Evolution

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Evolution refers to systematic change over time. During the nineteenth century, growing evidence about extinct species such as dinosaurs compelled scientists to explain such findings. Although speculations about evolution had been offered for over two millennia, Charles Darwin, in the mid-nineteenth century, proposed for the first time a coherent theory and mechanism for evolution and amassed supportive empirical evidence. Darwin's theory of evolution by natural selection offers a naturalistic explanation for the existence and diversity of life. Since its presentation in *On the Origin of Species* in 1859, the core of Darwin's theory has survived thousands of empirical tests. Over more than 150 years, scientists have added to, elaborated, and modified details of the theory. Yet, no empirical work has contradicted the core of the theory, and all empirical evidence supports the main tenets: populations change over time; this change is gradual; speciation occurs; all species share common ancestry; and the primary cause of evolution is natural selection.

The evidence for evolution includes empirical results generated within, for example, zoology, biochemistry, morphology, genetics, geography, and paleontology. To reject the evidence for evolution requires also rejecting well-supported results in these and other scientific fields. There is now as much evidence for evolution by natural selection as there is for the theory of gravity and the germ theory of disease (see Coyne, 2009). Furthermore, there is currently no empirically supported alternative theory. Evolution by natural selection is the only known process capable of producing complex biological systems. It is the unifying theory of the life and social sciences.

Biological evolution is change in gene frequencies in a population over time. It occurs gradually, over many generations (not within the lifetime of an individual). Individuals with variations that enhance survival and reproduction will replace those less suitably endowed. As a simple example, no individual anteater's tongue will lengthen due to its continued effort to reach inside an ant hole. Rather, those anteaters with slightly longer tongues secure and eat more ants than those with shorter tongues, and consequently have more offspring, which inherit their parents' "long-tongue" genes. Ant holes represent a selection pressure in favor of longer anteater tongues, and when such a pressure persists in the environment over many anteater generations, "long-tongue" gene frequency will increase in the population, and "short-tongue" gene frequency will decrease.

Selection acts on the replicating unit, which is the gene (and its identical copies). It is convenient to refer to an *individual's* fitness because individuals are the vehicles for genes, but ultimately *genes,* and not individuals, survive over evolutionary time (see Dawkins, 1976). Hence, an accurate description of evolutionary processes includes a gene's point of view. Of course, referring to genes as a having a point of view, or any other anthropomorphic character, is shorthand for ease of communication rather than a literal description of genetic material. In what follows, we refer often to individuals and mechanisms, but genes are the unit of replication, and their evolutionary success ultimately rests on maximizing the number of copies of themselves in the population.

Natural Selection

Natural selection is the primary engine that drives evolution, and the only known process that produces adaptations. Natural selection is beautifully simple, and it has no direction

or goal. Natural selection is a process that depends entirely on the interaction between genes and environments. Evolution by natural selection depends on three facts about populations: inheritance, variation, and differential reproduction. Traits must be genetically heritable and reliably passed from parent to offspring. For example, neck length in giraffes is a heritable trait; differences between individual's neck lengths are due mostly to differences in their genes (which they inherit from their parents).

Individuals in a population have different versions of genes (alleles) that code for different versions of such heritable traits. These variations arise from random mutations that do not lead to evolution, but which provide the raw materials for evolution. The selection of alleles by natural selection is highly nonrandom. The only variations on which natural selection can act are heritable ones; therefore, they must be present in the parents' sex cells at the time of fertilization (or in the case of asexual reproduction, present in the cell lineage from which the offspring arises). Mutations in the somatic cells of parents are not transmitted to their offspring, and therefore are not part of the evolutionary process that builds adaptations. For example, the offspring of giraffes with alleles coding for longer necks inherit those genes, which then interact with the environment to produce longer necks. However, those offspring will not inherit a parent's skin cancer growth, which involves mutations of existing parental skin cells.

Differential reproduction refers to the fact that some individuals propagate their genes more successfully than do others. To propagate their genes, individuals must survive long enough to reach sexual maturity and produce offspring. Survival is a prerequisite for reproduction, but it is the number of successful offspring that determines gene frequency in a population. Hence, reproductive success, more than survival, determines the fitness of an individual. Survival determines fitness to the degree that it contributes to gene propagation. For this reason, "survival of the fittest" does not mean "survival of the strongest." Rather, it refers to the fact that genes carried by successfully reproductive individuals are statistically more likely to proliferate in the population than those carried by less successfully reproductive individuals.

Fitness is a term that applies in the context of a specific environment. An individual that is fit in one environment may not be fit in another. Natural selection depends on gene–environment interaction, so relative environmental consistency is vital for significant allele frequency shifts and the construction of adaptations. Consistent environmental variables that pose reproductive challenges over many generations are referred to as selection pressures. Selection pressures vary across geographic areas and ecological systems. They consist of both the animate and inanimate natural environments.

Adaptations

All organisms recurrently face adaptive problems that ultimately affect reproduction. These include challenges such as avoiding predation, navigation, mate selection, and temperature regulation. Inherited traits that evolved by natural selection in response to such problems are referred to as adaptations. For example, environmental navigation is an adaptive problem for many organisms, and many spend much of their lives in sun-lit environments. A light-sensitive organ such as an eye is one solution to the adaptive problem of navigating in a sun-lit environment. Vision provides many organisms such a significant benefit that eyes (in one form or another) have evolved dozens of times independently in a process called convergent evolution. For example, mollusks evolved pinhole eyes that form a relatively sharp yet dark image but that helps the organism avoid predation; owls evolved eyes so large relative to their skulls that they have become tubular and provide superior nocturnal and binocular vision for hunting; and bees evolved compound eyes that are sensitive to ultraviolet light that helps them navigate.

Most adaptations, such as an eye, are complex and have the appearance of intentional design. Thus, it is easy to interpret them as thoughtfully constructed to serve a specific function, such as vision. However, a closer look at such adaptions reveals their beautiful yet imperfect "design." The human eye, for example, is built "backwards" such that light must pass through multiple tissue layers before it reaches the photoreceptors. A further limitation of the human eye is sensitivity to a remarkably restricted range of the electromagnetic spectrum; surely, we can imagine that X-ray vision might be wonderfully beneficial. Why do adaptations have these limitations? Why are they not perfectly designed?

Constraints on Optimal Design

Several forces constrain optimal design: time lags, historical constraints, lack of available genetic variation, costs, and coexistence with other adaptations (see Dawkins, 1982). Natural selection is always playing "catch-up" with the environment because it does not have foresight. There is often a time lag between an adaptive problem faced recurrently by an organism and the evolution of a mechanism "designed" to solve that problem. In modern times, for example, an organism may find itself in an environment different from the one in which its genes were naturally selected. Fear of snakes but lack of fear of cars illustrates that we are equipped with ancient brains that evolved to solve ancient adaptive problems (e.g., snakes), but not modern, urban-living problems (e.g., cars). Moreover, these differences in feared stimuli persist despite the fact that in modern, urban environments cars are far more likely than snakes to injure and kill people.

Natural selection can only modify an existing trait. Moreover, the modification process is gradual, and every intermediate must be more advantageous than alternative traits; otherwise, the trait will not be selected. Selection is not like an engineer who can start from scratch and optimally design according to predetermined specifications. Natural

selection can only operate on the available variations. Even if there is no optimal variant for a particular environmental pressure, the best one is selected and increases in frequency in the population. All adaptations entail costs and benefits. Because organisms have limited resources, natural selection favors compromises that lead to an overall positive outcome (measured by gene propagation). For example, eyes are metabolically expensive organs to build and maintain, so animals have eyes only to the degree to which they are useful in the environment in which they evolved.

Coexistence with other adaptations produces additional restrictions on an adaptation; it must play well with others. Many evolved mechanisms inhabit the same vehicle (i.e., the individual). Therefore, cooperation with, and facilitation of, other evolved mechanisms are often favored by selection. This is true even if such compromises come at the expense of a single adaptation's design. Given the numerous and substantial hurdles selection must work around, it is a wonder that so many sophisticated, specialized adaptations exist at all.

Sexual Selection

Sexual selection is an important element of natural selection for many species. It is directly related to the reproductive success of individuals within a species, and at times may even hinder survival. Ultimately, differential reproduction leads to changes in allele frequencies in the population. Competition for reproductive success is realized in intersexual selection (i.e., "mate choice," attracting a mate of the opposite sex) and intrasexual selection (competing with same-sex individuals). Intersexual selection drives members of the sex that invests less in offspring (often males) to evolve adaptations to attract members of the sex that invests more in offspring (often females). These adaptations sometimes do not facilitate survival. For example, the extravagant size and ornamentation of the peacock's tail is metabolically costly to grow and maintain, attracts predators, and reduces mobility.

How could such a trait evolve and persist in the population? There are four main hypotheses. According to the runaway hypothesis (also known as the "Fisherian model" or the "sexy son" hypothesis), mate choice initially evolved to facilitate adaptive choices for traits conferring a survival advantage. However, once a trait and a preference for it arise, they produce a self-reinforcing feedback loop (i.e., each becomes a selection pressure for the other). This can explain how, over generations, the peahens' preference for larger, more colorful tails increases, as does that type of tail in peacocks. Those peahens' and peacocks' female offspring inherit this preference, and their male offspring inherit a larger, more colorful tail, which in turn is more attractive to the next generation of peahens, and so on. The healthy mate hypothesis proposes that females prefer as mates males that look healthy, to thereby avoid exposure for themselves and their offspring to infectious diseases and parasites. Diseased peacocks are less likely to be able to maintain an extravagant tail, which leads females to prefer the larger, more vibrant tails in mates.

The handicap hypothesis (also known as the "good genes" hypothesis) posits that females prefer traits that signal the presence of high-quality genes, to increase their offspring's fitness. It is easy to imagine the peacock's tail as a "self-imposed handicap." The fact that a peacock survived long enough to reach reproductive age implies that the genes that built him are good enough to have overcome the challenges posed by his tail. Finally, the chase away hypothesis posits that traits that exploit existing sensory biases will be preferred. For example, the colors displayed by peacock tails might happen to reflect visual biases already present in peahens. Peahens prefer the more brilliant and colorful displays, and peacocks sporting the more colorful tails will be more reproductively successful, regardless of whether those peacocks have better genes or are healthier than rival peacocks.

Sexual selection is a product of the conflicting interests of males and females when they have unequal access to opposite-sex mates. This inequality is explained by Trivers's (1972) parental investment theory; the sex that invests more effort in producing offspring is more discriminating in mate selection than the opposite sex. Males and females have diverging interests and are in conflict. In most species, males invest less in offspring than do females. Consequently, females are choosier about with whom to mate.

One way for males to compete is by adjusting qualities of their ejaculates, in a process referred to as sperm competition. This competition can take place before, during, or after copulation. Some examples include the male dunnock pecking at his partners' cloaca (i.e., reproductive tract opening) to remove a previous male's sperm before copulating; the human penis shaped such that it mechanically displaces another male's sperm from the woman's reproductive tract while copulating; and male bumblebees leaving mating plugs after copulation as a barrier to other males' sperm. In turn, females evolve counteradaptations to maintain their ability to select the sire of their offspring. For example, the females of many insects have sperm storage organs that allow females to select particular sperm with which to fertilize their ova.

Sexual selection is an example of an evolutionary process analogous to an arms race (also referred to as antagonistic coevolution). An evolutionary arms race is an ongoing struggle between competing lineages of coevolving genes, which produces adaptations and counteradaptations in both lineages. As one lineage becomes better at manipulating the other, the latter improves in response to the selection pressure placed upon it by the former. The resulting refinements occur over evolutionary time, between lineages of the opposite sex; between lineages of the same sex in a species; between predator and prey lineages; between parasite and host lineages; and even between lineages of evolved mechanisms within a single population. This process affects the selection of both physical and psychological mechanisms, as demonstrated with the peacocks' tail and peahens' tail preferences.

Kin Selection

Another consequence of natural selection is captured by Hamilton's (1964) kin selection theory. Kin selection is an evolutionary theory that explains the otherwise puzzling existence of eusociality (e.g., sterile worker bees). Individual differential reproductive success cannot account for the existence of worker bees because they do not reproduce and pass on their genes (i.e., genes of a sterile worker). The basic idea behind kin selection is that individuals differentially care for others to the degree that they share genes with them by common descent. This allows for genes that "care" for identical copies of themselves to help and benefit from each other (essentially, to help themselves). Hence, "self-help" genes proliferate in the population, and caring for kin remains a common phenotypic trait (worker bees care for their siblings and mother, the queen). The concept of inclusive fitness broadens the kin selection model to include cases other than genetic relatedness in which "self-help" genes can "recognize" copies of themselves and benefit from helping those copies, in terms of frequency in the population.

As with all adaptations, organisms need not be consciously aware of their adaptations' evolutionary history and their underlying reproductive logic. For example, a squirrel does not calculate the likelihood of relatedness, and therefore of shared "self-help" genes, with other squirrels when it produces an alarm call that benefits others by alerting them to a predator. Natural selection builds simple cognitive "rules of thumb" that solve adaptive problems in the environments in which they evolved (e.g., if squirrels tended over evolutionary time to live with genetic relatives, a squirrel may follow a cognitive rule such as "produce an alarm call to alert others to predators").

Speciation and Common Ancestry

Striking adaptations such as the anteater's tongue, the human eye, and the peacock's tail are just a few exemplars of the stunning diversity found in living species. Speciation occurs when a single population branches into two or more populations that are different enough as to not regularly mate and produce fertile offspring. Speciation rates vary, and not every opportunity (e.g., sudden geographic isolation) guarantees that new species will evolve. Most species go extinct without leaving descendant species. Although speciation does not occur often, when it does occur, future speciation opportunities double. This explains the exponential increase in species over evolutionary time. It is a remarkable fact that although there are millions of species living today, all of us—humans, flies, and starfish—share characteristics. Common to all species are the standard four-letter DNA code, DNA replication processes, and DNA reading and translation into proteins. These similarities strongly support common ancestry.

Every species can be traced to a single ancestor from which it inherited common traits, and every extant species shares an ancestor with every other species. For example, lineages of different modern carnivores (dogs, cats, bears, etc.) can be traced to a common ancestor, the first carnivore from which each lineage eventually branched. Species that have split more recently (e.g., modern humans and modern chimps) have a more recent common ancestor than those that split a longer time ago (e.g., modern humans and modern macaques). Common ancestors are neither of the descendant species; they are a separate species altogether. For example, the common ancestor of humans and chimps is neither human nor chimp, but a third and different species. All life is related genealogically and genetically through common ancestry.

Implications for Psychology and Psychopathology

Evolution by natural selection built all organisms, including humans and their nervous system. Human psychology is a product of the nervous system that governs all conscious

and nonconscious mental phenomena. Psychological adaptations are sophisticated information-processing mechanisms that evolved to solve recurrent adaptive problems in human ancestral history. These specialized mechanisms are sensitive to an extremely narrow sliver of the infinite information available in the environment. Psychological adaptations are sensitive to information that has been recurrently present in the ancestral environment and that, on average, has been useful to solving each adaptation's corresponding adaptive problem. Inevitably, complete descriptions and causal explanations of any psychological phenomena are evolutionary explanations.

Psychopathological phenomena are no exception. From this perspective, a mental disorder might be analyzed as the extreme end of a continuum of the output of evolved mechanisms. Alternatively, a mental disorder might be analyzed as a discrete phenomenon that is the output of evolved mechanisms that are functioning as they were designed by natural selection to function, or as the output of evolved mechanisms that are not functioning as they were designed to function (Wakefield, 1992). An analysis of a mental disorder (e.g., delusional disorder – jealous type, "morbid jealousy") includes identifying a potential evolved mechanism and its range of functioning (e.g., typical sexual jealousy) (Easton, Schipper, & Shackelford, 2006). It is also important to consider the costs and benefits that may have been associated with the target disorder, in both the ancestral past and in the present. Comparing the potential evolved mechanism and its information-processing procedure to that of the target disorder (e.g., which cues are used to generate perceptions of infidelity?) may provide additional clues as to the nature of the potential disorder.

As with all adaptations (e.g., heart, kidney, teeth), psychological adaptations sometimes go awry, and for a variety of reasons (e.g., developmental disturbance, environmental perturbations). Understanding the function and processing of psychological mechanisms clarifies the normal range of species-typical, individual differences, and may help to identify abnormalities as measured by substantial deviations from that range. If we know how and why our information-processing mechanisms function, we can begin to understand how and why they malfunction. An evolutionarily informed approach to psychology and psychopathology creates continuity, coherence, and mutual beneficence between the two, and places them both within the larger picture of the social and life sciences.

Implications for Life and Social Sciences

Evolution by natural selection is the only theory that offers a causal, naturalistic explanation of why organisms are the way they are. All organisms possess adaptations constructed by natural selection. These evolved mechanisms ultimately exist because they propagate the genes that built them. This knowledge provides a unifying theoretical framework for the life and social sciences, and a source from which to generate novel hypotheses. All life and social sciences, not just biology, can benefit from applying evolutionary thinking to theoretical and empirical efforts. An evolutionary metatheory seamlessly bridges gaps within and across disciplines. Engaging in evolutionary thinking enlightens and inspires scientists in multiple realms, as evidenced by the fruitful and growing fields of evolutionary psychology and psychopathology, evolutionary medicine, evolutionary law, evolutionary anthropology, evolutionary economics, and many others.

As Dobzhansky (1973) put it, "Nothing in biology makes sense except in the light of evolution." When evolution by natural selection is properly understood and applied, nothing in the life and social sciences makes sense except in the light of evolution.

SEE ALSO: Behavior Genetics; Fisher, Ronald A. (1890 – 1962); Specific Phobia; Unity of Science

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