Richard Dawkins on Constraints on Natural Selection

Laith Al-Shawaf[1] and Kareem Zreik[2]
[1]Department of Psychology, University of Colorado – Colorado Springs, Colorado Springs, CO, USA
[2]Department of Economics, Lebanese American University, Beirut, Lebanon

Introduction

Richard Dawkins presents a nuanced take on optimality in his seminal work *The Extended Phenotype*. Dawkins's central argument is that optimality is *not* attainable in nature because of constraints on the process of natural selection. He focuses his discussion on six key constraints: time lags, historical constraints, tradeoffs (which he calls constraints of costs and materials), constraints due to available genetic variation, imperfection due to selection operating at different levels, and constraints due to environmental unpredictability.

Together, these six constraints on optimality offer a deeper understanding of how natural selection works and the kinds of outcomes it produces. They also help lay to rest the erroneous view that evolutionists endorse a Panglossian, pan-adaptationist view in which every aspect of animals' bodies and brains is optimally designed. No credible evolutionist thinks this. Instead, it is widely understood that natural selection builds suboptimal adaptations because of the following key constraints.

Time Lags

Evolution by natural selection is a gradual, step-by-step process. As a consequence, organisms are adapted to *past* circumstances, not present circumstances. If it so happens that the environment has not changed much, then organisms may be well-adapted to their current environment. But if the environment they inhabit has changed, organisms can exhibit maladaptive behaviors simply because environmental change has taken place faster than the slow, cumulative process of evolution by natural selection.

For example, humans are adapted to a time in which food was scarce. As such, our species has evolved taste preferences for calorie-dense foods, fat, and sugar (Buss 2015). In the calorie- and nutrient-scarce environments in which we evolved, these preferences were adaptive. By contrast, in modern environments with an overabundance of fast food, these evolved taste preferences lead to obesity, type II diabetes, and cardiovascular disease. They are no longer adaptive because of the discrepancy between the environment in which we evolved and the one we currently inhabit (Nesse and Williams 1994). Stated differently, the environment has changed too fast for selection to keep up: time lags have rendered our adaptive taste preferences maladaptive in modern environments.

T.K. Shackelford, V.A. Weekes-Shackelford (eds.), *Encyclopedia of Evolutionary Psychological Science*,
https://doi.org/10.1007/978-3-319-16999-6_2172-1

Historical Constraints

History provides a second key constraint on the power of natural selection. When an engineer sets out to build something, she can always start over if something goes wrong in the process. By contrast, natural selection is constrained by millions of years of history. Once a certain body plan or nervous system is in place, certain areas of evolutionary "design space" are closed off for that lineage, and others are rendered less "evolvable" (Dennett 1996). In other words, the phylogenetic background of a species affects what it is capable of evolving next: history constrains evolution.

Consider the case of how jet engines superseded propeller engines (Dawkins 1999). Designers of the first jet engine had a blank canvas from which to construct prototypes. This meant that they were not forced to stick with any initial mistakes or missteps they made – they were free to start from scratch if needed. Moreover, in the case of humanly engineered machines, there is no need for each new step in the process to be an improvement on its predecessor: our foresight enables us to add or change parts that have no immediate effect, but that will eventually improve the machine's functioning when the design is complete.

Natural selection has neither of these luxuries. It cannot start from scratch; it can only build upon what is already there – and every single intermediate step must function better than its predecessor. These constraints limit the power of natural selection to produce optimally designed mechanisms. The consequence is suboptimal designs such as the vertebrate eye, which has a blindspot and appears to be installed backwards (Dawkins 1999). Such a design is suboptimal by engineering standards – but there are limits on natural selection that do not exist in engineering.

Tradeoffs

Every adaptation comes with a cost, and this makes tradeoffs inevitable. For example, gazelles under predation pressure from wolves may evolve longer legs, enabling them to run faster and increase their likelihood of escape. But longer leg bones are more brittle and more likely to break. The gazelle thus faces a cost either way: more robust bones but diminished capacity to flee, or enhanced capacity to flee but more vulnerable bones. Some tradeoffs are simply unavoidable.

The blind Mexican cavefish (*Astyanax mexicanus*) illustrates the same point. Over millions of years, this fish has lost its sight. One hypothesis for how this happened involves tradeoffs: the Mexican cavefish may have lost its eyes because vision requires energy-hungry neurons, and in a pitch-black cave it is a waste of metabolic resources to build and maintain a visual system. In such an environment, those physiological resources can be more profitably channeled toward something else – cell repair, immune function, or a stronger tailfin, for example.

The key point is that every adaptation imposes a cost. These costs lead to unavoidable tradeoffs – and if the tradeoff is truly unavoidable, then it is impossible to optimize the traits being traded off against one another. Because of this, tradeoffs lead inexorably to suboptimal designs.

Available Genetic Variation

Natural selection cannot make new genes arise out of thin air; it can only work with whatever genetic material happens to be available in a population at a given time. As a result, the availability of genetic variation is a key constraint on natural selection. To put it differently, it is impossible for natural selection to produce an adaptation – let alone an optimally designed one – if the relevant genes are simply not present in the population.

It is difficult to exaggerate the importance of this point. The selection pressure for a particular trait may be exceedingly strong, but this will not matter at all if there is no genetic variation underlying that trait. No matter what other factors are in place, the trait in question will not evolve unless there happens to be genetic variation for it in the population. An analogous constraint in human engineering would be the following: it is impossible to build something – no matter how badly we need it – if we simply do not have the raw materials with which to build it.

Artificial selection on cattle illustrates this point. Researchers carried out experiments in an attempt to produce more heifer (female) calves rather than bull calves, as only heifers produce milk. However, it turned out that the genetic variation required for this outcome (producing more female offspring) did not exist, so the experimenters were unable to produce the desired sex ratio (Dawkins 1999). The key point is this: if the relevant genetic variation does not exist, the trait will not evolve – no matter how long natural selection operates and how strong the selection pressure is. Natural selection is unavoidably constrained by the raw material that happens to be available in the population at the time.

Imperfections at One Level Due to Selection at Another Level

Optimality in nature is also constrained by the fact that selection at one level can lead to maladaptive effects at another level. Dawkins describes this in the following way: "selection at the level of the gene can give rise to apparent imperfections at the level of the individual" (Dawkins 1999).

Heterozygous advantage provides an illustrative example. In such cases, a gene may be positively selected because of its beneficial effects when in a heterozygous state. But when in a homozygous state, the effects of such a gene are harmful. For example, the allele for sickle-cell anemia has been selected for because it is protective against malaria in a heterozygous state. However, if a person inherits *two* copies of this allele, he or she will develop sickle-cell anemia, which can be fatal (Allison 1954). It is thus possible for selection at the genic level to have detrimental effects on an organism's health. And because it is impossible to optimize two conflicting levels (genic and individual) simultaneously, suboptimal outcomes are unavoidable.

Mistakes Due to Environmental Unpredictability

Dawkins's final constraint is that of environmental unpredictability. Animals may be exceedingly well adapted to their environments, but since some environmental events are inherently unpredictable, mistakes and missteps are inevitable.

For example, a bird may be well adapted to fly in conditions that are, on average, favorable to flight. But it would not be surprising for the mechanism of flight to fail in a severe hurricane. Unpredictable catastrophes can kill even the most well-adapted organisms. As Dawkins puts it, "it will usually be impossible to cater to every conceivable contingency of detail, and any given animal will therefore frequently be observed to make 'mistakes', which can be fatal" (Dawkins 1999).

Stated differently, organisms are adapted, on average, to the statistical conditions of their environments. But no matter how well designed an animal's flight or vision or bipedalism might be, some environmental events are anomalous and unpredictable. Natural selection is constrained by this unpredictability, and cannot build biological mechanisms that are somehow immune to random environmental accidents. Environmental unpredictability thus acts as a sixth key constraint on the power of natural selection.

Further Constraints: Antagonistic pleiotropy and the conflict between survival & reproduction

These six limits on the power of natural selection to produce optimally designed mechanisms are not exhaustive, but space considerations prohibit us from offering a comprehensive account of all the constraints on natural selection. We briefly mention two others here: (a) conflicts between survival and reproduction and (b) antagonistic pleiotropy.

Survival and reproduction often come into conflict in nature. Because differential *reproduction*, not survival, is the bottom line of evolution, when they do conflict, reproduction inevitably trumps survival (Alcock 2009; Dawkins 1976; Williams 1966). The peacock's tail illustrates this well. It is a burden to survival: cumbersome, metabolically expensive, and a hindrance when it comes to escaping from predators. But peacock genes build these tails anyway because peahens are attracted to them – such is the power of sexual selection. The key point regarding the conflict between survival and reproduction is this: because it is impossible to simultaneously optimize two conflicting outcomes (survival and reproduction), suboptimal outcomes are inevitable. And because differential reproductive success – not survival – is the currency of evolution by natural selection, design for reproduction takes precedence. This often leads to suboptimal design for survival (see e.g., Al-Shawaf et al. 2015).

Antagonistic pleiotropy – a phenomenon in which a single gene may have conflicting effects (Nesse and Williams 1994; Williams 1957) – provides another constraint on optimality. For example, some genes have beneficial effects in early adulthood but detrimental effects in later adulthood. This is the case with genes for testosterone production, as testosterone enhances male reproductive success in early adulthood but increases susceptibility to a wide variety of diseases in later years (Trivers 1985; Williams and Nesse 1991). And because selection is more powerful earlier in the lifespan and weaker later in the lifespan (after reproduction has already occurred; Nesse and Williams 1994; Williams 1957) it will favor genes that help the organism early in the lifespan even if they hurt it later on. In this way, antagonistic pleiotropy – combined with the waning strength of selection across the lifespan – constitutes another key driver of suboptimal design in nature.

Conclusion

Summary

Richard Dawkins's seminal account of the limits of natural selection focused on six key constraints: time lags, historical constraints, constraints due to available genetic variation, tradeoffs, imperfection due to selection operating at different levels, and constraints due to environmental unpredictability. To these six key constraints, we briefly added two more: antagonistic pleiotropy and the conflict between survival and reproduction.

One more theoretical point bears mentioning. Natural selection should not be understood as an optimizing process at all – instead, it is a "meliorizing" process (Dawkins 1999). That is, natural selection does not produce the best design possible by engineering standards – rather, it produces designs that are *better*, on average, than the other available designs in the population at the time.

This definition of natural selection, together with the eight constraints discussed above, explains why natural selection cannot produce optimally designed mechanisms in nature.

We hope this entry helps elucidate the nature of these constraints on natural selection, why they exist, and the important role Dawkins has played in highlighting them. We also hope this entry underscores the erroneousness of the oft-repeated criticism that evolutionary scientists think adaptations are optimally designed. They are not, of course – for all the above reasons. More importantly, it is thanks to evolutionary scientists – key among them Richard Dawkins – that we understand the exact reasons *why* natural selection cannot achieve optimality in nature.

Cross-References

- ▶ Adaptations: Products of Evolution
- ▶ Antagonistic Pleiotropy
- ▶ Evolutionary Mismatch/Time Lag
- ▶ Misconceptions in Evolutionary Psychology
- ▶ Misunderstandings About Natural Selection
- ▶ Natural Selection
- ▶ Optimal Designs
- ▶ Sexual Selection
- ▶ Survival and Reproduction

References

Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2015). Human emotions: An evolutionary psychological perspective. *Emotion Review*, 1–14.

Alcock, J. (2009). *Animal behavior: An evolutionary approach*. Sunderland: Sinauer Associates.

Allison, A. C. (1954). Protection afforded by sickle-cell trait against subtertian malarial infection. *British Medical Journal, 1*(4857), 290–294.

Buss, D. M. (2015). *Evolutionary psychology: The new science of the mind* (5th ed.). Boston: Pearson Education, Inc..

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dawkins, R. (1999). *The extended phenotype: The long reach of the gene*. Oxford: Oxford University Press.

Dennett, D. C. (1996). *Darwin's dangerous idea: Evolution and the meanings of life*. London: Penguin Books.

Nesse, R. M., & Williams, G. C. (1994). *Why we get sick*. New York: Times Books Random House.

Trivers, R. (1985). *Social evolution*. Menlo Park: Benjamin-Cummings.

Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.

Williams, G. C. (1957). Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution, 11*(4), 398–411.

Williams, G. C., & Nesse, R. M. (1991). The dawn of Darwinian medicine. *Quarterly Review of Biology, 66*, 1–22.