Ayden International Journal of Biomedical Research and Technology, Volume 11 (1), 2023 / ISSN: 2997-1497

Original Article

THE DUAL CHALLENGES OF NATURAL SELECTION: ACHIEVING STASIS AND OPTIMIZATION SIMULTANEOUSLY

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Abstract: Students readily conflate evolution, gene-based change in organisms from one generation to the next, with natural selection. Natural selection is the main mechanism driving evolution, but these processes differ and the terms are not synonymous. A key point often overlooked is that in most situations, natural selection generally operates as a normalizing (stabilizing or optimizing) force that reinforces existing phenotypic variation. Paradoxically, natural selection usually works to prevent rather than promote evolutionary change. Relatedly, students often mischaracterize evolution as a drive for perfection. Natural selection is a normalizing yet optimizing process that does not yield optimal (ideal) design, but generates solutions just good enough to get by. This is because selection operates via elimination rather than addition, and because it works with existing phenotype rather than starting afresh. Thus, phenotypes often remain static and exhibit imperfections, ironically providing some of the best evidence for evolution.

Keywords: evolutionary stasis, selection, normalizing, optimizing, imperfection

1. Introduction

In a heavily publicized September 2013 interview with *Radio Times* (UK), Sir David Attenborough, arguably the world's most renowned naturalist, created a stir by flatly stating that human beings, alone among all species on Earth, are no longer subject to the laws of evolution (Furness, 2013). ―I think that we've stopped evolving. Because if natural selection, as proposed by Darwin, is the main mechanism of evolution… then we've stopped natural selection.‖

Attenborough's highly-touted pronouncement made a splash, and critics immediately pounced, but it was really nothing new. For almost a century, experts and outsiders alike have loudly proclaimed the end of evolution (Stock, 2008). In 2000, famed paleontologist Stephen Jay Gould, one of the world's foremost authorities on evolution, made headlines with an essay (―The Spice of Life‖) declaring that ―Natural selection has become almost irrelevant. There's been no biological change in humans in 40,000 or 50,000 years.‖ Gould in turn was echoing geneticist Steve Jones, who likewise argued (1995) that ―Natural selection has to some extent been repealed… Things have simply stopped getting better, or worse, for our species.‖ Like many of their colleagues, Attenborough, Gould, and Jones all suggested that human evolution slowed to a standstill thanks to the oft-cited suspects of medical care, contraception, agriculture, sanitation, and other culturally-induced changes to our environment (Stoneking, 2009). Such arguments have become so familiar that, in the words of anthropologist Henry Harpending, ―We've been almost indoctrinated with this notion that human evolution stopped long ago‖ (Sample, 2007).

Nonetheless, for as many scientists who have hopped on the ―no more evolution bandwagon,‖ an even greater number of researchers continue to issue strongly worded protests objecting to the notion of an end to evolution. The highly visible pronouncements of Jones, Gould, and Attenborough (decades apart) prompted dozens of scientists to pen vociferous rebuttals listing numerous recent changes in the human body, including body temperature, adaptation to altitude, lactose tolerance, and skeletal slenderness (Balter, 2005; Reed, 2008; Stock, 2008).

Indeed, Harpending argued that not only has culture *not* halted our evolution, but that instead it has sharply *accelerated* the pace of human evolution (Hawks et al. 2007; Hancock and DiRienzo, 2008; Cochran and Harpending, 2009). Geneticist Matt Ridley (2012) concurred with Harpending, contending that medicine has relaxed and thereby enhanced natural selection's influence on humans, leading to the appearance of ―a huge number‖ of new gene variants.

What is going on here? How does one make sense of this stunning divide? As with many hotly debated issues, one can easily find persuasive arguments and compelling evidence on both sides. Clearly, whether one considers human evolution to be alive and well or dead and gone is a matter of perspective. The same proves true for countless other species, particularly those often cited as living fossils whose appearance has remained unchanged for hundreds of millions of years—even as their genes and genomes continue to change unabated, in some cases at remarkably rapid rates, including ghost sharks, ginkgo trees, and tuataras (Hopkins and Lidgard, 2012; Werth and Shear, 2014). A recent study (Meyer et al., 2021) indicated that although lungfishes retain a primitive external appearance, their genome is the largest yet sequenced. But if these species' genes continue to evolve, why do their outward forms (**phenotype**) appear to remain strikingly unaltered?

A second crucial takeaway of the perennial ―end of evolution‖ kerfuffle involves distinctions between evolution and natural selection. For many people, including most beginning biology students, these terms are interchangeable and synonymous. However, this is decidedly not the case. As will be explained, one of the oddest paradoxes of biology is that whereas evolution involves change, natural selection, ironically, is nearly always about staying the same.

A third lesson from this debate involves the very reason why species keep changing: namely, continued changes in their environment. Because one does not, outside of rare and unusual circumstances, encounter instances of environments staying fixed for long, one should similarly expect species to keep changing. However, a key part of the reason that species can quickly change to suit new conditions is that as well as natural selection works, species never quite manage to become perfectly adapted. As will be explained, natural selection depends on a process of **optimization**, but the ultimate irony is that it arrives at solutions that are ―good enough‖ yet seldom truly optimal. These paradoxes are simple rather than subtle, and these distinctions are not merely academic or rhetorically semantic. Instead, they lie at biology's heart, and thus deserve a central place at the heart of science education. The passages that follow examine valuable, indeed fundamental, lessons of why natural selection generally means staying the same, and why it follows a process of optimization that rarely leads to **optimality**. In so doing three key questions are explored:

1) What is the relationship between natural selection and evolution?
2) Why do some species appear not to evolve? What lies behind apparent evolutionary stasis?
3) Why do principles of optimal design apply to human endeavors but not natural processes?

2. Evolution versus natural selection

Ask anyone to define ―evolution‖ with a single word and the response, from laypersons and expert scientists alike, will be as immediate as it is obvious: change. Ask people to define ―natural selection‖ and the reply will probably be ―evolution.‖ People are also likely to equate natural selection with ―survival of the fittest‖ (Werth, 2013), a phrase coined by philosopher Herbert Spencer seven years before Darwin's 1859 publication of *The Origin of Species*. Spencer, perhaps best known today for advocating ―Social Darwinism,‖ meant that the strongest, mightiest individuals will best their weaker counterparts, but Darwin, who grudgingly came to accept the popular ―survival of the fittest‖ phrase, quickly pointed out that it referred not to the strongest or smartest individuals, but rather those that best ―fit‖ a particular set of circumstances, such as a desert or polar region. Modern biologists would quickly emphasize that survival is important only if it leads to reproduction, for it is inherited traits (passed along to succeeding generations) that underlie natural selection.

Natural selection is a mindless, mechanistic process, not a goal-oriented agent that ―wants‖ or strives for progress (Werth, 2012). It operates as a modest algorithm of **blind variation and selective retention** (**BVSR**, a phrase introduced by psychologist Donald T. Campbell in 1960) based on differential survival and reproduction, via inheritance of genes creating the variation.

Although natural selection is not the same as evolution, it is widely understood to be the most important mechanism producing organic change, and therefore the principal engine of evolution (considering evolution both as a process and as the resulting process, the chronicle of life's history).

Other key components of evolution include **mutation**, **gene flow** (introduction of new genes into or out of a population via immigration/emigration), **genetic drift** (chance effects experienced by small populations, such as the founder effect or a bottleneck), and **non-random mating** (such as inbreeding). According to biology's basic **Hardy-Weinberg principle** (Stern, 1943), if these phenomena do not occur, populations remain the same: they do not evolve.

It should be obvious but must be noted: evolution is not just any change in organisms, but involves genebased change from one generation of organisms to the next (parent to offspring). Thus, developmental change (at any stage of the life cycle up until death) is not evolution, although developmental instructions and processes themselves readily evolve (Kampourakis and Minelli, 2014; Werth, 2014).

So central is natural selection to evolution that biologists Jones, Gould, and Attenborough essentially equated the two processes, as reflected in their above quotations. This notion—that natural selection and evolution are one and the same—is so widespread and uncontroversial that it has become ubiquitous orthodoxy. However, a crucial but seldom recognized difference is that whereas evolution refers to change, natural selection, oddly enough, routinely works *to prevent change*. This idea is so indisputable that it should be self-evident, but because it is counterintuitive, it nonetheless requires a bit of explanation.

As discussed by evolutionary biologist George C. Williams in his 1997 book *The Pony Fish's Glow*, ―Adaptationist stories are not about evolution so much as its absence.‖ Consider that Aristotle's descriptions of wild plants and animals from 2,500 years ago apply perfectly to the same flora and fauna of our world today. In stunning contrast, crops, livestock, and pets have changed remarkably quickly, as witnessed by the fact that Aristotle's accounts of domesticated species do not fit today's world (Williams, 1997). Some of the most popular dog breeds literally did not exist a century, or in some cases, even decades ago. Why, then, have the descendants of ancient wild animals and plants changed little if at all over extraordinarily long spans of history?

The answer, as Williams explained, is that these organisms effectively ―fit‖ their environment in precisely the way that Darwin described. Although each generation of every species includes new genetic variants yielding different traits, departure from the norm is not welcomed—instead, it is typically culled from the gene pool, leading to reaffirmation of the original condition. The ―selective retention‖ part of BVSR generally does not, under normal circumstances, reward experimentation. This is why the default mode of natural selection is called **normalizing** or **stabilizing selection**: it removes extremes and favors averages, resulting in an accentuation of normal traits (while also producing a normal distribution of characteristics).

Even when evolution occurs via a type of natural selection called **directional selection** (because it pushes the average trait in a particular direction), selection never works additively but always negatively. Like a sculptor chipping away at a block of marble, selection removes unwanted material, culling unfavorable substance to reveal desirable content. A classic example involves a population of peppered moths, most of which are gray but some of which are considerably lighter or darker in color. Which color is adaptive is entirely contextdependent, contingent upon the prevailing background coloration, which makes moths more or less conspicuous to predators who detect them visually (Cook and Saccheri, 2012). There is always variation in the population, and coloration depends (at least in part) on genes, which are inherited and hence passed from parent to offspring in successive generations. Substantial changes in the surrounding environment, as indeed happened when trees darkened from industrial air pollution, and then lightened following adoption of anti-pollution measures, caused evolutionary (directional) shifts of average moth color (Cook and Saccheri, 2012). But for the most part, being ―normal‖ or average is the best option, and this is enhanced by normalizing selection. Those that stray from the norm are culled, and by surviving and reproducing less often, their genes causing lighter or darker forms are discarded or at least tamped down. Absent major environmental change, ―the more things stay the same‖ as the saying goes.

To give another example in human terms, an atypical person with ―outlier‖ traits markedly departing from the norm—such as extremely tall or short stature—is considerably less likely to survive and reproduce as well as a person of normal height (Mitton, 1975). The same applies to any human trait: not just physical but also physiological, biochemical, or behavioral. People surely differ, at least outwardly. We each display a unique face, fingerprints, and voice. However, we do not possess our own hormones, enzymes, or antibodies. With very few rare exceptions, we are all virtually the same inside, and this is a good thing. For those who do not fit the standard, their incongruity is almost always a bad thing.

Even budding biologists will now loudly object that phenotypic variations (departures from the norm) are in fact truly important in enabling adaption to altered environmental conditions. This response is of course as correct as it is straightforward. Without the underlying variation, evolution could not occur.

Still, this does not erase the simple fact that *for the most part, natural selection works to eliminate rather than accentuate or magnify any departures from the norm*.

Consider what would happen if natural selection did work that way. What kind of world would this create, if people were born with fins or wings, if dogs had more or fewer than four legs and two eyes, and if trees tried to live without photosynthesizing? How long would your life have been without properly operating lungs, blood vessels, or digestive enzymes? These are of course extreme examples, but even minor variation (e.g., longer or shorter fingers) is usually unwelcome. Thanks to human intervention (i.e., **artificial selection**), roses need not always be red and violets are not invariably blue, but wild roses and violets display far, far less variation.

Certainly, natural selection can select different variants if a shifting environment so requires. The argument here is not that nature appears static because such shifts occur on vast geologic time scales virtually inconceivable to the human mind. Natural selection can and often does yield evolutionary change so rapid that we see it, particularly in laboratory studies (Lenski, 2010). Thus we know that organisms are capable of evolving far more rapidly than we usually observe, whether in the wild, in the lab, or in the fossil record. Such rapid evolution has been documented not only in microbes but also in large, complex organisms such as the famous Galapagos finches that were vital to the formulation of Darwin's ideas (Weiner, 1994). No, the point is that even over vast stretches of time, natural selection will not, in the absence of new environmental modification, modify an organism's blueprints. In the absence of altered operating conditions, selection operates to maintain the *status quo* (Asher, 2013). Without a ―need‖ to generate variation, it generates no variation.

Again, this is because natural selection's default mode is to reduce variation by eliminating outliers via normalizing selection. Even if outliers survive they generally have decreased evolutionary fitness; that is, they have fewer surviving offspring. This was demonstrated in a famous study conducted in the 1890s by ornithologist Herman Bumpus, who found that sparrows whose wings were larger or shorter than average were less likely to survive. He wrote that ―Selection is most destructive of those birds which have departed most from the ideal type, and its activity raises the general standard of excellence by favoring those birds which approach the structural ideal‖

(Bumpus, 1899). His account explains why normalizing (stabilizing) selection is also sometimes referred to as **optimizing selection**, in that it *optimizes* (improves) the resulting organisms (Smith, 1979; Travis, 1989; Ewens, 1992; Imai et al., 2016). It makes raccoons more raccoon-like and less cat-like or opossum-like. It reaffirms existing species types and thereby magnifies their differences. Why this is so is simple, and, upon brief reflection, painfully obvious: again, natural selection ―creates‖ solely by a process of elimination. It works only by culling individuals that don't ―fit.‖ Natural selection's ―selective retention‖ may be bland and boring—get rid of whatever doesn't match a search image of predefined expectations—but it's hard to argue with its success. Natural selection is the key to evolution precisely because of its stunning, foolproof simplicity. You can't dispute the results.

This applies equally well to our species. A classic example of stabilizing selection involves human birthweight, closely related to infant mortality (Mitton, 1975). Babies born abnormally large or small have markedly lower survival rates, which prevents outliers and preserves the status quo, keeping things the same from one generation to the next. As Williams wrote (1997), ―Even the weak directional selection that does take place is usually thought to be corrective.‖ Geneticist Roger Milkman (1982) summed it up: ―The main day-to-day effect of natural selection is the maintenance of the status quo, the stabilization of the phenotype.‖

In this way, natural selection, despite admittedly being the main driver of evolution, normally works *against* rather than *toward* evolutionary change. This explains why species often change little, even over long stretches of time (Eldredge and Gould, 1972; Eldredge et al., 2005). This is the first major paradox of natural (optimizing) selection, but not the only one.

3. Optimal design

Optimizing selection leads to an additional, second paradox: it does not result in optimality. Once again, this derives from the simple yet effective way in which selection works, by a process not of creative addition but of elimination. By removing less fit organisms, selection creates ―winners‖—other organisms better at surviving and reproducing. But these ―winners‖ need not be the best, and not only because of random, chance events (like droughts, floods, frosts, or forest fires) that sometimes eliminate more fit competitors. One need not be considerably better than one's opponents to win a competition; one need only be a bit better on that day. Just as the winner of an athletic tournament is not always the best team or individual, the winner of natural selection only has to be marginally better during the limited competition. But the main issue here is that one can be rather poorly fit, in the evolutionary sense, so long as one is better than the competition. As the old joke says, you need not outrun an attacking bear; you just need to outrun your companions.

Geneticist Sewall Wright introduced the term **―adaptive landscapes‖** in 1932 to describe this concept, which is typically depicted as a three dimensional topology with various peaks. As organisms become better adapted to local conditions, they rise up a theoretical peak. However, there are nearly always other, more distant peaks representing greater fitness.

The problem is that to reach another peak, an organism, or phenotype, would have to ―descend‖ and cross a valley or plain separating the peaks. This is unlikely. As a result, organisms evolve phenotypes that are ―good enough‖ but not ideal or optimal. Further, evolution often crafts traits as functional compromises between competing demands (Werth, 2012).

For example, the angled head of the human femur, which often breaks in elderly people, arose as a middle ground between a wide birth canal to accommodate our species' exceptionally large braincase and a more stable, column-like leg to accommodate our exceptional bipedal stance. Like a legislative concession negotiated to allow some progress, rather than none at all, compromise means that organisms solve important problems at the expense of others. Imperfection rules.

The obvious upshot is that although optimizing selection can improve existing traits, it virtually never makes them truly optimal. This is obvious and predictable when one realizes that evolution does not begin with fresh blueprints, but instead tinkers with what is on hand.

Alas, the fallacy of optimal design in nature is deeply rooted and widespread, especially among students or others not well trained in biology (Werth, 2009). We marvel at the complex intricacy of organic design and readily consider it perfect—until we realize that imperfections abound. Vestiges of evolution (Shubin, 2008; Werth, 2012) and of embryonic development, such as male nipples, remnants of embryonic circulation (e.g., the fossa ovalis of the heart and ligamentum arteriosum), and remnants of embryonic urogenital development (e.g., the inguinal canal and Wolffian and Mullerian ducts; Werth, 2014), are just some of the numerous imperfections found in the human body. People frequently have bad backs, flat feet, and impacted wisdom teeth to go along with our vestigial ear muscles, vermiform appendix, goose bumps, and ―tail bone‖ (coccyx). Like the panda's ―thumb,‖ a digit-like structure that is not really a thumb at all (Gould, 1980), organisms are jerry-rigged with makeshift solutions. These imperfections yield some of the best evidence that evolution occurs, and show how it works.

We like to believe that form follows function, but evolution generally modifies pre-existing form, such that form frequently precedes and hence determines function.

Consider the enormous phenotypic diversity exhibited within a single species: the domesticated dog (*Canis familiaris*). All of this remarkable variation has been unlocked by **artificial selection** (selective breeding) within a relatively short time. Dogs were domesticated from wolves in Asia just 10,000 years ago in Asia, according to recent studies (Larson et al., 2012). Wolves display remarkably little phenotypic diversity. Although some of the diversity of dogs—in external form, behavior, and so on—may be attributed to mutations that originated and accrued since the split of dogs from wolves, it is difficult to imagine that all of this ―new‖ variation is solely attributable to mutation. Rather, it is likely that the gene pool of wolves, like that of other species, encompasses large stores of genetic variants which are held in check by natural selection (Werth, 2014; Werth and Shear, 2014). When this preserving stabilizing pressure is relaxed via a major environmental change—as, in a way, domestication should be considered—this latent variation is poised to emerge in a rapid burst, just as a coiled, spring-loaded jack-in-the-box is unleashed. The same is true of other domesticated animals and plants, including the wild cabbage, *Brassica oleracea*, that has given rise to many cultivars, including broccoli, cauliflower, Brussels sprouts, and kale.

Of course, mutations can never be tamped down or eliminated, and this is why variation will always be present. It explains why people who breed dogs or cultivars of plants can modify, via culling, the path of artificial selection, but they can never fully control its course or eradicate new mutants. Their work is never done. This also explains why misguided efforts to ―purify‖ humans via **eugenics**, such as Hitler's plan to create a superior Aryan master ace by exterminating unwanted peoples, are doomed to fail. You can remove all mutants from a population, but you can't keep them from recurring. Mutation can of course be a positive force for adaptation, but the ceaseless presence of mutation (springing up eternally like unwanted weeds) is another reason why organisms are not and will never be perfect.

Limits to evolutionary diversity come not only from within but also outside of organisms. Species of tropical regions often tend to display little phenotypic variation. Many tropical trees, insects, and other species tend to be highly specialized due to tight niche partitioning for resources. Because of this, tropical organisms tend to be less abundant that those of species at higher latitudes, although there is great alpha diversity (i.e., an exorbitantly high number of species) in tropical regions.

Nonetheless, when searching for tropical organisms, it is not uncommon for one to find a single representative of a given species but be unable to find another individual. Likewise many tropical species within curated museum collections are represented by a single type specimen**. Conclusion: Imperfect is Perfectly Fine**

Darwin is universally recognized as the founder of evolutionary biology, yet regrettably he is not rightly credited by scientists and historians as the de facto founder of **ecology**. Nonetheless Darwin delineated and defined key concepts of what would become known as ecology (Vorzimmer, 1965). Chief among these are concepts relating organisms to their **habitat** and, although Darwin did not use the term, their **niche**. These concepts are of course central to Darwin's (and our) understanding of adaptation by natural selection, which describes interactions between organisms and their environment: the fundamental basis of ecology.

This is embodied by Darwin's frequent references to the principle, tracing back to Linnaeus, of the **economy of nature**. Darwin grasped that nature was not profligately wasteful but stingy: ―good enough‖ is sufficient to survive and reproduce.

This explains why natural selection often works to stifle phenotypic change, and thus why natural selection often results in an absence of evolutionary change. This stasis results from external (environmental) forces, such as the competition from other organisms, as well as internal (genetic) forces, which limit the solutions that evolution generates. As Kardong (2008) noted, birds would be better off with wings of aluminum or steel; predators would be improved with wheels instead of legs. We do not live in a perfect world—either of our own making, or by natural design. Nature produces many wonders to behold and celebrate, but it does not produce optimality, even as it chiefly operates by a simple, recurrent process of optimization.

The concepts discussed here are simple yet fundamental, and although they are second nature to advanced students and biologists, they are surprisingly counterintuitive to beginning students. It is not immediately obvious that natural selection, the prime mechanism of evolutionary change, typically prevents rather than promotes change, causing phenotypes to remain static. Likewise, it is not obvious that natural selection produces flaws and imperfections rather than flawless perfection. Ironically, the absence of change and the absence of perfection together constitute powerful evidence for the fact of evolution. These basic yet nuanced points are central to modern biology and medicine, and their importance must therefore be stressed by educators.

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