Convergence as Evidence

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Abstract

The comparative method grants epistemic access to the biological past. Comparing lineages provides empirical traction on both hypotheses about particular lineages and models of trait evolution. Understanding this evidential role is important. Although philosophers have recently turned their attention to relations of descent (homology), very little work exists exploring the status of evidence from convergences (analogy). I argue that, where they exist, convergences play a central role in the confirmation of adaptive hypotheses. I focus on 'analogous inferences' (inferences which take a trait/environment dyad from one lineage and project it to another), show how such inferences ought to be analyzed and suggest three methods for strengthening their evidential weight.

Introduction

This paper fills a gap in philosophical understanding of biological reasoning: the use of analogy (roughly the independent evolution of similar traits) as evidence. As appeal to analogous evidence is ubiquitous in supporting evolutionary explanation, understanding its role is important. Moreover, a growing body of work has examined and emphasized the role of homologies - traits which are ancestrally related. No similar philosophical corpus exists for analogy. If relations by descent are important, then we might think that the contrasting notion of analogy also deserves attention. The central aim of this paper is to show that analogy has a primarily *evidential* role in biology and to outline how hypotheses, explanations and theories are supported by analogies. We need a handle on what kind of explanations they support, and what an analogy is. I begin with an illustration of a hypothesis, show how analogies test it, and then motivate a philosophical account of analogy as evidence.

Explanations in evolutionary biology rely on claims about the past. Henneburg et al ([1997]), for instance, claim that human fingerprints are an adaptation for grasping branches. In our ancestors' arboreal environment there was selection pressure against falling from trees. Fingerprints, the story goes, helped avoid this - individuals with this feature tended to survive when their conspecifics did not. Over evolutionary time, then, the trait spread throughout the population. How do we test this hypothesis against competing explanations? After all, fingerprints may have been an ancestral trait; our forbearers may have been fingerprinted prior to taking to the trees. Fingerprints could be an exaptation: evolved for some other purpose, they were put to use in grasping. Perhaps fingerprints are unrelated to arboreal environments. We need evidence about timing and distribution: that fingerprints evolved in our lineage while in an arboreal environment; and evidence about function: that they evolved because they assisted in grasping. Similarities between different lineages provide empirical traction on such claims. This approach to supporting evolutionary hypotheses is part of the 'comparative method' in biology.

The comparative method plays a central role in the epistemology of evolutionary biology. Examining molecular, morphological and functional similarities between contemporary and preserved lineages allows biologists to test hypotheses of the relatedness of lineages; the timing of evolutionary events; the character of previous environments and ecologies; the morphological and functional organization of extant and extinct organisms. One way to conceptualize the relationships between similar traits in different lineages is in terms of common descent (homology) and independent evolution (homoplasy). If a trait is held by two lineages, and their common ancestor also had it, then the trait is *homologous*. If the common ancestor does not hold the trait, then it is *homoplastic* – it has evolved independently[i].

An analogy is a similarity between two lineages that meets the following conditions, (1) the trait must be present in the two lineages, but not in their common ancestor (it must be homoplastic); (2) the trait must have evolved in the two lineages *non-accidentally*. The point of the second clause is to disqualify those cases where similarity has the wrong etiology to support inferences. For the purposes of this paper, where I focus on *adaptive* explanation, ‘non-accidental’ should be read as ‘due to the same selective environment’. For other contexts, other readings may be appropriate[ii].

This definition of analogy is a departure from ordinary biological usage. Typically an analogy is taken to be any similarity in traits between distantly related lineages, while homoplasy is contrasted with homology (technically synapomorphy) in systematics. ‘Convergence’ itself is typically contrasted with ‘parallel’ (both of which are homoplastic) and so is unsuitable for my purposes. I have here taken *homoplasy* to refer to a phylogenetic concept – two traits are homoplastic just in case the common ancestor did not have the trait. This is not enough to support evolutionary explanations however, as the trait must have evolved due to the same selection pressures. I count something as an analogy when it meets these two criteria.

This account of homology, homoplasy and analogy skates over vexing conceptual issues. In particular, it appears that judgments of homology or homoplasy depend on our perspective. Frequently analogous traits make use of homologous developmental resources, for instance the use of *pax6* in the development of analogous eyes. If underlying developmental continuities are to blame for analogies then this might undermine their independence. Indeed Hall ([2003], [2007]) has argued that we take analogy and homology as *continuous* rather than binary. I have two responses to this. First, it seems that analogy and homology are not continuous so long as we have a fixed *level of description*. An example of Hall’s is the divergent mechanisms in the development of homologous tetrapod digits. In most tetrapods, digits develop through cell pruning. In urodele amphibians, however, digits grow independently. Yet these divergent developmental mechanisms produce homologous traits. This does not commit us to a graded account: *qua trait* the digits of tetrapods are homologous and *qua developmental mechanism* they are not. Second, my analysis of analogy in evolutionary biology takes such concerns into account. If one wants to think of homology and analogy as a single concept then everything I have to say retains its value. The concern of this paper is with the use of analogies as evidence, and so to an extent such ontological issues must be put aside (they are touched upon in my discussion of parallelisms in 2.1)

With an account of analogy under our belt, we can now see it in biological play. If two lineages have independently evolved relevantly similar adaptations in similar selective environments, this provides evidence for natural selection's role in shaping phenotype. Analogies are taken to be 'natural experiments' which support adaptive hypotheses.

There is a similarity between us and (of all things) koalas. Organisms from both lineages have fingerprints. The fingerprints are so similar that an electron microscope cannot differentiate between an adult koala's and a human's. Moreover, the similarity is homoplastic: it is very unlikely that the common ancestor of humans and koalas had fingerprints. Henneberg et al claim that fingerprints in both humans and koalas are adaptations. Their function is to aid grasping branches, and they evolved due to arboreal selective environments. If so, then fingerprints are analogous between humans and koalas. Henneberg et al cite this as evidence for their hypothesis that human fingerprints are an adaptation for clinging to branches. That a trait-environment dyad is found in one lineage is reason to think it would be found in another.

So, analogies support adaptive hypotheses, but how good is analogous evidence? Despite traditional philosophical and biological interest in adaptation, most uses of analogy are tentative, uncertain and evidentially opaque[iii]. Is it enough, for instance, to cite a single case? An account of analogy as evidence provides answers to these questions and allows us to examine the empirical support they provide for natural selection's role in evolution.

Such an account is important on several grounds. First, it illuminates debates about the importance of natural selection in evolutionary explanation. Work on testing adaptive hypotheses and adaptationism in general has focused on either optimality modeling (Orzack & Sober [1994]) or the role of homology (Griffiths [1996]). If analogues are evidence for adaptive hypotheses then they provide a further empirical inroad to testing Neo-Darwinian ideas. Evolutionary theorists take worries about adaptive explanation increasingly seriously, and this both undermines the potential value of analogy as evidence and increases the urgency of using them to support adaptive claims.

Second, philosophical accounts of evolutionary evidence have ignored analogies to their detriment. Elliot Sober has given excellent treatments of inference in evolutionary biology covering common ancestry (Sober [1999]), drift versus selective models (Sober [2008] section 3) and the evidence for evolution against intelligent design (Ibid section 2). No attention is paid to the role of analogies. Philosophical accounts which do mention analogies are insufficient. Turner ([2011]) discusses convergence in relation to macro-evolutionary contingency but only as a set up to discussion of other methods of testing such hypotheses. Griffiths ([1994], [1996], [2007b]) discusses analogy, but in unfavorable comparison to homology. His concerns may well be right, but do not illuminate the use of analogy in inferences. Sterelny & Griffiths ([1999]) has a brief discussion of analogies as evidence but something more systematic is required.

Tucker (chapter 3, [2004]), in a broad discussion of historical inference, discusses analogy in the context of comparing explanations which refer to common and separate causes. He points out that separate causes may be more likely if there is some functional similarity between them: the construction of pyramids in both Egypt and the Americas is explained by the common engineering difficulties faced (not cultural exchange); the stream-lined forms of dolphins and sharks is explained by the selective environments both inhabit (not common ancestry). I am amenable to Tucker's Bayesian formalization of these inferences, but take several important departures. First, this paper is not concerned with contrasting the relative merits of inferences relying on homology and analogy. This would require a more developed analysis of those concepts, which I leave for later work. Second, the point of this paper is to exposit the role of analogies in supporting biological (in particular adaptive) explanations of traits, rather than a unified story including cultural, textural, linguistic and biological inference. There are interesting similarities between these inference-patterns, but their differences run deep enough to motivate a separate treatment.

There is an extended discussion of the role of analogies in historical inferences in Turner ([2007]) (chapter 4), and his pessimistic take is an interesting counter to my views. He argues that the use of analogy, although necessary for historical inquiry, does not grant any epistemic advantage due to the unreliability of such evidence. Too often reference to contemporary analogues has led us astray. Of course, picking the wrong model frequently does lead to problems for scientists, but I don't see how this is a problem for historical inferences *in particular*. Moreover, comparing my project with Turner's is misleading, as we have different targets. By 'analogy' Turner seems to refer to the use of contemporary animals to reconstruct past lineages, without distinguishing between homologous and analogous evidence or focusing on any particular kind of explanation. My focus is much narrower: I am interested in how a particular kind of similarity (traits which have independently evolved due to similar conditions) support historical inferences about adaptations. For Turner, reliance on analogy is necessitated by the epistemic disadvantages we face in uncovering facts about the past. A discussion of the relative epistemic situations faced by 'historical' and 'experimental' science (or for that matter what this distinction amounts to) is beyond the scope of this paper. I do not deny that the use of analogues can be misleading – indeed a primary purpose here is to promote the careful use of analogies which avoids the pitfalls Turner illustrates.

Given the ubiquity of appeals to analogous data in biological reasoning (see below), such meager treatments are surprising.

Third, an account of analogy as evidence can complement philosophical work on homology. In contrast to analogy, comparative inferences using descent have a quantified, well-supported method in phylogenetics (See, for example, Sober [1999], [2008], [1988]) and homology's presence in scientific literature is robust and unapologetic. Philosophers, too, have discussed the nature of homology (Griffiths [2007b]), its explanatory and evidential role (Brigandt & Griffiths [2007], Coates [1993], Franz [2005], as well as Sober's work), its relation to broader questions in biology (Love [2007], Matthen [2007], Griffiths [1994]) and to broader questions in philosophy (Griffiths [2006]). There is room for analogy in this fertile philosophical soil; given analogy's contrastive relationship with homology an account focusing on homology alone provides only half the story. There is much to be said about the relationship between homology and analogy in the context of these discussions, but that is not the focus of this paper.

Fourth, in some quarters there has been an increasing sophistication in the use of analogies to support hypotheses and there could be a fruitful dialogue between philosophy and biology in this area. Faith & Cranston ([1992]), for instance, give a Popperian gloss on phylogenetic delineation of analogy and homology (see also Faith et al [2011]). Evidence for a hypothesis is judged by considering and falsifying alternative explanations for that evidence. Braun & Harshman et al ([2008]), for instance, argue for polyphyly (multiple evolution events) in ratite flightlessness by methodically eliminating possible biasing explanations in their phylogenies[iv].

This paper in part bridges the gap between this biological theory and philosophical work on evolutionary evidence. However, there is a significant *philosophical* difference between accounts like Faith's and mine. Popperian corroboration cannot explain the success of analogous inferences (particularly in what I shall call 'integrated explanations') because it does not increase our credence in hypotheses. Moreover, a Popperian reading is far too strict for the historical sciences which very rarely deal in certainties. I have a more optimistic take on the relationship between evidence and credence. An approach more amenable to my view of confirmation would be to understand the elimination of biasing explanations in reference to Ian Hacking's ([1965]) *law of likelihood:*

Observation O favors H_1 over H_2 when $p(O|H_1) > p(O|H_2)$

This is to say that an observation counts as evidence for one hypothesis over another just in case the observation increases the *likelihood* of that hypothesis more than the other. 'Likelihood' is not mere probability, but the probability of an observation *given* a hypothesis. The law describes when a hypothesis is more probable in virtue of its evidence. We should understand Braun et al's elimination process as testing that their evidence does in fact count as such. The *strength* of the evidence is a further question, which this paper addresses.

And so a philosophical account of analogy is necessary and promises to be fruitful. Before moving on to the paper proper, I ought to make good on my claims about the ubiquity of analogous reasoning in biology.

Analogies are important for the work of ethologists, comparative psychologists and evolutionary psychologists. Marino et al ([2008]) propose a decoupling of neural and cognitive evolution due to divergent neuro-architecture, but convergent cognition, in primates and cetaceans[v]. Sayers and Lovejoy ([2008]) suggest we examine social carnivores, which '… hunt big game and cache meat, both of which approximate human hunting behavior…' (pp 95), as an inroad to our own hunting past. Plotnik et al ([2006]) claim that the discovery of mirror-recognition in a (single) Indian Elephant is good evidence of parallel cognitive evolution between elephants, apes and cetaceans. Nathan Emery ([2006]) points to the (impressive) cognitive prowess of parrots and corvids – '… it has been suggested that intelligence in these taxa can only have arisen by convergent evolution, driven by the need to solve comparable social and ecological problems (pp37).' The independent evolution of traits is taken to be illuminative of the forces which drive them.

In fact, everywhere you look in organismic biology you find appeals to analogy as evidence. The most well known convergences are morphological: the flight of bats, birds and pterosaurs; the stream-lined forms of dolphins, sharks and ichthyosaurs; the parallels between antipodean marsupials ('moles', 'tigers', 'anteaters', etc…) and birds (fairy-wrens, robins, etc…) and their northern counter-parts. Martin et al ([2007]) examine the visual apparatus of Kiwi, pointing out that their small eyes and limited neural vision-centers are surprising in a nocturnal, flightless bird (typically birds emphasize sight, and the birds with the biggest eyes are usually either nocturnal, like owls, or flightless, like other ratites). Their studies confirm that kiwi emphasize both tactile and olfactory information, similarly to many nocturnal mammals. ‘This suggests the independent evolution in Kiwi and in these mammals of similar sensory performance that is tuned to a common set of perceptual challenges presented by the forest floor environment at night that cannot be met by vision (Martin et al pp4).’ Again, a link is presented between a particular environment and a particular trait.

Paleontologists frequently appeal to analogous evidence. Senter [2007] argues that sauropods did not raise their necks on analogous grounds. ‘Keystone-shaped cervical centra (‘ventral bodies’ in mammalian nomenclature) at the bases of their necks allow giraffes, camelids and birds to hold their necks vertically, but sauropod cervical centra lack such shapes, even among sauropods that are typically portrayed with vertical necks (46).’ Here several unrelated animals are referred to in order to establish a link between a morphological trait and behavior. Sophisticated phylogenetic approaches use analogies to test macro-evolutionary hypotheses. Flowers, Galal and Bromham ([2010]), for example, use a large data set to hypothesize the spread of halophytes (salt tolerant plants) amongst angiosperms. The spread is polyphyletic (containing many homoplasies) but not random: some clades appear more likely to evolve salt tolerance than others. The paper claims that these analogies provide a research strategy to understanding salt tolerance. Explaining why some clades are more likely to evolve halophytes would be illuminative of the evolution of that trait in plants generally.

And so appeals to analogy as evidence are ubiquitous in evolutionary biology. An account of biological reasoning ignores this to its detriment, and philosophical work on homology cannot stand alone. This paper covers some distance towards remedying this.

The paper is in two parts. In the first I explain the use of analogies as evidence and what factors affect their evidential weight. As we have seen, independent evolution events can test adaptive hypotheses about those lineages. That koalas have fingerprints and live in an arboreal environment supports the claim that human fingerprints are adaptations for branch-grasping. They also support more general claims: predictions about other lineages and claims about evolution itself (I will call these ‘analogous inferences’). Given the evidence from humans and koalas we might make the general claim that arboreal environments select for fingerprints, and expect coupling in other cases as well. I present a set of ‘dimensions’ which determine our credence in adaptive inferences. As we shall see, some analogies are better evidence than others.

Given these concerns the second part investigates how we can bolster the evidential weight of analogies. Illustrations will be sketchy and toy-like, but I hope their applicability to more complex cases will be clear. In *parallel modeling* scientists restrict analogies to close relatives. As differences between related lineages are more likely to be caused by divergence in environment as opposed to development, restricting analogues to close relatives increases their evidential weight. *Integrated explanations* combine analogies with other streams of evidence. If independent evidence streams both support a hypothesis, this increases our credence. I argue that in such cases independent evidence is ‘mutually supporting’: their combined evidential weight is higher than the sum of the individual support they provide. *Convergent modeling* tests a proposed niche-adaptation dyad across several instantiations. This both supports the model and provides opportunity for refinement. These methods allay concerns about adaptive claims and show how analogies are an important stream of evidence for the construction and testing of historical hypotheses about biological form and function.

1. Analogous Inferences

This section examines the evidential relationship between adaptive explanation and analogy; focusing on cases I shall call ‘analogous inferences’. In 1.1 I explain the relationship between analogies and adaptive explanations, 1.2 introduces analogous inferences and 1.3 discusses the factors which influence credence in such inferences.

Analogies are evidence for two kinds of claim. On one hand, the explanatory target could be the lineage. Henneburg et al cite koalas as support for their hypothesis that human fingerprints are an adaptation to an arboreal niche. Alternatively, the target could be a general model for the evolution of the trait. They argue that given an arboreal niche, fingerprints will be selected for – and both humans and koalas count as evidence for this. By either reading, using analogies as evidence require that matches between selective environments and traits in different lineages inform us about the selective requirements of trait evolution. In the next part I make explicit the relationship between analogy and adaptive explanation.

1.1 Adaptive Explanations and Analogies

What is the relationship between adaptive explanation and analogy? Analogies support adaptive claims; particularly in *analogous inferences*. The success of such inferences turns on both contextual information and background assumptions about natural selection. This section explain how analogies relate to adaptive explanation and lays out the factors which determine our initial credence in whether two traits are in fact analogues.

An adaptive explanation of a trait has two steps. First, we postulate an evolutionary function, second, that function is explained in terms of selection pressures from previous environments. Henneberg et al claim that human fingerprints function to assist grip, and evolved due to selection pressures in our ancestral, arboreal environment. It paid our ancestors not to fall from trees, and this explains the evolution of fingerprints. The claim that koalas count as evidence for this leans on our belief that fingerprints in the two lineages are analogues, which requires that both be adaptations to the same environment.

What factors might determine our initial credence in the claim that fingerprints are adaptations? Two things to consider in determining adaptation are *fit* and *complexity*. If the trait exhibits a clear function, and that function is tied to a particular environment, then our job is easy. If fingerprints clearly aid grasping, and grasping only, then irrelevant of analogous information we might be happy to infer from their function to a previous environment. If, however, the trait is functionally ambiguous we need more evidence. If we have well supported adaptive claims about both traits, and it turns out the traits evolved independently for the same purpose due to the same environment, then they are analogous. So, the fit of the trait-niche dyad partly determines our initial credence of inferences made on analogous bases. Additionally, highly complex structures (take, say, a lens eye) are unlikely to evolve simply by drift, or for different purposes. The more complex the structure, the less likely it is for the structure to have evolved – the demand for an adaptive explanation becomes more pressing (Block [1997,] Dennett [1995], Sterelny [2003]). Further, a complex structure is more likely to be closely tied to a particular function – and thus fit closer to a selective environment.

Whether we take koala fingerprints as an adaptation turns in part on how complex the structure of fingerprints is, and how closely they match the postulated function.

Finally, whether two adaptations are analogous depends on their evolutionary relationship. If the traits are homologous they do not count as independent data points, as we do not need to appeal to common selective environments to explain the similarity. Homologous and homoplastic relationships are inferred using phylogenetic techniques, producing phylogenetic trees which are hypotheses of the pattern of ancestry and descent.

The methods are uncertain, sometimes contentious – and necessary for distinguishing homology from homoplasy, and thus for the use of analogy.

1.2 Analogous Inferences

Which inferences do analogies support? First, our confidence in the koala case should increase our confidence in the human case, and vice versa. This is to say that the observation of fingerprints in koalas, given their grasping, arboreal niche, increases our credence that fingerprints in humans evolved for that same function and due to the same environment.

Second, and more interestingly, humans and koalas could count as data points for an *analogous inference*. An analogous inference takes a known analogy and projects it onto a target lineage. If a particular trait-environment dyad exists in one lineage, this could be evidence that it exists in another. Analogies, then, support general adaptive claims. To say a dyad is projectable is to say that given certain conditions, occupation of a certain selective environment leads to the evolution of a certain adaptation. These adaptive regularities are applied in two ways by biologists.

An *organism to world* inference takes the form trait → environment. If we discover a lineage with fingerprints, then we have reason to think they previously inhabited an arboreal, grasping niche. In organism to world inferences there are three facts that we are relatively confident of, and use these to infer a fourth. We know the analogue’s trait and the selective environment in which it evolved (and thus the trait's function), we also know our target's trait. As the analogue and the target share traits, this is reason to think they also inhabited similar environments in the evolutionary past. In Henneberg et al's case, of course, we have good reason to think that human ancestors were arboreal. Their claim is about the *function* of fingerprints as opposed to selective environments. There are, then, two forms of organism to world inferences. One uses the analogy to infer the selective environment the trait evolved in, the other infers the function of the trait[vi]. The fingerprints of koalas support an adaptive regularity suggesting *both* that human fingerprints evolved to assist grip, and that this evolved due selection pressure from tree-grasping. In combination both analogues are evidence for the general claim that a lineage with fingerprints occupies, or once occupied, an arboreal niche

A *world to organism*[vii] inference is, unsurprisingly, the inverse: environment → trait. Given an arboreal, grasping environment, fingerprints will evolve. Say we are reconstructing an extinct mammal which lived in an arboreal environment and grasped branches. Will it have fingerprints? If we think yes, based on analogous evidence, then we make a world to organism inference. Indeed, Henneberg et al claim that '… dermal ridge patterns [fingerprints] are heritable structures occurring on the skin of those mammalian extremities that are prehensile *irrespective of the taxonomic affiliation of an animal*… (Ibid pp 2, my italics)' Which is to say, in all mammals with prehensile digits, given the right environment, fingerprints will evolve. We contrast our target with the adaptive model the analogues support, and infer the target's phenotype given their environment.

So far, in 1.1 we have seen that our initial credence in whether traits are analogous, our confidence that they are adaptations for the same purposes fitted to the same selective environment, is partly set by their complexity and fit. Also, whether the adaptations are analogues depends on phylogenetics. In 1.2 we saw that analogues both support adaptive claims and are the basis of analogous inferences, which project a trait-environment match onto another lineage. These inferences take two forms: organism to world, in which we infer a previous environment from a trait; and world to organism, in which a trait (or function) is inferred from a previous environment. The next section discusses which factors determine credence in analogous inferences above and beyond our background confidence set by complexity, fit and phylogenetics.

1.3 Scope, Grain and Specificity

The evidential support of analogous inferences are determined by three dimensions. The *grain* of similarity between the traits and the environment, the *scope*, or phylogenetic distance, captured by the inference, and the *specificity*, or satisfaction conditions, the claim requires.

How similar the analogues are, their *grain*, affect our confidence in analogous inferences. How similar, we might ask, are human and koala fingerprints? Surprisingly so, microscope evidence suggests. At a coarse grain convergences in flight are striking, having evolved independently in reptile, bird and mammal lineages. However, each flies differently utilizing different structures – at a finer grain the analogies are no longer similar (Griffiths [2007a]). Fine grained similarities are more remarkable than coarse ones, and more likely to have common selective causes. We can also consider grain from the perspective of selective environments. It seems reasonable to suppose *ceteris paribus* that niches that are similar in fine grained details, such as biogeography, available resources, etc… are more likely to produce similar phenotypes than coarse grained environmental similarities. Fine grained niche spaces will specify adaptations at a fine grain. There will be less 'give' in available adaptive pathways: evolution will be constrained.

Ceteris Paribus, the finer grained the analogues, be it in trait or environment, the higher credence we should assign the analogous inference.

The *scope* of an analogous inference is the phylogenetic distance it covers. It might appear that Henneberg et al's claim has a narrow scope, as it involves only two lineages. However, given the phylogenetic distance between marsupial and placental mammals the scope is relatively wide. Their claim assumes that, phenotypically, an evolutionary path taken by a marsupial lineage is likely to be taken by a placental lineage as well. This involves commitments to the kinds of constraints and potentiality those clades hold in common. An inference with smaller scope would cover a smaller clade, for instance an inference between humans and our closest relatives, *Pan*, would have a very small scope indeed. Note that scope is relative: what we consider to be 'wide' or 'narrow' will depend upon our purposes, the explanatory context, and background assumptions.

A wide scope, then, relies on the postulation of a larger regularity across life than a thin scope. As a rule of thumb, we ought to consider wide-scope claims as more contentious, as the large genetic, developmental and phenotypic differences between distantly related lineages are more likely to skew common results from natural selection. *Ceteris Paribus*, we should have higher credence in a narrow scoped inference than a wide scoped inference.

A caveat about small-scope inference: in such cases it becomes increasingly difficult to identify analogies. As mentioned above, homoplasy and homology are distinguished via phylogenetic inference. With a small data set and closely related lineages it is harder to confidently distinguish them. It is extremely unlikely that the lens eyes of cephalopods and mammals are homologous: their ancient common ancestor only had primitive proto-eyes at best. Are the patrilocal kin structures of, say, chimpanzees and bonobos (*Pan*) convergent or retained? We can say they are *probably* retained as most primates are matrilocal, and so the most parsimonious arrangement has the common ancestor of *Pan* evolving the trait, as opposed to independent evolution in chimp and bonobo. However, given the small data set, our confidence oughtn’t be too high (see Rodseth & Shannon [2006] and Chapais [2008] for general discussion of kin distribution in primates). So although small-scoped inferences are generally better supported than those of a large scope, we might become less confident of the independence of the analogues.

Wide-scoped analogies typically lack fineness of grain. After all, large phylogenetic distances typically correlate with divergence, take the structural (and perhaps functional) differences between the lens eyes of humans and cephalopods, for example. These divergences do not completely undermine inferences on the basis of such analogies: two arguments in the latter half of this paper show how we can bolster inferences made using wide-scope, coarse-grained analogies.

An inference's s*pecificity* determines the level of credence required for belief in that inference, it measures the level of detail required by a hypothesis or explanation. Compare Henneberg et al's claim that dermal ridge patterns evolve due to selection in arboreal environments to a much less plausible version which argues for the evolution of, say, particular patterns in fingerprints. The former claim is less specific as it is less detailed. The higher the specificity of a claim the more demanding it is. It would be more surprising if a particular pattern of fingerprints was selected for than merely fingerprints themselves. The less specific the claim, the less support it requires: the bar of required credence is set lower.

Specificity and grain have a close relationship. Grain refers to facts in the world, specificity to the demands of the inference. It is important that the facts are fine grained enough to support the level of specificity the inference requires. Wing analogues between bats, birds and pterosaurs are quite coarse: they are similar in some aerodynamic properties and in terms of function, but each uses different structures and different movements in flight. For instance, birds fly using their 'arms', whereas the wings of bats are stretched across their fingers. The analogy is coarse grained and this has consequences for the level of specificity it can support. Take two analogous inferences. The first is less specific, claiming that *some* adaptation to flight would evolve given the right set of ecological conditions. The second has higher specificity: given some set of ecological conditions, flight with (say) bird-like morphology would evolve. The analogy between bats and birds might be at the right grain to support the former inference, but not the latter. Because bats use a different morphological arrangement in flight than birds, they cannot be used as a data point to support an inference about bird-like morphological structure. Coarse analogies, then, are evidence for inferences of low specificity. Fine analogies can support claims of both low and high specificity[viii].

Examining Henneburg et al's organism to world inference, then, we can draw the following conclusions. Their claim has relatively wide scope as it requires projection from a marsupial to a placental lineage. All things being equal, this should count against the inference as it is less likely to be true across a wide swathe of mammalian life then it would be if it were constrained to close relatives. The trait is fine grained, as human and koala fingerprints are almost indistinguishable[ix]. This counts for the inference, as such similarities are unlikely to have evolved for different purposes. The claim is fairly non-specific, as they merely propose the evolution of fingerprints, not fingerprints of particular proportions or pattern. This also is in their favour. These three dimensions, in combination with background considerations such as complexity and fit, set our credence in analogous inferences.

A further factor that could affect our credence in analogous inferences (and adaptive explanations overall) is our commitment to natural selection's ability to shape phenotype in general. For those who take non-selective influences such as drift, exaptation, and so on seriously, claims about adaptations need to be well supported. Fortunately, there are strategies for bolstering the evidential weight of analogous inferences, to which I now turn.

2. Parallel Modeling, Integrated Explanations and Convergent Modeling

> …analogy is at least as powerful a comparative tool as homology… Evolutionary hypotheses are well supported when independently derived data repeatedly suggest that a particular selection pressure consistently favours a specific character. (Kevin Laland and Gillian Brown in Sayers & Lovejoy [2008])

I have argued that analogy plays a central evidential role in supporting adaptive hypotheses and cashed out which factors influence the support they provide. I now take up the challenge of explaining how analogous inferences are strengthened, outlining three credence-bolstering methods.

2.1 Parallel Modeling

> [an analogy is parallel]… if the underlying homology prescribes a highly distinctive, detailed and strongly determinative channel of constraint (Gould [2002], pp 1135).

One method is *Parallel Modeling.* Here, we constrain our scope of analogues to close relations. Because phylogenetic history constrains evolutionary paths, closely related lineages will be *more likely* to evolve similar phenotypes. As closely related lineages share similar developmental resources, the *differences* between them are more likely to be due to environment. By sticking to 'parallel' lineages, then, we control for developmental noise. Our models are constrained – they describe a putative regularity restricted to a particular clade (see Hall [2003], [2007]). This solution is related to the 'historical turn' (Griffiths [1996], Sansom [2003]) in adaptationism. Because phylogenetic history plays a large role in shaping phenotype, it ought to be incorporated into explanations of it, even adaptationist ones. What then are parallelisms?

Not all analogies are created equal. Some closely related animals have independently evolved the same trait from the same 'starting point'; utilizing very similar developmental systems. This is 'parallel' evolution. There are conceptual issues here. Given that all life on earth evolved from a single event (and so from the same starting point) and given that all life utilizes developmental systems based on the same four-base genetic structure (and so utilize similar developmental systems), it seems as if *all* analogies are parallel. I need an account of parallelisms that is appropriate for restricting the scope of analogous inferences. This involves a return to Hall's proposal that we take homology and analogy as graded concepts. Here I claim that parallelisms should be understood in a similar way and argue briefly that an appropriate account refers to the kind of causal role played by the underlying developmental resources.

‘Parallelism’ is a graded concept. Some analogies will be ‘more parallel’ than others, and what determines this will *not* simply be closeness of relation, or similarity of developmental system, but similarities in developmental systems with the correct *causal relation* to the target phenotype. Take the oft-cited homeobox *Pax6* gene, for instance[x]. *Pax6*’s standard description is as a ‘master-control’ gene for eye development. Removal of the gene causes the failure of eye development, duplication causes extra eye development. Crucially, *Pax6* controls eye tokens, not eye types: cross species mixing causes extra eye development, but the extra eyes are typical of the receiving species, not the donor. Moreover, homologues of *Pax6* are used in the development of the convergent camera-like eyes of mammals and cephalopods (Tomarev et al [1996]) and the divergent compound eyes of insects. *Pax6* does not constrain eye-type evolution because it lacks *causal specificity* (Woodward [2010]) – it does not affect the phenomena of interest sufficiently[xi]. As *Pax6* is utilized across the cases we wish to contrast in explanations of eye evolution, it cannot explain those differences. A useful account of parallelism, then, must exclude causes like *Pax 6* and include those which constrain adaptive paths[xii].

In parallel cases natural selection is more likely to be an important cause of the evolution of the target trait, as developmental constraints are held in common across the lineages. Differences between closely related lineages are more likely to be due to extrinsic, rather than intrinsic differences. So, given close relatives, an environment-trait dyad is more likely to be robust and easier to test. In terms of analogous inference, if our scope has the right kind of constraints, our credence should increase.

Henneberg et al's hypothesis has a wide scope as they rely on an adaptive regularity across marsupial and placental clades. In their paper they do consider other marsupial lineages, which could support a narrower scoped claim about fingerprints in marsupials. First, koalas share a clade with the wombats, *vombatiformes* (see Phillips & Pratt [2008] for phylogenetic analysis), and wombats are neither arboreal, nor have fingerprints. Second, the short-tailed spotted cuscus, a more distantly related marsupial (clade *phalangeriformes*), is arboreal, grasps branches, and has fingerprints. Third, tree kangaroos are arboreal *but do not grasp,* and do not have fingerprints. Each piece of evidence supports the hypothesis that *in marsupials* fingerprints evolve in response to arboreal grasping. The first and third strengthen the connection between phenotype and selective environment and the second adds another data point.

If the scope of the hypothesis were restricted in this manner we would have higher credence in it: because marsupials have similar developmental systems, it is more likely that differences in selective environments are to blame for differences in fingerprint evolution.

2.2 Integrated Explanations

Scientific evidence and theories do not work in a vacuum. The best historical hypotheses draw upon as many evidential paths as possible. Comparative information, then, may be an important *part* of a hypothesis' support. Our credence is based on the support of the hypothesis as a whole, not its parts in isolation. We can incorporate analogies into *integrated explanations* which utilize multiple evidence streams.

There are two claims I want to make about analogies and integrated explanations. First, we take a total-evidence view: we examine the hypothesis and its components as a whole when determining credence. This is in part due to my second claim: the evidence for a hypothesis can be mutually-supporting. Consider the following case study.

John Horner's ([1983]) theory that some dinosaurs were altricial (nestbound and requiring parental care during youth) relies upon both comparative and fossil evidence. He and Robert Makela's discovery of fossilized Maiasaura nests in 1979 provided physical evidence that young were cared for. The fossilized remains showed that adult Maiasaur remained at the nest site post hatching and infants did not immediately leave the nest. In addition, the *design* of the Maiasaur nests was similar to bird's nests (Horner [1994]). Basically, because Maiasaur nests *look* like birds nests, Horner concluded that Maiasaur infants had a similar upbringing to extant birds.

Horner draws on two evidence streams to support his hypothesis: fossil and analogy. The fossils provide material evidence of Maiasaur life-ways and nest structure which suggest altricial behaviour. The analogy with birds supports the claim through a world to organism inference. If the structure of bird nests is an adaptation for altricial behaviour this is evidence that bird-like nest design evolves in response to selection for parental care in oviparous lineages. The hope is that the design of Maiasaur nests evolved as a response to the same pressure[xiii].

How would we determine credence in Horner's conjecture? The evidence both individually and in combination paint a picture of altricial behaviour in Maiasaur. We cannot treat the evidence individually, taking our total credence as the sum of the evidence, as the evidence is related. For instance, the analogy to bird-nest design is used by Horner to *explain* the fossils. The existence of bird nests designed to facilitate altriciality makes Maiasaur nests *less surprising.* This is to say the likelihood of discovering fossil nests from altricial lineages is higher given that birds utilize the same design for the same purpose. The analogous evidence makes the fossil evidence more likely, and vice-versa. If we buy this line, then we must conclude that the *total* evidence for Horner's hypothesis is in fact higher than the sum of the individual evidence.

Analogous inferences are strengthened when incorporated into integrated explanations. Because of the mutually-supporting nature of the evidence, independent and robust confirmation dramatically increases credence in the analogous inference.

2.3 Convergent Modeling

I now turn to analogous inferences which are not as constrained as parallel models, or parts of integrated explanations. Under certain circumstances, *convergent models,* tested and refined across several analogues, can increase our credence in analogous inferences.

The difference between a convergent and a parallel model is one of degree. In the latter case we restrict ourselves to a narrow scope, in the former we test across a wide scope.

What is a convergent model? Analogous inferences rely on adaptive regularities matching trait/niche dyads. Henneberg et al hypothesize that across all mammals fingerprints will evolve given prehensile extremities and occupation of an arboreal grasping niche. In convergent modeling, we test this wide-scoped hypothesis across a set of analogues. This has two results. First, the model is supported by confirming cases. Second, the model can be refined as we discover exceptions.

Hoppit et al's ([2008]) model of the evolution of teaching in hominids uses meerkats as an analogue and is an excellent opportunity for convergent modeling. Thornton & Mcauliffe ([2006]) demonstrate that meerkats teach scorpion hunting to their pups by providing debilitated scorpions in response to begging calls. This counts as teaching according to Caro & Houser's ([1992]) *functional* definition. Roughly, an individual is teaching just in case they modify their behavior in some way which does not benefit their carrying out of the skill in question, but increases the chance of uptake. If your aim is to hunt and kill a scorpion, biting off its sting and giving it to a pup to play with is terribly inefficient; however, if you want your offspring to learn to hunt scorpions, this behavior will help.

Based on their observations of meerkats, Hoppit et al hypothesize that teaching evolves given three variables. First, the population must include inadvertent social learners; they must have the cognitive acumen to learn through trial and error. Indeed, Meerkats do learn through trial and error. Second, there must be a selective advantage for the *tutor* if the pupil picks up the skill. As teaching is a change in tutor behavior, for this to be visible to selection it must benefit the tutor. Meerkats are cooperative breeders, and the faster pups can fend for themselves the better, so it is a reasonable conjecture for their lineage. Third, inadvertent social learning must be inadequate, costly, or at least inefficient, for the passing on of the skill; otherwise there would be no reason for selection to favor teaching over inadvertent social learning. And indeed trial and error learning is an *awful* way to learn venomous scorpion hunting.

As the first two variables are true of our closest relatives, Hoppit et al suppose that teaching evolved in humans due to selective pressure to learn new and more complicated skills:

> Unlike in other apes, in humans, teaching could have been favored by the requirement to transmit complicated skills and technology that are not easily acquired through inadvertent social learning. (Hoppitt et al [2008])

This hypothesis covers a fairly wide scope: *carnivora* and primates share a common ancestor around 85 million years ago, the rodents, primates and carnivores falling within that clade (Dawkins [2004]). Hoppitt et al’s organism to world inference, then, has an implicit assumption that (for most placental mammals) teaching will most likely evolve given those conditions. At such a scope, we might worry that natural selection's path would be too easily confused by non-selective factors.

Fortunately, teaching has been proposed in many lineages since Caro & Hauser's paper. Hoppitt et al cite eusocial insects (ants and bees), non-human primates (callitrichid monkeys), *carnivora* (cheetah, domestic cats, meerkats) and birds (pied babblers and domestic fowl). Marino et al ([2007]) also propose teaching in *cetacea*. It seems reasonable to count five analogues: non-human primates, *carnivora*, birds, cetaceans and eusocial insects. In convergent modeling, we would test the model across these five analogues. Clarke ([2009]), for instance, shows that feeding calls in White-tailed ptarmigan (a species of alpine grouse) influences diet-choice in chicks:

> White-tailed ptarmigan hens display a multimodal signal composed of food calling (a distinctive guttural clucking) and tid-bitting (dropping bits of a food item with active head bobbing) only in the presence of their precocial chicks… Invariably, the chick then pecks at and consumes morsels of the specific food item indicated by the hen (Ibid pp27).

The White-tailed ptarmigan meets the requirements of Hoppitt et al's model. The hen points out protein-rich food sources which are difficult to identify[xiv], in an alpine environment food is scarce and so trial and error learning could lead to starvation, the chicks retain eating preferences into adulthood, birds typically learn through trial and error, and so on. This supports Hoppitt et al's model, increasing our credence both in the model and the hypothesis that teaching evolved in our lineage in response to similar needs.

Both convergent and parallel modeling can have a further effect: refining the model. Exceptions are not necessarily falsifying but can lead to improvement. An example of refinement comes from primatology. Testicular size is used a measure of sperm competition in primates (Harcourt [1995]). In a promiscuous environment there is selection for male investment in sperm production, which is manifested in larger teste size. As there is selection against heavy sperm production in non-promiscuous environments, a primate's testicle to body ratio ought to be a signal of their breeding strategy. This is the basis of a quantified model: teste size against body mass predicts breeding strategy.

In Jolly & Phillips-Conroy's ([2006]) study of teste size in baboons, yellow baboons did not fit the model. By a measure of body-mass to testicular size their testes were too small given their promiscuous breeding strategy. On reflection, Jolly & Phillips-Conroy realized that the unusually long, heavy arms of that lineage skewed the result. 'It is evidently the relatively long (and thus proportionately heavy) limbs of yellow baboons that make them *appear* to have smaller testes, when total body mass is used as the standard (Ibid pp 267).' By measuring teste size relative to *trunk* mass the yellow baboons were fit to the model – and the model itself was refined. Moreover, this approach provides research strategies: given Hoppit et al's hypothesis we should examine teaching in particular animals, and its phylogenetic spread overall.

And so testing adaptive models across groups of analogues both increases our credence in the model even if the scope is wide, and can result in refinements.

Conclusion

Analogy is an important empirical stream of evidence for both inspiring and corroborating adaptive hypotheses. It deserves some measure of the philosophical attention paid to homology. I have explained analogy's use in supporting adaptive claims both about single lineages and evolution more generally, as well as showing which factors affect their evidential weight. Coarse grained analogies supporting wide scope, highly specific inferences are problematic. However, through parallel and convergent modeling, as well as incorporating analogies into integrated explanations, such worries can be partly mitigated.

Much work remains. In light of the importance of analogy as evidence, a reassessment of the ontological and epistemic relationship between homology and analogy is in order. Also, historical linguistics, archaeology, and other fields make use of something very similar to analogy and whether this paper's position is extendable into those domains is an open question. Moreover, the use of non-adaptive analogies in biology deserves attention. Finally, a general account of biological epistemology must incorporate the role of analogies into its framework.

If we are to draw on the bounty of natural analogous experiments, while respecting contemporary concerns about constraint and non-selective forces in evolution, we must adopt a more careful approach to analogous inference. After all, our window to the past is opaque – so any available solvents ought to be rigorously applied.

Adrian Currie

c/o Philosophy, ANU RSSS
Coombs (building 9)
ACT, 0200

Adrian.currie@anu.edu.au

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[i] This is a *taxic* definition of homology and homoplasy, tied to phylogenetics. There are other approaches which are quite different in character. I think Griffiths ([2007b]) is right in claiming that taxic homology should be understood as an *explanation* of similarity in biology. Given that my target is the explanatory and evidential uses of analogy, the taxic account is appropriate.

[ii] For instance, we might infer the nature of developmental constraint in reference to two independently evolved non-functional characters.

[iii] Simon Conway-Morris ([2003]) is a striking exception. It is a rich source of examples of analogy; however his claim that convergence provides evidence that life is massively non-contingent due to *selective* constraint is not supported by the analogies he cites (see Sterelny [2005] for critical discussion). In terms of the analysis I introduce later, the wide scope and high specificity of Conway-Morris' claim demand a very high standard of evidence indeed, which extant cases of analogy simply cannot provide.

[iv] I am grateful to an anonymous referee for drawing my attention to this work.

[v] Interestingly, Clayton et al [2007] make a similar claim in relation to avian cognition: '… since birds do not have the typical six-layered cortex found in humans and other mammals, this divergence in structural organization of the brain raises the question of whether these cognitive abilities are achieved by similar or different neurocognitive mechanisms in the avian and mammalian brain (pp 520).'

[vi] We might question whether claims about function are claims about the world. I take it that there are truths about whether a trait was selected for in previous environments, and insofar as this sets the proper function of the trait, then this is a fact about the world. Further, 'activity' function, which makes no claim about the evolutionary history of a trait (see Amundsen & Lauder [1994] & Love [2007]), is at least in part a claim about the world. Our interests may set the functions we seek, but those functions are found in the organization of the phenomenon and its components.

[vii] Thanks to Kim Sterelny for the 'organism to world' and 'world to organism' terms here.

[viii] The question of grain is important for Paul Griffiths' issues with *shallowness* in analogy. As he puts it, 'It is a truism in comparative biology that similarities due to analogy (shared selective function) are "shallow". The deeper you dig the more things diverge (Griffiths [2007a], pp 216).' If it turns out that analogies are usually coarse grained, then we can only employ them in the defense of 'shallow', or less specific, claims. In part, the considerations in the second half of the paper serve to counter these worries.

[ix] The environment, however, is not particularly fine grained: merely inhabiting an arboreal, grasping niche is mentioned. However, given the specificity this is perhaps all that is required.

[x] See Callearts et al ([1997]) for a thorough, if dated, overview

[xi] See Powell ([2007]) for a similar approach to parallelisms, as well as Gould's ([2002]) discussion of 'pharaonic bricks' and 'corinthian columns'

[xii] Gould ([2002]) provides a example in the form of maxillipedalism, the transformation of limbs into eating apparatus in *crustacea.* The developmental triggers which controls these transformations across the clade have been identified and provide an '… operational basis… to firm and testable explanations… (Ibid pp 1132).'

[xiii] Of course the appropriateness of this example turns on whether nest-building in birds and Maiasaur is homologous or homoplastic. This is a difficult claim to support or undermine, given the difficulty of tracing dinosaur nesting behaviour. Even if the example fails in the details, its lesson does not: *if* nest building is analogous between the two lineages, then Horner's argument is best cashed out in my terms. I am grateful to an anonymous referee for pointing this out.

[xiv] Fowl have very few tastebuds, and Clarke suggests that without motherly intervention the chicks do not identify these protein-rich foods.