Agency in Evolutionary Biology

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1 Why Does Evolutionary Biology Give a Privileged Role for DNA?

Contemporary evolutionary biology is a vast and loosely-connected discipline, so it is very hard to give an all-encompassing account of what it is all 'for', but I am nevertheless going to try. The vast majority of evolutionary biologists are working within a tradition that stems from Charles Darwin's (1859) *The Origin of Species* (hence the label 'Darwinism').[1] However, the contemporary tradition of evolutionary biology has been arrived at after a great discontinuity, which has been described as 'the eclipse of Darwinism'.[2] In this way, the contemporary tradition is often considered to have its foundations laid after the discontinuity in the research tradition stemming from Julian Huxley's (1942) *The Modern Synthesis*. To many critics of contemporary evolutionary biology—not least those like Noble (2006, 2016) concerned with the privileged role of DNA in evolutionary theory, the 'Neo-Darwinism' in *The Modern Synthesis* was where it all went wrong. I am going to address what happened at this critical juncture circuitously, by following the chain of reasoning from the statement of a problem that evolutionary theory sets out to explain and to the capitulation of 'the privileged role of DNA' on the way to its resolution.

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[1] "*The point I want to make now is that all attempts to answer that question* [evolution, especially of humans] *before 1859 are worthless and that we will be better off if we ignore them completely*" (Simpson 1966, p. 1).

[2] This description is a chapter heading of Huxley's (1942) *The Modern Synthesis.*

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1.1 What Is Evolutionary Biology All About?

Although Darwin's *The Origin of Species* represents the intellectual birth of mainstream evolutionary biology, the question at the heart of this book was a much older one: the problem of adaptation.[3] Yet, the way of approaching the problem was comparatively contemporary. Following in the tradition of British empiricism,[4] Darwin sought to explain adaptations with reference to features that were 'external' to the organism. The choice of this approach was heavily influenced by William Paley, who was by no means the originator of this externalism, but was amongst its most effective and influential advocates. Paley contended that the reason why the forms and behaviours we see in nature are one way rather than another has nothing to do with the individuals in question.[5] Instead, Paley argued, the forms and behaviours must be explained by the existence of a Creator. Darwin naturalised Paley's teleological argument and repurposed it to support his theory of adaptation through evolution by natural selection, which is famously based on a great analogy to animal and plant breeding.[6] *The Origin of Species* is, for the most part—and almost to the point of

[3]There are numerous books that frame the question of adaptation within a pre-Darwinian historical context, which trace adaptationist thinking back to the Ancient Greeks (Bowler 1983; Riskin 2016; Stott 2012), especially Aristotle who is even accredited by Darwin (1859) in later editions of *The Origin of Species.*

[4]I am using this term to refer particularly to the philosophical perspective epitomised by David Hume. These views differ from what John Locke referred to as 'continental rationalism', which is equally epitomised by Rene Descartes. 'British empiricism' is a contemporary term, which I use following (Godfrey-Smith 1996).

[5]"*If an account must be given of the contrivance which we observe; if it be demanded, whence arose either the contrivance by which the young animal is produced, or the contrivance manifested in the young animal itself, it is not from the reason of the parent that any such account can be drawn. He is the cause of his offspring in the same sense as that in which a gardener is the cause of the tulip which grows upon his parterre, and in no other. We admire the flower; we examine the plant; we perceive the conduciveness of many of its parts to their end and office; we observe a provision for its nourishment, growth, protection, and fecundity; but we never think of the gardener in all this. We attribute nothing of this to his agency; yet it may still be true, that without the gardener we should not have had the tulip: just so it is with the succession of animals even of the highest order. For the contrivance discovered in the structure of the thing produced, we want a contriver. The parent is not that contriver. His consciousness decides that question. He is in total ignorance why that which is produced took its present form rather than any other. It is for him only to be astonished by the effect*" (Paley 1802, p. 34).

[6]"*One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. … we must, I think, look further than to mere variability. We can not suppose that all the breeds were suddenly produced as perfect and as useful as we now see them; indeed, in many cases, we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to have made for himself useful breeds. The great power of this principle of selection is not hypothetical. It is certain that several of our eminent breeders have, even within a single lifetime, modified to a large extent their breeds of cattle and sheep. In order fully to realise what they have done it is almost necessary to read several of the many treatise devoted to this subject, and to inspect the animals*" (Darwin 1859, p. 23–24).

tediousness, a great catalogue of evidence collected from 'the many treatise devoted to this subject' of selection by breeders. But, in all important senses, Darwin left unchanged the externalist style of reasoning that was championed by Paley wherein individuals have adaptations because of some feature external to those individuals. Such externalism was in great contrast to the thrust of pre-Darwinian evolutionary theory, especially stemming from Lamarck (and continental rationalism).[7] So, what is the aim of evolutionary biology? In sweeping terms: to explain adaptation. But, to the extent that a research tradition is both a problem and a way of approaching that problem,[8] the problem of evolutionary biology is also set within an externalist method of enquiry.

As I have eluded to already, Darwin did not instigate a successful research tradition within his own lifetime—though he was nonetheless well-respected.[9] Instead, there were many apparently insurmountable criticisms, though it is interesting that the constructed history of this time by evolutionary biologists tends to focus on one: "*The biggest blank on the evolutionary map, however, concerned variation and its inheritance. The theory of mutation on a mendelian basis is the first adequate attempt to fill the gap*" (Huxley 1942, p. 109). Or, as was remarked after *The Modern Synthesis* (from which the quote above is taken) was published: "*The question Darwin failed to answer was actually a simple one. Survival of the fittest* what*?*" (Alexander 1979, p. 23). Progress toward an answer to this question started with the studies of the mechanism of inheritance by Gregor Mendel, which led to the development of population genetics. For those involved in this new field, the world of individual organisms rapidly becomes reconceptualised in terms of a genetic accounting.[10] Underlying this

[7] "*All major evolutionary theories before Darwin, and nearly all important versions that followed his enunciation of natural selection as well, retained fealty to an ancient Western tradition, dating to Plato and other classical authors, by presenting a fundamentally "internalist" account, based upon intrinsic and predictable patterns set by the nature of living systems, for development or "unfolding" through time*" (Gould 2002, p. 160).

[8] "*As the student proceeds from his freshman course to and through his doctoral dissertation, the problems assigned to him become more complex and less completely precedented. But they continue to be closely modelled on previous achievements as are the problems that normally occupy him during his subsequent independent scientific career. One is at liberty to suppose that some—where along the way the scientist has intuitively abstracted rules of the game for himself, but there is little reason to believe it. Though many scientists talk easily and well about the particular individual hypotheses that underlie a concrete piece of current research, they are little better than laymen at characterizing the established bases of their field, its legitimate problems and methods. If they have learned such abstractions at all, they show it mainly through their ability to do successful research. That ability can, however, be understood without recourse to hypothetical rules of the game*" (Kuhn 1962, p. 47).

[9] This respect can be seen in Darwin's 'major funeral' in Westminster Abbey, where he was honoured more as a public intellectual than as the father of evolutionary biology (Bowler 1984; Desmond and Moore 1991; Gould 1978; Mayr 1982).

[10] "*Suppose, for example, that a group of distinguished families possess potential or actual versatility to the extent of being able successfully to fill the role, either of a landed gentleman administering his estates, or of a soldier. A is the eldest son, and stays at home; his brother B goes to the wars; then so long as A has some eight children, it does not matter, genetically, if B gets killed, or dies childless, there will be nephews to fill his place*" (Fisher 1914, p. 315).

shift in focus from individuals to genes, there was also a drastic reconceptualization of the very phenomena at the heart of scientific enquiry: "*evolution is a change in the genetic composition of populations*" (Dobzhansky 1937, p. 11).

In this way, *The Modern Synthesis* is actually a rather curious text: on the one hand it was revolutionary, but on the other it was also incredibly dated. For example, Huxley explains natural selection in the form that Darwin presented in *The Origin of Species—i.e.* in the form that was not watertight and hence experienced an 'eclipse'. Huxley thought that population genetics vindicated Darwin's argument, when instead it radically transformed it. For this reason, Peter Medawar is reported to have remarked after Huxley delivered a talk: "*The trouble with Julian* [Huxley] *is that he really doesn't* understand *evolution*" (Dawkins 2013, p. 269). For this reason, the constructed history of this time by mainstream evolutionary biologists gives much more attention to a later work by George Williams (1966), called *Adaptation and Natural Selection.*[11] This book was enormously influential in firmly placing the externalist approach to adaptation from Paley, which is so prominent in Darwin's description of evolution by natural selection, in centre-stage.[12]

Williams brings a new philosophical rigour to the concept of adaptation, only licensing its use under restrictive circumstances: describing a trait as an adaptation is a specific hypothesis about what trait is being considered, what functions that trait serves and what aspect of the environment drives the trait's selection.[13] Central to this reinstatement of Darwin's question of adaptation was an abandonment the individual-centric description of evolution by natural selection on traits and a rehousing of the basic idea within a gene-centric framework.[14] This may seem a little confusing, because Williams is also looked back to for asserting individual selection over group selection, but this assertion is made because Williams is thinking about those entities as genetically-accounted.[10] This line of reasoning was taken to its logical extreme by Richard Dawkins (1976) in *The Selfish Gene*, who extolled Williams' gene-centric approach to evolution with great flare.[15] Within Dawkins' 'seductive' description,

[11] "*Williams'* [1966] *shift in emphasis from individuals to genes went almost unnoticed. His interpretation has not only peacefully coexisted with the synthetic theory for two decades, but has also been typically regarded as a brilliant defence of it. Williams' genic selection, however, has taken on a new-found importance. When genic selection was contrasted with selection on populations, it drew little attention, as most people mentally equated genic selection with individual selection. However, with the publication of Richard Dawkins's The Selfish Gene, genic selection was pitted against individual selection. In Dawkins's work, the significance of Williams' seemingly subtle shift in emphasis became focused and clearly associated with a fundamental shift in the language of evolution*" (Buss 1987, p. 175).

[12] "*I hope that this book will help to purge biology of what I regard as unnecessary distractions that impede the progress of evolutionary theory and the development of a disciplined science for analysing adaptation*" (Williams 1966, p. 4).

[13] "*The decision as to the purpose of a mechanism must be based on an examination of the machinery and an argument as to the appropriateness of the means to the end*" (Williams 1966, p. 12).

[14] "*The natural selection of phenotypes cannot in itself produce cumulative change, because phenotypes are extremely temporary manifestations*" (Williams 1966, p. 23).

[15] "*Was there to be any end to the gradual improvement in the techniques and artifices used by the replicators to ensure their own continuation in the world? There would be plenty of time*

there is a definite hardening of what evolutionary biology is all about. When individuals are viewed as 'throwaway survival machines', attention necessarily refocuses on what is more permanent—the genes. But, one might think, surely there are other entities that could have enough permanence to also be an important part of evolutionary change? Dawkins gives a thorough exhibition of this point to discuss why genes take centre-stage: "*What, after all, is so special about genes? The answer is that they are replicators*" (Dawkins 1976, p. 191). Thus, whilst biologists might say 'genes', it is really replicators that are at the heart of evolutionary explanations. As Dawkins described, replicators have a degree of permanence unlike any other biological entities because they have the stability, fecundity and fidelity (of replication) to survive on evolutionary timescales. Whilst Dawkins does flirt with the idea of a second replicator within human culture (coining the term 'meme'), he does not think that biological evolution is impacted by any replicator other than genes[16]—and mainstream thought still concurs with this opinion.[17] The hard-won replicator perspective on evolution is widely celebrated because it makes us think clearly about 'what' is being selected.[18]

So, what is evolutionary biology all about? In the broadest sense, it is about how living things change over the generations. But, for the most part, this line of enquiry is about the genetics of adaptation: why we see one trait rather than another, from the

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for improvement. What weird engines of self-preservation would the millennia bring forth? Four thousand million years on, what was to be the fate of the ancient replicators? They did not die out, for they are past masters of the survival arts. But do not look for them floating loose in the sea; they gave up that cavalier freedom long ago. Now they swarm in huge colonies, safe inside gigantic lumbering robots, sealed off from the outside world, communicating with it by tortuous indirect routes, manipulating it by remote control. They are in you and in me; they created us, body and mind; and their preservation is the ultimate rationale for our existence. They have come a long way, those replicators. Now they go by the name of genes, and we are their survival machines" (Dawkins 1976, p. 19–20).

[16] "*My primary intention [by introducing memes], however, was not to make a contribution to the theory of human culture, but to downplay the gene as the only conceivable replicator that might lie at the root of a Darwinian process. I was trying to push 'Universal Darwinism' (the title of a later paper, based on my lecture to the 1982 conference commemorating Darwin's death). Nevertheless I am delighted that… others have run, so productively, with the meme ball*" (Dawkins 2013, p. 280).

[17] That cultural variants are not viewed as replicators is not universally agreed upon, but the argument on both sides has become dominated by what words imply. For example, those in favour of memes (*e.g.* Dennett 2017) cite those who are not in favour as supporting their argument (*e.g.* Richerson and Boyd 2005)—despite explicitly rejecting the term 'meme' because it implies that cultural variants are replicators. In general, I would favour the approach of Richerson and Boyd's perspective because it explicitly acknowledges that the mechanism of cultural inheritance is critical to exactly what is being preserved (and does not loosely apply the replicator concept in the absence of a clear understanding of what is replicated).

[18] "*If a genetic change that lengthens the bone also curves the eyebrow, then our adaptive explanation should recognise that; we should be interested in the genetic differences that give rise not merely to differences in toe-length but to differences in toe-length-plus-eyebrow-shape, even if eyebrow shape should turn out to be selectively neutral. This is an answer that would not have been obvious to the organism-centred view of classical Darwinism but comes readily to a theory that is gene-centred*" (Cronin 1991, p. 107).

externalist perspective of the features of the environment that lead to the selection of some genetic variants rather than others.

1.2 What Is Evolutionary Biology's Concept of Agency?

I have set evolutionary biology firmly on the philosophical foundations of British empiricism. In this light, unsurprisingly, evolutionary biology's concept of agency is very much in-keeping with this tradition[19] in viewing agency as a metaphor—not a 'fact of nature'. Consequently, there is no problem in talking about genes, individuals or groups as agents, but there is a need to be disciplined. Agency is a useful way of talking about entities that take decisions, so can in principle be applied to many biological entities. But, as Williams (1966) argues in *Adaptation and Natural Selection*, we should not confuse scenarios where a single or multiple agencies are at work because the outcome can be very different (which was the cause of Wynne-Edwards' group selection controversy).

Evolutionary biologists tend to use this concept of agency in very loose ways. For example, although I have stated that agency can be a useful way of talking about genes, individuals or groups, in each case most evolutionary biologists discuss individuals and groups as genetically-accounted (*i.e.* as collections of genes). Because natural selection acts on phenotypes and acts by changing genotypes, evolutionary explanations often focus on a genotypic change but explain it via the phenotypic consequences of competing genotypes. The blurring of this replicator-vehicle distinction is something of a bad habit, but it can make arguments much easier to follow by observing the convention that the 'individual' refers to whatever genotypes of that individual are currently relevant. I would also add, here, that there is now a thriving research tradition stemming from Leo Buss's (1987) *The Evolution of Individuality* where the coherence of biological entities as discrete individuals is understood as a derived trait along a continuum of individuation at different phenotypic (or vehicular) levels across the diversity of current lifeforms (see also Maynard Smith and Szathmáry (1995) *The Major Transitions in Evolution*).

One may wonder, how does this concept of agency gel with common-sense notions like free will? When *The Selfish Gene* was published, I think that the philosophical

[19] "*For my part, when I enter most intimately into what I call myself, I always stumble on some particular perception or other, of heat or cold, light or shade, love or hatred, pain or pleasure. I never can catch myself at any time without a perception, and never can observe any thing but the perception. When my perceptions are removed for any time, as by sound sleep, so long am I insensible of myself, and may truly be said not to exist. And were all my perceptions removed by death, and could I neither think, nor feel, nor see, nor love, nor hate, after the dissolution of my body, I should be entirely annihilated, nor do I conceive what is further requisite to make me a perfect nonentity. If any one, upon serious and unprejudiced reflection, thinks he has a different notion of himself, I must confess I can reason no longer with him. All I can allow him is, that he may be in the right as well as I, and that we are essentially different in this particular. He may, perhaps, perceive something simple and continued, which he calls himself; though I am certain there is no such principle in me*" (Hume 1738, p. 134).

impact of the idea that your genes may have contrary interests to your own presented the 'self' as something of that old Cartesian duality in suggesting a 'ghost in the survival machine'. This is not what evolutionary biology implies. Instead, following empiricism, the general view is one of compatibilism between causal determinism and human freedom[20]: all events are seen as part of chains of cause and effect, irrespective of whether or not those causes or effects are necessarily observable, and human freedom is viewed as a subjective statement about our incomprehension of how our own causal mechanisms work (rather than inviting speculation on whether or not there are unaccounted supernatural sources of causation).

1.3 Why Does Evolutionary Biology Give a Privileged Role for DNA?

I have stated, in broad terms, that evolutionary biology is about how living things change over generations, and this means understanding why we see one trait rather than another, from the externalist perspective of features of the environment that lead to the selection of some genetic variants rather than others. So, when thinking about the claim that evolutionary biology gives a privileged role to DNA, there are two basic responses here. The first is to deny that evolutionary biology does give a privileged role to DNA in its explanations of how traits change. I think it would be possible to argue that this misunderstands the way in which genetic explanations of adaptation draw links between the environment and DNA, as a hypothesis that connects some external feature of the environment with some internal feature of individuals. The second is to accept that there is a kind of privilege at work, which is afforded to replicators. As the only widely-accepted replicator is the gene (*i.e.* DNA), mainstream evolutionary biology is principally about the genetics of adaptation. Most evolutionary biologists would launch into the first response, but what would follow would be a rather dull, long-winded case-by-case exposition of paradigmatic examples of how evolutionary biology asks a question and finds its answer in a genetic

[20] "*There is a doctrine about the nature and place of the mind which is prevalent among theorists, to which most philosophers, psychologists and religious teachers subscribe with minor reservations.… The official doctrine, which hails chiefly from Descartes, is something like this. With the doubtful exceptions of the mentally-incompetent and infants in arms, every human being has both a body and a mind. Some would prefer to say that every human being is both a body and a mind. The body and the mind are ordinarily harnessed together, but after the death of the body the mind may continue to exist and function. Human bodies are in space and are subject to mechanical laws which govern all other bodies in space. … But minds are not in space, nor are their operations subject to mechanical laws. … Such in outline is the official theory. I shall often speak of it, with deliberate abusiveness, as "the dogma of the Ghost in the Machine." I hope to prove that it is entirely false, and false not in detail but in principle. It is not merely an assemblage of particular mistakes. It is one big mistake and a mistake of a special kind. It is, namely, a category mistake. … [p. 66] … In short, then, the doctrine of volitions is a causal hypothesis, adopted because it was wrongly supposed that the question, 'What makes a bodily movement voluntary?' was a causal question*" (Ryle 1949, p. 17 and p. 66 as marked).

difference. But I am not really sure that gives a serious treatment of the criticism, which I think is less about paradigmatic examples and more about the way in which the genetic focus of research can *by assumption* exclude alternative (and interesting) sources of explanation from the enquiry. In this way, I am going to only address this second response.

Claims of replicators that are built of other materials than DNA are controversial, but they are 'in the air' at the moment with the rise of epigenetics. These are not woolly suggestions of 'memes' or suchlike, which have dropped out of favour because it is not clear that the study of 'cultural variants' really gains very much from the analogy to genes (because the mechanism of genetic replication is nothing like how organisms learn).[15] This is actually a critical point: the 'eclipse of Darwinism' was made possible by the fact that Darwin's argument in the absence of a mechanism of inheritance was not guaranteed to be correct. For a non-DNA replicator, the mechanism of inheritance would have to be known for it to be more than an interesting speculation—and perhaps some epigenetic systems are sufficiently well-characterised to be worthy of exploration.

What would need to be demonstrated to evidence a non-DNA replicator? I don't view this as a systematic answer, but there would (at least) need to be a clear demonstration that the candidate biochemical was capable of traits that are independent from variation in the DNA-replicator. Consequently, instances where a candidate biochemical is inherited but not replicated would be insufficient. These might include, for example, regulatory biochemicals that are given by a mother to her unborn infant during pregnancy to 'prime' that individual for the environment they are about the experience. Even if these molecules were inherited across multiple generations, they would only survive on evolutionary timescales if they were being replicated. Regeneration of a regulator does not count as replication, because it is still under the control of the DNA-replicator. That is not to say that I, as an evolutionary biologist, do not find this fascinating, but I would tend to view priming as interesting from a different perspective. The question that interests me is about the selection on the genetic variant that enables priming rather than whether or not individuals have a primed phenotype. To date, and to my knowledge, there are not epigenetic molecules that are anything more than inherited-regulatory molecules that act as primers.[21]

For those interested in epigenetic replicators, I think there is one consideration that is always worth bearing in mind. Even if a non-DNA replicator were discovered, which I would keep an open mind toward: how would evolutionary biology change were a non-DNA replicator discovered? I would suggest, not very much. The vast majority of genetic explanations of adaptation would still hold, because the vast majority rest on the experimental manipulation of individuals with different genetic variants in order to confirm what feature of the environment selects a particular genetic variant (and its associated traits). Given this, genetic change must be the predominant explanation of how living things evolve. However, a non-DNA replicator would introduce a new dimension for evolutionary biology. Just as the quirks of the genetic mechanism influence how traits evolve, quirks of the new replicator's

[21] There is a thorough Neo-Darwinian discussion of epigenetics in Haig (2007).

mechanism would presumably do likewise. And, I would suppose, there would also be room for conflict between types of replicator. In the history of life on earth, it is generally thought that there have been other types of replicator and that the genetic code (built on DNA) has selectively out-competed other systems because it is a good medium of replication.[22] But, it is not widely held that other types of replicator beyond those built from nucleic acids are important for the 3.8 billion years of life on earth that we currently know about. And, of course, if there were convincing evidence to contrary, opinions would change.

So, why does evolutionary biology give a privileged role to DNA? Given that evolutionary biology is trying to explain why traits change over time in one way rather than another, evolutionary biology privileges DNA in its explanations because the only genes (*i.e.* DNA-replicators) can persist on the relevant evolutionary timescales.

2 Why Is Popper's 'Active Darwinism' Problematic?

I have presented an explanation of why evolutionary biology is set up the way it is, and now I want to turn to the alternative concept that was advocated by Popper and pushed for with renewed vision by Noble.

2.1 What Is Popper's Reading of Evolutionary Biology?

Popper's earliest evolutionary ideas were first expressed in *The Poverty of Historicism* (1957) and came to the fore in *The Logic of Scientific Discovery* (1959) where the growth of knowledge was described as a process of cumulative error elimination. But Popper did not see an immediate parallel with his theory of scientific progress and evolutionary biology. By the time of his *Intellectual Autobiography* (1974), Popper started to make these connections but was rather wary of 'Darwinism': "*I have come to the conclusion that Darwinism is not a testable scientific theory, but a* metaphysical research programme—*a possible framework for testable scientific theories*" (p. 134). For him, this rests of the premise that: "*Darwinism does not really* predict *the evolution of variety. It therefore cannot really* explain *it. At best, it can predict the evolution of variety under "favourable conditions". But it is hardly possible to describe in general terms what favourable conditions are—except that, in their presence, a variety of forms will emerge*" (p. 136). It is nonetheless clear that evolutionary biology is especially problematic for his understanding of scientific progress, but he firmly states: "*And yet, the theory is invaluable*" (p. 137). In this early interaction, I think we can see how Popper is seeking to isolate a specific strand

[22] These ideas are put forward by Cairns-Smith (1982), and enthusiastically discussed by Dawkins (1986). A more modern treatment is given by the seminal Maynard Smith and Szathmary (1995).

of evolutionary biology as 'Darwinism', as opposed to a more general evolutionary approach which he sees himself as a contributor toward.

Following on from ideas developed in the Spencer Lecture (1961) entitled *Evolution and the tree of knowledge*—which was the basis of a chapter in *Objective Knowledge* (1972), Popper controversially expresses dissatisfaction that evolutionary biology can adequately explain cumulative adaptation, following the suggestions of others that there must be 'orthogenetic trends' to funnel variation in specific directions. But at the time of completing *Objective Knowledge* (1972), unambiguously stated that the "*Neo-Darwinist theory of evolution is assumed*" (p. 242), and he went on to elucidate twelve theses on which evolutionary theory rests, which can be broadly summarised en-masse as applying his thinking of cumulative error elimination within scientific progress to nature. I would suggest that he was starting to see his ideas on the growth of knowledge within the broader context of evolutionary thought (*i.e.* seeing epistemology as an evolutionary science), alongside a long-standing unease with something in the contemporary science. Popper's insistence that there is a common mechanism at work within scientific progress in knowledge and adaptive evolution in nature[23] was in tune with the *zeitgeist*, where there was enthusiasm for 'Universal Darwinism'[24] and the broader development of 'evolutionary' subdisciplines (most notably) in economics, computer science and psychology.

Although it is not clear at exactly what stage Popper read various works of Samuel Butler, especially *Evolution: Old and New* (1879) where the basic distinction between 'active' and 'passive' Darwinism is first made,[25] Popper acknowledges a debt toward him in his *Intellectual Autobiography* (1974) whilst expressing a general disdain

[23] "*In my opinion, passive Darwinism turns out, when confronted by active Darwinism, to be a mistaken interpretation of the process of adaptation. Adaptation is, I suggest, essentially a trial and error learning process that extends over many generations. … [p. 121] … We should regard the whole of evolution as a huge learning process going in all sorts of directions and specialisations*" (Popper 1986, in Niemann 2014, p. 120 and p. 121).

[24] "*My general point is that there is one limiting constraint upon all speculations about life in the universe. If a life-form displays adaptive complexity, it must possess an evolution mechanism capable of generating adaptive complexity. However diverse evolutionary mechanisms may be, if there is no other generalization that can be made about life all around the Universe, I am betting it will always be recognizable as Darwinian life*" (Dawkins 1983, in Bendall 1983, p. 423).

[25] "*In like manner we say that the designer of all organisms is so incorporate with the organisms themselves—so lives, moves, and has its being in those organisms, and is so one with them—they in it, and it in them—that it is more consistent with reason and the common use of words to see the designer of each living form in the living form itself, than to look for its designer in some other place or person. Thus we have a third alternative presented to us. Mr. Charles Darwin and his followers deny design, as having any appreciable share in the formation of organism at all. Paley and the theologians insist on design, but upon a designer outside the universe and the organism. The third opinion is that suggested in the first instance, and carried out to a very high degree of development by Buffon. It was improved, and, indeed, made almost perfect by Dr. Erasmus Darwin, but too much neglected by him after he had put it forward. It was borrowed, as I think we may say with some confidence, from Dr. Darwin by Lamarck*, and was followed up by him ardently thenceforth, during the remainder of his life, though somewhat less perfectly comprehended by him than it had been by Dr. Darwin. It is that the design which has designed organisms, has resided with, and been embodied in, the organisms themselves" (Butler 1879, p. 24–33).

for other 'evolutionary philosophers'. Many of the concepts of Popper's Medawar Lecture (1986, published in Niemann 2014) are within Butler's *Evolution: Old and New*, but I suspect that Popper arrived at Butler's perspective semi-independently in marrying together a dissatisfaction with a specific strand of evolutionary thought and the comparisons with (and generalisation of) his ideas on the growth of the scientific knowledge.

Within the Medawar Lecture, Popper clearly expressed an understanding of the essential aim of what evolutionary biology was about,[26] but disagreed with much of the language in which ideas are presented. This disagreement led him to discuss natural and sexual selection as competing theories,[27] when most evolutionary biologists would the latter as a subcategory of the former. Popper viewed the role of organisms' preferences for choosing their own niche to be broadly ignored with contemporary evolutionary theory,[28] and consequently asserted a much greater role for problem-solving (*i.e.* learning) in the general picture of how organisms are selected. Nevertheless, I think is important to remember is that Popper was contrasting two forms of Darwinism, in that he wasn't suggesting that Darwin's research tradition was 'wrong'—or advocating some alternative like Lamarckism.[29] Instead, I think his aims in the Medawar Lecture were more in the vein of stating some things that appeared odd within the framework of contemporary evolutionary theory from the opinion of an outsider. And, in short, what struck him as odd was evolutionary biology's concept of agency.

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[26] "*My problem exists because some excellent Darwinists even believe that evolution can be fully explained by only two things: (1) The variability of the genome whose variations are obviously a matter of chance are completely independent of the organisms' activities and preferences; and (2) The physical environment, where 'physical' may include, of course, the physical presence of other organisms*" (Popper 1986, in Niemann 2014, p. 119).

[27] "*Darwin, as you all know, believed in sexual selection. And he believed that sexual selection was a kind of natural selection. But this is only if we take the niche of the male, to which the female belongs, as the niche that is here important. It can be easily show, all of you can think of this when you go home, that if we take a niche that covers both male and female, then sexual selection is a refutation of natural selection. So it depends on the concept of niches whether sexual selection fits into the scheme of natural selection or refutes it. If you take the niche of the male, then the female is part of the niche and the male must please the female by such things as tail or horns, or I do not know what, which may not be very useful for natural selection. But if you take the niche for male and female together, then most of the examples of sexual selection are a worsening of adjustment, of the adaptation, to this common niche. They are an improvement of adaptation to the niche of the male and a worsening of adaptation to the common niche of male and female*" (Popper 1986, in Niemann 2014, p. 127–128).

[28] "*One of my assertions is that the preference for better niches is the main thing that leads to Darwinian evolution. The organisms are active. They search a better niche. And then this niche, this environment, ensures somehow that the better adapted organisms leave more offspring. And in this manner we get specialisation and more adaptation*" (Popper 1986, in Niemann 2014, p. 122).

[29] "*I do not defend Lamarckism as it is today called, that is to say, the inheritance of acquired properties*" (Popper 1986, in Niemann 2014, p. 127–128).

2.2 What Is Popper's Concept of Agency?

Popper defends a common-sense notion of agency, which he exclusively attributes to organisms, based on the fact that you have free will in the very literal sense that you have real choice that is not determined by any prior events (*contra* causal determinism)—but it is fair to say that his views here are quite hard to discern. Prior to the Medawar Lecture, Popper takes the view that human agency is somewhat exceptional in contrast to other animals' agency—though we share some basic features.[30] But, whilst human knowledge is primarily learnt about their world and consequently agency develop as an ability to make choices,[31] animal knowledge is primarily genetic—having been acquired through natural selection.[32] Popper clearly had an uneasy relationship with what he referred to as either 'materialism'[33] or 'determinism'[34]—but what I will refer to as (British) empiricism. My reading is that Popper struggled to work out what kind of a claim he was wanting to make: was free will a claim about our imperfect understanding of human behaviour or a claim about how humans are? Here, Popper sided with rationalism rather than empiricism, to assert that consciousness (and hence free will) is an undeniable objective fact.[35] To a rationalist, consciousness is the first and most undeniably true fact of existence because it does not rest on anything other than introspection. But, following

[30] "*I assert that every animal is born with expectations or anticipations, which could be framed as hypotheses; a kind of hypothetical knowledge. And I assert that we have, in this sense, some degree of inborn knowledge from which we may begin, even though it may be quite unreliable. This inborn knowledge, these inborn expectations, will, if disappointed create our first problems; and the ensuing growth of our knowledge may therefore be described as consisting throughout of corrections and modifications of previous knowledge*" (Popper 1972, p. 258–259).

[31] "*It seems to me of considerable importance that we are not born as selves, but that we have to learn that we are selves; in fact we have to learn to be selves. … [by] developing theories about ourselves*" (Popper and Eccles 1977, p. 109).

[32] "The believer—whether animal or man—perishes with his false beliefs." (Popper 1972, p. 122)

[33] "*I do not claim that I have refuted materialism. But I think that I have shown that materialism has no right to claim that it can be supported by rational argument—argument that is rational by logical principles. Materialism may be true, but it is incompatible with rationalism, with the acceptance of the standards of critical arguments; for these standards appear from the materialist point of view as an illusion, or at least as an ideology*" (Popper and Eccles 1977, p. 81).

[34] "Indeterminism—*or more precisely, physical indeterminism—is merely the doctrine that not all events in the physical world are predetermined with absolute precision, in all their infinitesimal details*" (Popper 1972, p. 220).

[35] "*We have to assume, difficult as this may be, that it [consciousness] is a product of evolution, of natural selection. Although this might constitute a programme for a reduction, it is not itself a reduction, and the situation for the reductionist looks somewhat desperate; which explains why reductionists have either adopted the hypothesis of panpsychism or why, more recently, they have denied the existence of consciousness (the consciousness say, of toothache) altogether. Though this behaviourist philosophy is quite fashionable at present, a theory of the nonexistence of consciousness cannot be taken any more seriously, I suggest, than a theory of the nonexistence of matter. Both theories 'solve' the problem of the relationship between body and mind. The solution is in both cases a radical simplification: it is the denial either of body or of mind*" (Popper 1974, p. 272–273).

Searle's (1999) terminology, Popper seems to conflate statements that are epistemically objective (*i.e.* claims about what is from my perspective) with statements that are ontologically objective (*i.e.* claims about what is). The former are dependent on current evidence, but the latter are not. In contrast with the empiricist tradition, free will is an epistemically objective 'illusion'[19]—but that is not to say that behavioural science would ever have enough knowledge to predict human behaviour with any reasonable accuracy. I have often wondered whether Popper's view was influenced by his point in history, where he had seen the damage that could be done by entertaining a nihilistic view of the objective world.[36] I might also add that I have always been baffled why indeterminism might somehow make room for free will in the objective world (what Popper called World 1), when its behaviours remain statistically definite.

2.3 Why Is Popper's 'Active Darwinism' Problematic?

I do not think there is any other way to construe my reading of Popper's division of 'active' and 'passive' Darwinism: it is a false dichotomy. The thing that really makes me firm about this conclusion is Popper's treatment of sexual selection, which he argues contradicts natural selection.[23] I understand what he means, namely that what makes an individual adapted to survival can differ from what makes an individual adapted for reproduction—which is not a controversial statement. But natural selection is generally used as the overarching idea of any type of selection, of which sexual selection, kin selection, fecundity selection, mortality selection etc. are subtypes. More to the point, I see no deficit in the current research paradigm stemming from Darwin, who gave us both the concepts of natural and sexual selection. I reject Popper's assessment of theory only treating the male's choice (or niche), which probably stems from Popper being unaware of traits that are associated with female choice—but nevertheless if he was aware of these cases then he glossed over them as he was running out of time at the end of the lecture. In this way, much of this disagreement about sexual and natural selection must surely reflect a problem of language, as Popper was clearly using terms in a different way than evolutionary biologists' do. I wonder how much of the general idea of 'active Darwinism' is of the same flavour, but I am not going to focus on this exposition because it seems rather dull.

At a deeper level, the problem with 'active Darwinism'—in as far as there is one that extends beyond a rephrasing of the ideas in 'passive Darwinism'—relates to Popper's discussion of how organism's choices impact how they evolve. I do not

[36] "*Compton describes here [in a preceding quote] what I shall call 'the nightmare of the physical determinist'. A deterministic physical clockwork mechanism is, above all, completely self-contained: in the perfect deterministic physical world there is simply no room for any outside intervention. Everything that happens in such a world is physically predetermined, including all our movements and therefore all our actions. Thus all our thoughts, feelings, and efforts can have no practical influence upon what happens in the physical world: they are, if not mere illusions, at best superfluous byproducts ('epiphenomena') of physical events*" (Popper 1972, p. 217).

think that there is any disagreement that, say, the sexual preferences of organisms can be important in determining how evolution proceeds. I think there is room to doubt two things: first is the generality with which this applies, and second is the essentiality to a general explanation of natural selection.

Popper is right to assert that many organisms have preferences that change how they interact with the environment, and consequently how selection acts on them; but when Popper encounters this, he asks "How do those preferences impact evolution?" when an evolutionary biologist would ask "Why are those preferences adaptive?". If those preferences were arrived at randomly, they would be of little interest to me as an evolutionary biologist because they would not be adaptive. Preferences are only going to be adaptations if they have the ability to be passed on in the longer-term (*i.e.* over many generations), which would need them to be produced by replicators. So, the fact that preferences change evolution is point of agreement, but Popper has inverted the causality to suggest the preference evolves before the gene that enables an individual to express that preference. Popper gives little indication about where this preference might come from beyond 'active problem-solving', which both Popper and his commentators have likened to a Baldwin effect, where learnt preferences (*i.e.* non-genetic adaptations) impact genetic evolution. As Popper seems to be aware, there is nothing incompatible between the Baldwin effect and what he calls 'passive Darwinism'—and the Baldwin effect is even incorporated into Huxley's *The Modern Synthesis*. The difference is more that Popper assumes that the Baldwin effect is the 'general case' and other cases are the exception (hence favouring the phrasing of his active Darwinism), whilst evolutionary biologists assume the opposite. In defence of the position of most evolutionary biologists, I could now launch into a set of evidence that not many organisms (if not only one) are capable of generalised learning in such a way that their learnt preferences meaningfully impact their genetic evolution in order to show that most lifeforms evolve in a much more 'passive' way that Popper supposed.[37] But, for me, the crux is really settled by my second point.

[37]To push this point further, in the Medawar Lecture, I think it is revealing that Popper spends his term advocating 'active' Darwinism in the discussion of animals *only*—and I would read him more specifically as talking about vertebrates because only they have a kind of generalised learning because of their centralised nervous system (in a way that makes individual capable of expressing its own unique personality). Further, Popper gives little consideration of the animals, plants and micro-organisms that form sedentary (or sessile) individuals that do not have much control over their environment. I do not mean to imply that they cannot engage in 'niche construction', but sedentary species clearly must have a restricted ability to do so in comparison to motile species. The fact that there are degrees to which Popper's 'active Darwinism' might be better for understanding some species over others is very different from disputing the 'general case', as Popper does. Additionally, Popper gives no discussion of selfish genetic elements, intragenomic conflict and horizontal gene transfer and other phenomena of living things that undermine the importance of individuals as coherent/unified learning agents. From an empiricist perspective, I think that Popper falls into a rationalist trap, which was eloquently stated by Hume: "*What peculiar privilege has this little agitation of the brain which we call thought, that we must thus make it the model of the whole universe?*" (Hume 1779, p. 134). In this reading, Popper applies the structure of his own way of thinking to the objective world as if the objective world had the same structure; hence why Popper thought it was legitimate to draw parallels between the growth of scientific knowledge and evolution

Organisms do not need to be active problem-solvers for them to evolve by natural selection, and so problem-solving does not really explain adaptation in general terms. It may well be true that generalised learning has a much greater role in evolution than most evolutionary biologists tend to think, but natural selection would work on entities that are incapable of learning. Indeed, evolutionary biologists tend to mostly work with genes, which may react to different environments in different ways (which we can understand as a probabilistic 'reaction norm') but are fundamentally inert chemicals that do not change their own base composition. Instead, environmental factors may cause them to mutate as they are passed down the generations, and therefore any adaptations that they contribute toward are only the result of natural selection. On this point, it can be useful to follow evolutionary epistemology's portioning of an adaptation into components of instruction and selection (Plotkin 1994). The basic idea here is that adaptation can come about through two basic sources: instruction refers to following some 'rules', and selection refers to environmental feedback on blindly-generated variation.[38] Classically, these two sources of adaptation can be thought of as extremes on a continuum between rules uniquely specifying a single adaptive variant and the generation of multiple variants that are then whittled down to a single adaptive variant. A preference is an instruction, but the question is how any adaptive properties were arrived at. If the preference is innate, then it was arrived at through selection on genotypic variants. If the preference is learnt, then it was arrived at through instruction by some phenotypic set of rules. The continuum perspective masks that those phenotypic rules are only going to successfully lead to adaptation if they are the result of a selective process (*i.e.* by selection on genotypic variants that specify learning rules). Therefore no matter how you look at it, in the ultimate sense, adaptation is arrived at through natural selection somewhere in the system, but it doesn't necessarily have to be natural selection in a straight-forward manner. I would also say, tying this back to biology, adaptation is arrived at because of the natural selection of genotypic variants that underlie behaviour, or the learning rules that govern behaviour. In this way, it is natural selection not problem-solving (*i.e.* learning) that is essential to adaptation.[39]

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by natural selection. In other words, I think that Popper over-states the degree to which organisms choose their environment because his philosophy lends him toward being anthropocentric.

[38] The critical feature of selection is sometimes misconstrued (as Noble does so), and so I will clarify. Although the paradigmatic selection process would be random variation, a bias in the process of mutation does not matter in as far as the bias does not influence the outcome of the selective process—which is to do with a feature of the environment that does the selecting. This is why the word 'blind' is often preferred to 'random'.

[39] As an aside, I think it would be possible to make the reverse argument that instruction underlies selection, but to do so would require the physical laws of the universe to be construed as 'instructions'. In this implicitly causally deterministic framework, natural selection would proceed from the physical laws of the universe because the physical laws permit selection to operate. This argument is not totally vacuous, hence why natural selection can be simulated in a computer that operates by a series of instructions. However, I would argue that this argument alienates an important aspect of natural selection, which is the medium of the replicator. The mechanics of genome replication has a huge impact on the direction of the evolutionary change resulting from selection—and the degree to which different kinds of traits can be more or less adaptive, so I am not sure how useful

Perhaps one could argue that this restricts the scope of evolutionary biology's explanation of adaptation, but I think it clarifies something very important. If there is any adaptation as a result of learning, that adaptation is either the result of the natural selection of genes governing how behaviour changes in response to some feature of the environment or the result of a secondary phenotypic process of selection that is enabled (but not directed) by genes. The second case, we might consider as 'open-ended' or 'generalised' learning, though of course how open-ended it is depends on the system's constraints (just as modern genes are constrained by protein biochemistry). To explain a trait as an adaptation would require an intimate knowledge of the way selection works in that system (just as natural selection only made sense given genetics). In the context of genes, this is often described as suggesting that genetic 'constraints' are an important part of adaptive explanation because of their creative role in how selection works.[40] What little we do know about learning systems is that they vary across the diversity of life, and so the constraints in these systems are never going to be universally shared (unlike for the genetic code, which is pretty much universal). The point I want to make here is this: even if evolutionary biologists were interested in learnt adaptations, we would explain them with the same externalist mindset as we apply to genetic adaptations. In this way, we would still direct focus toward how features of the external environment cause features of the internal structure that we see, rather than really treating individuals as active problem-solvers.

3 What Was Popper's Criticism Really About?

This brings me on to my final set of thoughts. I find it hard to believe that Popper cannot have considered most of the arguments that I have just raised both for evolutionary biology's framework and against his suggested alternative. The question is, why did he continued anyway? I don't think that he was really trying to revolutionise evolutionary biology by unveiling some fatal flaw in contemporary research. Instead, I think he was trying to push the analogy of evolutionary change as a learning process in order to expose something odd about the way evolutionary biology conceptualises agency. I think Popper rightly sensed the externalist tendency of evolutionary biology

this perspective is. Further, given its causal determinacy, I am not sure how much is reinforces the active problem-solving perspective of organisms.

[40] "*It is common to think of constraints in a negative fashion – as preventing things from happening, and thereby reducing the variety found in nature. But if the process of producing variation is open-ended, the introduction of constraints can channel the variation, and by directing it, produce much further or deeper exploration in a given direction than would otherwise be possible. Constraints can thus play a creative and, in one sense, ultimately progressive role. This is a deep truth, not only about evolution, but about problem-solving and exploration in general. It is why Darwin was right in 1859 when he saw natural selection as a creative force, and why his critics who saw selection only as playing a negative role by eliminating variety were wrong*" (Wimsatt and Schank 1988, in Nitecki 1988, p. 235).

to explain adaptations with appeal to features of the environment, though I do not think that he recognised this externalism explicitly. Given that Popper is the champion of common-sense, I think Popper's discomfort with evolutionary biology came from his unease with the way that it flaunts agency as a metaphor—which stands very much in contradiction of his rationalist account of science as yielding objective knowledge about reality. I think that many people would instinctively sympathise with Popper's position, especially for those in contemporary thought that look to evolutionary biology as orchestrating a modern (and atheistic) Creation Myth, whereupon I think it is natural for many people to feel like there should be some greater prominence of the individual within this scientific epic. The way in which evolutionary biology asserts the insignificance of agency is omnipresent in the way in which, even when organisms are discussed, organisms tend to be talked of in terms of their genetic accounting only.

Prior to the Medawar Lecture, I have suggested that there was a tension in Popper's thoughts on evolutionary biology—hence why he both lavished it with praise and yet gave it special treatment as an inconvenient anomaly. By the time of the Medawar Lecture, I think that Popper had resolved some of this tension by asserting that agency objectively exists and is an important part of the causal structure of the objective world, rather than asserting that agency has a subjective existence as a metaphorical way of thinking about the objective world. However, I do not think that Popper critically assessed why this disagreement about agency came about. I have characterised this as Popper's favouring of rationalism over empiricism in asserting the existence of agency prior to any evidence which may suggest an alternative conclusion. Within rationalism, agency is the bedrock of all human understanding which is built from ontologically objective knowledge; within empiricism, agency is more often used as a metaphor (or 'thinking tool'), and human understanding is built from epistemically objective knowledge (which may or may not turn out to ontologically objective). In this regard, Popper's own philosophy of 'critical rationalism' is—to some extent—bridging the divide, but in other ways it is also a bridge built from one side on a rationalist foundation. Along with other scientists, evolutionary biologists tend to admire Popper as 'their' philosopher of science, in defending a common-sense world-view held by most scientists. But, in the details, I think that many scientists would defend the same world-view but from an empiricist foundation (perhaps, 'critical empiricism'?).

In this way, I think it is inaccurate for Noble and others to use Popper as someone who was 'on their side' against the views expressed in *The Modern Synthesis* because I think that Popper's complaint with evolutionary biology was a philosophical one relating to agency. Popper thought very favourably of Medawar's critique of Teilhard de Chardin's evolutionary theology, wherein scientific research was described as the 'art of the soluble'.[41] Perhaps influenced by the empiricist foundations of

[41] "*No scientist is admired for failing in the attempt to solve problems that lie beyond his competence. The most he can hope for is the kindly contempt earned by the Utopian politician. If politics is the art of the possible, research is surely the art of the soluble. Both are immensely practically-minded affairs*" (Medawar 1967, p. 97).

evolutionary biology, Medawar was expressing the fact that a good research scientist spends their time solving problems rather than building syntheses. Particularly in biology, a synthesis is always going to be constructed as a teaching aid for general intuition rather than as a rigorous statement of universal truth because there will always be an exception. To my mind, focusing criticism on *The Modern Synthesis* as a seminal work is a fascinating construction of the history of evolutionary theory because, as I and others have argued, it actually had very little impact compared to other contemporary works. Further, the word 'synthesis' makes it a wonderful straw-man; ecology does not have a 'modern synthesis' equivalent but is instead a looser collection of canonical concepts and so it is much harder to decry its failures in this way.

4 Conclusion

So, where does this leave us? Popper's foray into evolutionary biology is fascinating because it represents a collision of world-views. I am not sure that Popper gets everything right, and I am not sure that Noble is correct that we need to rehabilitate Popper's views of evolutionary biology—nor do I think we will ever agree on that one. But I respect that there is something non-trivial about these disagreements, which deserves further discussion. I think much of the disagreement comes from the competing treatments of agency within rationalist and empiricist traditions, and so I think that the non-trivial elements of the disagreement are philosophical in nature, rather than relating to anything that could be changed on the practical side of the established facts that either tradition could use to support their position. Perhaps by simply recognising the nature of this disagreement, a lot of misrepresented 'hot air' can be avoided.

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