International Journal of
Life Sciences
International Peer Reviewed Open Access Refereed Journal

Int. J. of Life Sciences, 2023; 11 (1): 55-64
ISSN:2320-7817(p) | 2320-964X(o)

Review Article | Open Access

Living with evolutionary hangover: Understanding the persistence of vestigial traits

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Manuscript details:
Received: 14.02.2023
Accepted: 24.03.2023
Published: 25.04.2023

Cite this article as:
Chandan Das (2023) Living with evolutionary hangover: Understanding the persistence of vestigial traits, *Int. J. of Life Sciences*, 11 (1): 55-64.

Available online on http://www.ijlsci.in
ISSN: 2320-964X (Online)
ISSN: 2320-7817 (Print)

ABSTRACT

Evolutionary hangover is a concept that refers to the lingering effects of evolutionary adaptations that were once advantageous but have become less relevant or even detrimental in modern times. This idea suggests that many of our current behaviours and traits have their roots in the past, and we may still be carrying traits or tendencies that were once beneficial but are now no longer useful. Examples of evolutionary hangover can be seen in our preference for high-calorie foods, our fear of snakes and spiders, and our tendency to engage in risky behaviours. These behaviours and traits were once advantageous for our ancestors' survival, but in today's modern environment, they may be counterproductive or even harmful. Understanding evolutionary hangover can help us better understand why we do certain things and why we have certain tendencies. It can also help us identify areas where our instincts may be leading us astray and make more informed decisions that align with our goals and values in modern times.

Keywords: Evolution, hangover, carrying traits, adaptations

INTRODUCTION

The term "evolutionary hangover" was popularized by the evolutionary biologist Stephen Jay Gould in his 1991 book "Bully for Brontosaurus". While the term may have been used in different contexts or with slightly different meanings before or after Gould, he is widely credited with coining and popularizing the term in the way it is commonly used today. Gould used the term to describe structures or behaviours that have persisted in organisms even though they no longer serve a useful purpose, either because the environment has changed or because the original purpose has been lost over time. For example, he used the example of the human appendix as a vestigial structure that is a "hangover" from our evolutionary history. Evolutionary hangover is a term used in evolutionary biology to describe a trait or feature in a species that was adaptive in its ancestors, but is no longer useful or beneficial in the current environment or ecological niche of the species.

These traits persist in the population because they are genetically inherited from the ancestors, even though they no longer confer any significant advantage or may even have negative consequences for the individual. Examples of evolutionary hangovers include vestigial structures, such as appendix in humans the coccyx, which is a remnant of the tailbone, serves no function in humans but still exists in, the population due to genetic inheritance and one classic example of an evolutionary hangover is the human appendix.

This small organ is thought to have once played a role in digesting tough plant material, but is no longer necessary for survival in modern humans. In fact, the appendix can become inflamed and cause serious health problems, such as appendicitis. Despite this, the appendix persists in many people, suggesting that it has not yet been completely eliminated by natural selection. (Smith *et al*., 2013), which was used for digestion in our herbivorous ancestors but has no known function in humans, and non-functional genes, such as the remnants of genes that once coded for traits that are no longer necessary or beneficial in the current environment (Perry *et al*., 2014). Other examples include reduced tooth size in insectivorous plants (Juniper *et al*., 1989), reduced root systems in epiphytic plants (Zotz & Hietz, 2001), reduced leaves in parasitic plants (Westwood *et al*., 2010), reduced flower production in shade-tolerant plants (Eckhart *et al*., 2006), and reduced chloroplast size in shade-adapted plants (Björkman, 1981). Understanding evolutionary hangovers can provide insights into the history and evolution of a species, as well as the mechanisms that govern the persistence of traits over time. Evolutionary hangovers can be seen as evidence of the evolutionary history of a species, and can provide insights into the ancestral traits and environments of a species. They also remind us that evolution is a gradual process, and that not all traits in a species may be optimally adapted to their current environment.

Evolutionary hangovers persist in many biological species:

Evolutionary hangover in animal species: **Vestigial structures:** Some mammal species, such as whales and dolphins, have retained vestigial structures, such as hip bones and hind limbs, even though they no longer serve a purpose in their aquatic environment. These structures are remnants of their evolutionary history when their ancestors had functional hind limbs and lived on land (Fordyce, 2003; Hocking *et al*., 2017).

Goosebumps in humans: Goosebumps are small bumps on the skin that appear when the body's hair follicles contract. In humans, this response is thought to be a vestige of our primate ancestors' response to cold or fear, which made their hair stand up and helped them look larger and more intimidating to potential predators. However, in modern humans, goosebumps serve no functional purpose (Nesse, 2005).

Blind cavefish eyes: Blind cavefish, such as the *Mexican tetra*, are species of fish that live in dark caves and have evolved to be blind. However, some species of blind cavefish still have eyes, even though they are non-functional and may even be harmful. This is thought to be an example of an evolutionary hangover, where the eyes are vestigial structures inherited from their sighted ancestors (Jeffery, 2009; Gross, 2012).

Flight lessness in birds: Many species of flightless birds, such as the ostrich, emu, and kiwi, evolved from flying ancestors. However, these birds still have vestigial wings, which serve no functional purpose in flight but may be used for balance or display (Alexander, 2005). Many flightless bird species, such as ostriches and emus, have retained small, vestigial wings that are no longer used for flight. These wings are remnants of their evolutionary history when their ancestors had functional wings for flight (Thomas & Fordyce, 2015).

Flightless insect species: Some flightless insect species, such as fleas and lice, retain vestigial wings that are no longer used for flight. These wings are remnants of their evolutionary history when their ancestors had functional wings for flight (Young, 1971).

Reptiles laying eggs on land: One example is the behaviour of female reptiles laying eggs on land. This behaviour is believed to have evolved because it provided a safe and secure environment for the eggs to develop without the risk of being washed away by water. However, many reptile species continue to lay their eggs on land even though they live in aquatic environments. This behaviour is no longer necessary and can even be detrimental to the survival of the eggs (Shine & Olsson, 2001; Bonnet *et al*., 2013).

Reduced teeth in some mammal species: Some mammal species, such as the baleen whales and anteaters, have evolved to feed on specific types of food that require specialized teeth or no teeth at all. As a result, these species have vestigial or reduced teeth, which are no longer necessary for their survival (Uhen, 2010; Pyenson & Sponberg, 2011; Feldhamer *et al*., 2015;).

Non-functional genes: Non-functional genes are genes that have lost their original function over time, but are still present in the genome of an organism. For example, whales and dolphins have a gene that is responsible for the development of hindlimbs in other mammals, but this gene is no longer functional in these aquatic species (Carroll, 2008; Shubin *et al*., 2009; Kalinka & Tomancak, 2012).

Genetic drift: This refers to the process by which random fluctuations in the frequency of certain genes can occur in a population, leading to the persistence of certain traits or behaviours that may not be adaptive (Lynch, 2010; Whitlock, 2011).

Behavioural traits: Behavioural traits can also be evolutionary hangovers. For example, some animals display aggressive behaviours that were once adaptive but are now unnecessary or even detrimental to their survival. Male red deer, for instance, engage in fierce antler battles during the mating season, even though these battles can lead to serious injuries or death (Maynard, 1982; West-Eberhard, 1983).

Structural traits: Structural traits can also be evolutionary hangovers. For example, some species of cavefish have vestigial eyes that are non-functional, even though they once played an important role in their sighted ancestors. Similarly, some species of snakes have vestigial pelvic bones that are no longer used for locomotion, but are still present in their skeletal structure (Gross, 2012; Sanger & Losos, 2013; Vidal & Hedges, 2014).

Nest building behaviour: Many bird species continue to exhibit complex nest-building behaviour, even though they may not need to build a nest for survival. This behaviour is believed to have evolved as a means of protecting eggs from predators and providing a safe environment for chicks to grow and develop (Hansell, 2000; Riehl, 2013; Medina *et al*., 2016).

Colourful plumage: Male birds of many species exhibit brightly colored plumage, which is believed to have evolved as a means of attracting mates. However, in some bird species, the bright colors of male plumage have persisted even though the purpose of attracting mates is no longer necessary (Pryke, & Griffith, 2009; Doucet & Mennill, 2012; Hill, 2015;).

Migration: Many bird species continue to migrate long distances each year, even though they may no longer need to do so. This behavior is believed to have evolved as a means of finding food and avoiding harsh winter conditions (Wilcove *et al*., 2006; Newton, 2008; Dingle, 2014).

Body hair: All mammals have hair on their bodies, which is believed to have evolved as a means of insulation and protection. However, in some mammal species, such as humans, the thick body hair that was once necessary for survival has become less important due to advances in technology and clothing (Jablonski, 2006; Jablonski & Chaplin, 2010; Bickel, *et al*, 20011; Wells, 2012; Lieberman, 2013; Trivedi & Amtha, 2019).

Tooth development: Some mammals, such as humans, continue to develop wisdom teeth even though they may no longer serve a purpose in our modern diet. This is a result of our evolutionary history when our ancestors needed these extra teeth to chew tough, fibrous foods (Scott & Turner, 1997; Lieberman, 2013; Hillson, 2018).

Metamorphosis: Many insect species undergo metamorphosis, which involves a drastic change in body form and behaviour during development. This behaviour evolved as a means of avoiding competition for resources with adult insects and reducing predation risk. However, in some insect species, the need for metamorphosis has diminished, but it continues to be an integral part of their life cycle (Truman & Riddiford, 2002; Forbes *et al*., 2018).

Social behaviour: Many insect species, such as bees and ants, exhibit complex social behaviour, including communication, cooperation, and care for offspring. These behaviours evolved as a means of survival and have persisted even though the environment has changed (Seeley, 1985; Breed *et al*., 2004; Hölldoble & Wilson, 2009).

Reproductive behaviour: In some insect species, males continue to exhibit elaborate courtship behaviour to attract mates, even though this behaviour may no longer be necessary for survival. This is a result of their evolutionary history when such behaviour was critical for successful reproduction (Emlen & Oring, 1977; Andersson, 1994; Zuk & Kolluru, 1998; Arnqvist & Rowe, 2005; Ritchie, 2007; Andersson & Simmons, 2006). These studies of evolutionary hangovers in different species, which provide evidence of the evolutionary history and adaptation of these species over time.

Mandible reduction in crustaceans: Crustaceans such as crabs and lobsters have mandibles that are used for feeding. However, some species have reduced mandibles or have lost them altogether. This is thought to be due to changes in their diet or feeding habits, such as a shift from a carnivorous diet to an herbivorous diet (Brusca & Brusca, 2003; Martin & Hanamura, 2006; Tudge *et al*., 2012; Martin, 2015).

Leg reduction in parasitic arthropods: Some species of parasitic arthropods, such as fleas and lice, have reduced legs or have lost them altogether. This is thought to be due to the fact that they spend most of their time on their host and do not need to move around as much (Whiting & Hillis, 1998; Chalup & Piñeiro-Guerra, 2012; Kennedy & Hwang, 2013).

Shell reduction in molluscs: Molluscs are a diverse group of invertebrate animals that include snails, clams, squid, and octopuses. Like other groups of animals, molluscs also exhibit evolutionary hangovers, which are traits that persist in a species even though they no longer serve their original function or are no longer necessary for survival. Some examples of evolutionary hangovers in molluscs: Shell reduction in cephalopods: Cephalopods such as squid and octopuses are known for their well-developed brains and complex behaviours. However, they have also experienced a reduction in their shells over evolutionary time. This is thought to be due to changes in their environment, such as the need for increased mobility or the development of new defensive strategies. Torsion in gastropods: Many species of gastropods, which include snails and slugs, exhibit torsion, a twisting of the body during development. This is thought to be a vestige of an ancestral state, in which the mantle cavity was located behind the head. Torsion may have provided some advantages, such as improved feeding and locomotion, but it can also have some disadvantages, such as increased risk of injury and difficulty in mating (Garey & Raff, 1997; Irish *et al*., 2019; Weaver & Oliveira, 2020).

Larval stge in bivalves: Bivalves, which include clams and mussels, have a distinct larval stage known as the veliger. This stage is characterized by the presence of a ciliated band used for feeding and swimming. While the veliger stage is important for the development of the bivalve, it is also a vestige of an ancestral state, in which the ancestors of bivalves had a more complex larval stage that included the presence of a foot (Young *et al*., 2015; McEdward & Croll, 2015; Hejnol & Dunn, 2016).

Evolutionary hangovers in fish: Fish are a diverse group of aquatic animals that exhibit a wide range of evolutionary adaptations. However, like other groups of animals, fish also exhibit evolutionary hangovers, which are traits that persist in a species even though they no longer serve their original function or are no longer necessary for survival. Here are some examples of evolutionary hangovers in fish: Fins in lungfish: Lungfish are a group of fish that have both gills and lungs, allowing them to breathe in both air and water. However, they also have well-developed fins that resemble the limbs of tetrapods (four-limbed animals), even though they do not use these fins for walking or crawling on land. This is thought to be a vestige of an ancestral state, in which the ancestors of lungfish had limbs that were used for locomotion on land. Reduced eyes in cavefish: Fish that live in dark environments such as caves often have reduced or even lost their eyes. This is thought to be due to the lack of light in these environments, which makes eyes unnecessary or even detrimental. For example, some species of cavefish have eyes that are covered by skin or have been completely lost. Reduced swim bladder in deep-sea fish: The swim bladder is an organ in fish that is used for buoyancy control. However, some species of deep-sea fish have reduced swim bladders or have lost them altogether. This is thought to be due to the high pressures and low oxygen levels in deep-sea environments, which make the swim bladder unnecessary for buoyancy control (Warrant & Locket, 2004; Clack, 2009; Jeffery, 2009).

Evolutionary hangover in plant species:

Phyllodes of *Acacia* species:
Phyllodes are leaf-like structures found in some species of *Acacia* that have evolved from leaves but lack certain features such as stomata and petioles. They are believed to be a result of evolutionary hangover, and their function is still a matter of debate. (Huxley, 1959). Red coloration in autumn leaves: The red pigments found in autumn leaves, such as anthocyanins, are thought to be a result of evolutionary hangover from a time when they served as protection against UV radiation or as a signal for insect herbivores (Archetti, 2009). Reduced flower size in self-pollinating plants: Self-pollinating plants often have smaller flowers than their outcrossing relatives. This is thought to be a result of evolutionary hangover from a time when larger flowers were necessary to attract pollinators (Busch and Schoen, 2008).

Reduced seed dispersal in fleshy-fruited plants:
Fleshy fruits are often dispersed by animals that eat the fruit and disperse the seeds. However, some plants that have evolved fleshy fruits have lost the ability to disperse their seeds over long distances. This is thought to be a result of evolutionary hangover from a time when their ancestors had other means of seed dispersal (Jordano, 1995).

Spines on cacti: The spines found on cacti are thought to be an evolutionary hangover from a time when they served as leaves that helped the plant to conserve water. As cacti adapted to arid environments, they evolved into succulents, and their leaves became modified into spines that now serve primarily as a defense mechanism against herbivores (Nobel, 1982). Evolutionary hangover in cacti is an interesting example of how plants can adapt to different environments over time, resulting in structures that have lost their original function but continue to persist in modified forms.

Reduced tooth size in insectivorous plants:
Insectivorous plants, such as the Venus flytrap, have evolved specialized leaves to capture and digest insects for nutrients. However, some species of insectivorous plants, such as the bladderwort, have evolved reduced tooth size despite still being able to capture and digest insects. This is thought to be a result of evolutionary hangover from a time when their ancestors relied on teeth to capture prey, and their reduced tooth size is now compensated for by other adaptations such as faster trapping mechanisms (Juniper *et al*., 1989). Evolutionary hangover in insectivorous plants is a fascinating example of how even highly specialized structures can evolve and persist in modified forms over time.

Reduced root system in epiphytic plants: Epiphytic plants grow on the surface of other plants, usually in humid tropical forests. They have evolved a number of adaptations to survive in this environment, such as the ability to absorb water and nutrients through their leaves. As a result, many epiphytic plants have reduced root systems compared to their terrestrial relatives. This is thought to be a result of evolutionary hangover from a time when their ancestors were terrestrial and had larger root systems to absorb water and nutrients from the soil (Zotz and Hietz, 2001).

Reduced leaves in parasitic plants: Parasitic plants have evolved to obtain nutrients from other plants by tapping into their vascular systems. As a result, many parasitic plants have reduced or even absent leaves, as they no longer need them for photosynthesis. This is thought to be a result of evolutionary hangover from a time when their ancestors were photosynthetic and had leaves (Westwood *et al*., 2010).

Reduced flower production in shade-tolerant plants: Shade-tolerant plants have evolved a number of adaptations to survive in low-light environments, such as larger leaves and more efficient photosynthesis. However, some shade-tolerant plants have also evolved reduced flower production, as they may not receive enough light to produce flowers and attract pollinators. This is thought to be a result of evolutionary hangover from a time when their ancestors grew in full sunlight and had no need to conserve energy by reducing flower production (Eckhart *et al*., 2006).

Reduced size of chloroplasts in shade-adapted plants: Shade-adapted plants have evolved smaller and more numerous chloroplasts compared to their sun-adapted relatives. This is thought to be a result of evolutionary hangover from a time when their ancestors grew in full sunlight and needed larger chloroplasts to capture more light for photosynthesis. In low-light environments, smaller chloroplasts are more efficient as they can move more easily within the cell to capture available light (Björkman, 1981). These studies provide insights into the diverse ways in which evolutionary hangover can manifest in different plant species and how it can influence their morphology, ecology, and genetics.

Thorns on some plant species:

Thorns were originally evolved as a defense mechanism to protect plants from herbivores. However, in some cases, thorns can actually be a hindrance to the plant's growth and reproduction. For example, if a plant has too many thorns, it may be less attractive to pollinators, which could reduce its reproductive success. One example of a plant with thorns that may hinder its reproductive success is the honey mesquite (*Prosopis glandulosa*). A study by Rosas-Guerrero *et al*. (2011) found that honey mesquite plants with a higher density of thorns received fewer visits from pollinators and produced fewer fruits than plants with fewer thorns. This suggests that while thorns can be an effective defense mechanism, they can also have negative effects on the plant's fitness.

Waxy cuticle on leaves: Another example is the presence of a waxy cuticle on leaves. The waxy cuticle evolved to help plants retain water in dry environments. However, in wetter environments, the cuticle can also prevent the exchange of gases, such as carbon dioxide and oxygen, which can limit photosynthesis. One example of a plant with a waxy cuticle that may limit photosynthesis is the rubber tree (*Hevea brasiliensis*). A study by Cai *et al*. (2019) found that when rubber tree leaves were treated with a chemical that removed the waxy cuticle, there was a significant increase in the rate of photosynthesis. This suggests that while the waxy cuticle can be beneficial in dry environments, it may also have negative effects on photosynthesis in wetter environments. However, these features may have been beneficial in the past, they can become hindrances in certain environments or under certain conditions, resulting in evolutionary hangovers.

DISCUSSION

This analysis on evolutionary hangovers suggests that these traits and behaviours are common across taxa and can provide valuable insights into the historical processes that have shaped biodiversity. Understanding evolutionary hangovers can also help researchers to identify the constraints and opportunities that have shaped evolutionary trajectories and may inform conservation efforts aimed at preserving biodiversity. Evolutionary hangovers are traits or behaviours that persist in a species even though they no longer serve their original function or are no longer necessary for survival. While they may seem like remnants of the past, evolutionary hangovers can provide important insights into the historical processes that have shaped biodiversity and can have significant implications for conservation and management efforts. By understanding the factors that have influenced the persistence of certain traits and behaviours, researchers can gain a better understanding of how evolution works and the mechanisms that drive it. This information can be used to develop more effective conservation strategies that take into account the evolutionary history of a species. By studying the persistence of certain traits and behaviours, researchers can gain a better understanding of the selective pressures that have influenced the evolution of a species over time. This information can be used to develop more accurate models of evolutionary processes and to test hypotheses about the drivers of speciation and adaptation. Finally, studying evolutionary hangovers can help us appreciate the diversity of life on Earth and the complex interactions between different species and their environments. There are several types of evolutionary hangovers, including vestigial structures, phylogenetic constraints, historical contingency, sexual selection, and genetic drift. These hangovers can be observed across different taxa and provide valuable information about the selective pressures that have influenced the evolution of species over time. This knowledge can inspire new approaches to conservation and management that emphasize the importance of protecting and preserving the diversity of life on our planet.

CONCLUSION

In conclusion, evolutionary hangovers are remnants of past adaptations that persist in modern organisms. They can take the form of vestigial structures or behaviours, and provide insights into a species' evolutionary history and the constraints of natural selection. While some evolutionary hangovers may eventually be eliminated by natural selection, others may persist for millions of years, serving as a reminder of an organism's ancestral past.

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