it seemed that females avoid individuals with a similar combination of MHC proteins as themselves. This would allow them to avoid inbreeding or ensure a broader repertoire of MHC gene alleles for their offspring, thus increasing their ability to recognize the largest number of foreign peptides. However, it now seems that the entire process is more complex. Females also seem to avoid mating with males who have too many different MHC gene alleles. This is usually interpreted as there being an optimal degree of heterozygosity in MHC genes – a low number of different alleles results in a small sample of peptides being presented on cells, while too many alleles cause a large percentage of T cells to commit suicide in the thymus, as they recognize a peptide derived from the body's own proteins presented on one of the many MHC gene alleles.

It is possible, however, that polymorphism in MHC genes and the high complexity of the system are created and maintained by a coevolutionary elevator mechanism. If a male, through a mutation, acquires a new MHC gene allele that transports a unique group of peptides to the cell surface, not carried by other MHC alleles, this male will consequently have a distinct odor compared to other males. If, in the same population, there is a female that exhibits a preference for the given odor, a new runaway process will be triggered, which, through the coevolutionary elevator mechanism, will spread both the new MHC gene allele and the female allele for preference of the particular body odor within the population.

It is known that in the genomes of many mammalian species, there are numerous genes for olfactory receptors, and many of these exhibit high polymorphism. This, in itself, may not mean much, as the number of olfactory signals in the environment can be high, and it may be essential for a species to recognize as many of them as possible. What is unusual is that genes for olfactory receptors are among the few groups of genes that are primarily subject to positive selection, meaning that evolution favors change. The vast majority of genes are mainly subject to negative selection, where non-synonymous mutations, those that result not only in a nucleotide substitution in the triplet but also lead to the replacement of the amino acid encoded by the mutated triplet, are constantly eliminated by selection (any change in the amino acid sequence of the respective protein usually harms and reduces the fitness of the mutated individual).

However, there are three groups of genes where the opposite is true, and non-synonymous mutations prevail over synonymous

ones. Firstly, these are genes involved in immunity, such as interleukins or peptide-binding parts in MHC proteins (Hughes & Nei, *1988*). The reason for this is apparent – the selection pressure for evolutionary change is driven by the coevolutionary struggle between the host and parasites. The parasite tries to get rid of peptides that the host's T cells can recognize as foreign through mutations, while the host attempts to generate new MHC gene alleles through mutations that could recognize previously unrecognized peptides in the parasite's proteome (Zemkova et al., *2017*). In the case of MHC proteins, the coevolutionary elevator mechanism, i.e., the coevolutionary cooperation between MHC gene alleles and the allele for preference of the respective odor, could also be the driving force.

The second group of genes exhibiting molecular signs of positive selection for change are those involved in reproduction (Swanson & Vacquier, *2002*). These genes are expressed in gametes and the tissues of reproductive organs. At first glance, it may seem that males and females share common biological interests, specifically producing numerous and high-quality offspring. In reality, however, the interests of both parents can differ significantly. For example, females aim to have their eggs fertilized by the highest quality male in the population, while even low-quality males strive to fertilize the female's eggs themselves. The resulting struggle, occurring at both behavioral and physiological levels, is often intense, and the evolutionary processes stemming from it are rapid. It is known that when one sex is prevented from evolutionarily responding to the other sex's evolutionary tactics (e.g., naive females from a reserve population with no prior contact with the local male lineage are introduced in each generation), males quickly outcompete females in promoting their reproductive interests.

The third group of genes showing clear traces of positive selection (prevalence of non-synonymous mutations over synonymous ones) lacks a widely accepted explanation. These genes are the numerous olfactory receptor genes (Gilad et al., *2003*; Niimura & Nei, *2007*). It is possible that their involvement in the coevolutionary elevator, which ensures the joint spread of new MHC alleles and olfactory receptor alleles responding to the corresponding peptides in species that rely on olfactory cues for mate selection, could account for this observation.

The Role of Coevolutionary Elevators in the Evolution of Excessive Traits: Insights from Plant Sexual Selection

Sexual selection also applies to insect-pollinated plants. In this case, however, the choice of mating partners is not made by individuals of both sexes, but rather through pollinators. Individual plants compete with each other to attract insect pollinators. If pollinators are guided by the relative intensity of expression of a particular trait, such as flower size, they could theoretically cause the development of an excessive trait, as they would preferentially visit plants with the largest flowers. Nevertheless, plants rarely exhibit excessive traits in the true sense of the word, meaning traits that would reduce their carriers' viability.

A likely explanation for the absence of excessive traits is the fact that, in this case, alleles for the preferred trait are present in the plant's gene pool, while alleles for trait preference are present in the pollinator's gene pool. As a result, the coevolutionary elevator cannot function here. A pollinator with a preference for a new trait, such as larger flower size, may help spread the allele for the preferred trait (flower size), but not the allele for the preference of the trait. The pollinator and the plant do not have shared offspring in which both alleles could be passed on simultaneously.

However, a form of Fisherian runaway selection may still occur in plants. A pollinator with a new allele that allows it to prefer a new trait will enable faster reproduction and more successful dissemination of plants with this trait, thus benefiting pollinators that prefer this trait. The existence of this positive feedback loop, which Fisher relied on, is evidently not sufficient to trigger a runaway process that could lead to the development of excessive traits. Therefore, it is possible that the existence of a coevolutionary elevator is a necessary condition for the emergence of excessive traits through sexual selection.

Human Traits Driven by Coevolutionary Elevator: Intelligence, Music, and Immunity?

Runaway sexual selection could have played a significant role in human evolution as well. Although humans do not have obvious excessive morphological traits, such as large antlers, the coevolutionary elevator could still have played an important role in our evolution. One of the key characteristics of our species is the size of the brain and the ability to think. While we cannot assess the ability to think based on paleontological findings, it is highly likely that it correlates well with the size of the cranial cavity. We know that the cranial cavity size increased very rapidly, even though there was no apparent reason for this change at the time. This happened during a period when the environmental conditions and the lifestyle of our ancestors did not change significantly (Mchenry, *1994*).

It is possible that intelligence, and thus the associated brain volume, increased in humans due to sexual selection, and that the human brain essentially represents an excessive trait created by the coevolutionary elevator mechanism. When a large sample of men and women were surveyed about the qualities they would like in a lifelong partner, both men and women assigned the most points to faithfulness out of 11 offered qualities (altruism, dominance, faithfulness, generosity, sense of humor, charisma, intelligence, kindness, masculinity, wealth, and youth). However, when a special technique was used to determine which of these qualities were truly prioritized, faithfulness dropped to the ninth place among male evaluators and eighth place among females, while sense of humor, a trait that likely reflects intelligence, moved to the first place for both. Intelligence itself ranked a respectable fourth place for both men and women (for men, after humor, charisma, and kindness; for women, after humor, kindness, and altruism) (Flegr et al., *2019*).

Another group of traits that play a significant role in mate selection among humans is related to singing and engaging in music. People, especially those in their early reproductive years, devote a lot of time and energy to these activities, and members of our species often achieve considerable virtuosity in both disciplines. Ethological experiments have shown that women preferred suitors who held a guitar case over those who held a sports bag (Gueguen et al., *2014*). Again, it is possible that, just like in songbirds, the coevolutionary elevator contributed to the development of musical abilities and the ability to appreciate music.

As previously mentioned, the coevolutionary elevator may have indeed played a role in shaping the evolution of human individual scents, particularly through the MHC genes that contribute to their composition. This process might have created a preadaptation, see the chapter Preadaptations for a high-quality immune system, which later allowed our species to survive and thrive in dense and populous communities spread over vast, continuous geographic regions. Consequently, the coevolutionary elevator could have laid the groundwork for the ecological success of the human species.

Conclusions

Runaway selection is a complex evolutionary mechanism that contributes to the development of exaggerated secondary sexual characteristics within species through sexual selection. This process entails a multifaceted interplay between female mate preferences, male trait displays, and external factors such as the costs of female choice and mutational bias. The *sexy sons* and *sexy males-preferring daughters hypotheses* highlight the challenge of reversing runaway selection and underscore the adaptive implications of reproductive choices. However, runaway selection might not completely account for the emergence of exaggerated traits. Alternative theories like *coevolutionary elevator*, *indicator*, and *handicap hypotheses* offer valuable insights regarding the initiation and maintenance of extreme traits.

Coevolutionary elevator models, in particular, furnish an improved understanding of the mechanisms driving the evolution of exaggerated traits. These models contribute significant insights into species diversification and the development of various observable and cryptic phenomena, as well as reveal the emergence of intricate patterns and structures in numerous organisms, ultimately providing a more comprehensive perspective on the evolution of beauty and the forces shaping it.

Visual, acoustic, and olfactory signals can also participate in runaway sexual selection, leading to intricate and temporally variable traits in species. Exploring the roles of olfactory signals and their links to MHC gene polymorphism in mate choice and sexual selection further elucidates factors influencing mate choice within vertebrate species. Specifically, in the context of human evolution, runaway sexual selection and the coevolutionary elevator may have played a considerable role in developing unique traits such as intelligence, music, and immunity. These processes may have laid the groundwork for the ecological success of humans across diverse, populated communities and extensive geographic areas.

As the field of evolutionary biology advances, future research may unveil new understanding of the runaway selection process, the coevolutionary elevator model, and their impacts on species diversity, adaptation, and the complexity of life on Earth.

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