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The Epistemic Functions of Biological Agency in Evolutionary Biology

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Abstract
Explanations for adaptive change tend to emphasize what happens to organisms rather than what organisms do, or how they do it. The surging interest in the relationship between developmental plasticity and evolution demonstrates that biological agency can structure research agendas, and raises a number of general issues concerning explanatory power and the nature of explanation in evolutionary biology.

Key Words
Agency; developmental plasticity; explanation

Human cultural practices have differentiated into a bewildering diversity of forms and functions. Explanations for such cultural change can draw on a range of factors. Some factors can be seen to impose change from the outside; drought being one example. But cultural change can also be initiated and directed by factors that can be considered endogenous or internal to individual humans, including their goals, ambitions, and needs. The connection between human agency and agriculture, social stratification, or local customs may be tortuous and difficult to establish, but it is hard to deny that human agency can carry explanatory weight for why human cultures change, or why they change in particular ways.

Explanations for biological evolution are supposed to be fundamentally different in this regard. The explanation for adaptive behavioural change in a population of fish encountering a novel predator is not supposed to refer to how fish responded to the predator in their attempts to survive, but to the selection of slight behavioural differences, underpinned by genetic variation. As vertebrates colonized land, limbs did not evolve because the bones and muscles of fins tried to accommodate awkward movement, but their evolution should be explained by cumulative natural selection of small variants in fin morphology, underpinned by genetic differences. Of course, individual fish that encounter a new predator frequently do modify their behaviour vin ways that help them survive, and bones and muscles do accommodate mechanical stress to maintain functional integration. In this sense, organisms and their parts can be said to act and respond purposefully, or to exhibit agency.[1] However, in contrast to explanations for human cultural change, the goal-oriented behaviour and development of fish seem to 'have no real status as centres of causal agency' (Goodwin, 1999) for biological evolution. Evolutionary biology, like any good natural science, explains in terms of causes and forces rather than appealing to goals and purposes.

It is commonly considered that evolutionary biologists not only rule out explanations that refer to organismal goals (i.e., teleological explanations), but that one should not grant the 'proximate' causes or mechanisms that underpin goal-oriented behaviour and development any explanatory power either (Mayr, 1961; Laland et al., 2011). Proximate causes are supposed to explain how biological systems work, but not why they evolve. Instead, as in the examples above, explanations for adaptive diversification should rely entirely on fitness differences between individuals (or genotypes) – natural selection – as the 'ultimate' cause.[2]

The distinction between proximate and ultimate causes can be found in virtually every modern textbook on evolution, where it is intended to help students identify what is an evolutionary explanation

and what is not. Keeping the mechanisms of development, physiology and cognition out of evolutionary explanation implies that it does not matter to evolution what kind of entity organisms actually are, or how they work. This ensures 'an impermeable barrier between individual agency and evolutionary transformation' (Riskin, 2020, p. 273) that many scientists consider central and essential to evolutionary explanations (e.g., Scott-Phillips et al., 2011; Charlesworth et al., 2017; see Laland et al., 2011; 2014). In practice, however, biologists commonly make use of concepts that refer to goal-oriented processes when they explain evolutionary change. Behavioural ecology, for example, is rife with references to strategies and goals, and the selfish gene perspective even seem to grant agency to DNA. Biologists typically explain their use of agential language as a convenient metaphor. Genes, cells or organisms do not really try to maximize their biological fitness; the choice of words is simply a short-hand for saying (something along the lines of) that competition over limited resources will result in an increase in those features of genes, cells or organisms that cause particular variants to have more descendants than others. This *metaphorical short-hand function* of agential concepts in evolutionary explanations is widely considered a legitimate and effective way to communicate, but its shortcomings continue to be a matter of debate (e.g., Godfrey-Smith, 2009; Okasha, 2018; Veit, 2021).[3]

In this essay, I will outline three other possible epistemic functions of biological agency in evolutionary biology (see Uller, 2023). Firstly, thinking of genes, organisms or other entities as agents can make evolutionary theory intelligible to the scientists themselves. This reason for adopting agential language is compatible with considering goal-oriented processes, like development, irrelevant for explaining adaptive evolution. Nevertheless, it identifies a distinct epistemic function of agency in evolutionary explanations that is not primarily communicative. The second function of biological agency is rather different, because it is the result of a rejection of the traditional separation of proximate and ultimate causation/explanation. By granting that organismal development and behaviour provide directionality to adaptive evolution, this perspective sets an alternative explanatory agenda with its own criteria of explanatory adequacy (Love, 2008; Brigandt, 2011). Finally, it is possible that reference to organismal goals themselves can be explanatory, perhaps not unlike the relationship between human agency and cultural change that opened up this chapter. On this account, organismal agency makes biology sufficiently different from physics and chemistry to support a kind of explanation that other natural sciences dismiss, but one that it shares with the human sciences.

Biological Agency Could Make Evolutionary Theory Intelligible

Evolutionary models may be heavy on mathematics, but one can get quite far in evolutionary theory on standard algebra and statistics. If you understand the theory, that is. The philosopher Henk de Regt has pointed out that scientists will struggle to use a particular theory unless they can grasp the consequences of the theory without performing detailed calculations (de Regt, 2017). For example, to develop a population genetic model to study how dispersal influences the evolution of cooperation, the scientist must make a number of assumptions about the structure of the model. These decisions are not easy to make unless the scientist can intuitively grasp the consequences of varying assumptions, such as the number of loci or the size and number of patches that can be occupied. In other words, population genetic theory must be intelligible to the scientists as a theory for it to be successfully applied to explain evolutionary phenomena.

Scientists use a wide range of conceptual tools to facilitate the intelligibility of theories. One famous example in evolutionary biology is the metaphor of the adaptive landscape, which allows graphical representation of the consequences of selection and genetic drift without knowing the details of the mathematics. Thinking of genes or organisms as maximizing agents arguably has a similar epistemic function, at least for some biologists. Perhaps agential thinking comes naturally to humans and therefore easily adopted as a conceptual tool. Not everyone will find the same conceptual tool useful (e.g., Kaplan 2008; see Skipper & Dietrich 2012), however, and this may therefore be one source of the controversy surrounding the use of biological agency in evolutionary biology. Moreover, since

conceptual tools are designed to facilitate intelligibility of theoies rather than understanding of phenomena, biologists may say one thing about the entities they study (e.g., 'bacteria try to maximize their inclusive fitness') but consider those entities to have entirely different properties (e.g., 'bacteria do not really try to do anything because they do not have agency'). Yet, scientific intelligibility and metaphysical views likely interact, and the success of agential thinking in evolutionary theory may very well have influenced wide-spread beliefs about the causal and informational privilege of genes, that the genome is a program or blueprint, and so on.

Biological Agency Could Set Explanatory Standards

The distinction between proximate and ultimate causes can make it difficult to see how biological agency could have any other epistemic function in evolutionary biology except serving as a metaphorical short-hand or conceptual tool. However, the logic of explaining adaptive change solely in terms of natural selection has come under quite some pressure over the past two decades (not for the first time, though). One of the challenges come from evolutionary biologist Mary-Jane West-Eberhard.[4] Her highly influential book Developmental Plasticity and Evolution (West-Eberhard, 2003) can be read as one long argument for the explanatory relevance of goal-oriented developmental processes in evolution. In brief, West-Eberhard points out that it is perfectly valid to begin an evolutionary explanation with the developmental responses to genetic or environmental perturbation. These responses determine the distribution of phenotypes that can be selected, and they may facilitate adaptive evolution because the mechanisms of development often allow the mutual, adaptive adjustment of different parts of the organism. For example, a mutation that increase bone growth can be beneficial only because muscles and tendons adjust to the growing bone and thus ensures that the modified limb will remain functional. West-Eberhard therefore consider the first order of adaptive design in nature to be development, not natural selection.

To begin with the flexible phenotype implies that proximate responses to environmental change, or *phenotypic plasticity,* also can have evolutionary consequences. Consider again a population of fish encountering a new predator. How individuals respond plastically will (together with genetic variation) determine the distribution of phenotypes that selection can act upon.[5] Moreover, those responses are more likely than not to reduce the risk of predation even if the predator is novel, because the more general principle of being exposed to a threat is not novel. Thus, it is partly because individual fish respond to predators in a goal-oriented manner that the population can adapt, and how the individuals respond determines in part how the population will adapt. This argument applies even if genetic variation is the only heritable source of within-population phenotypic variation. Similarly, when the bones, muscles and tendons of fins adjust to support a moving body on land, the mechanisms of development are presenting phenotypes to be selected, and the ability of parts to respond functionally to each other facilitates adaptive evolution. More generally, what organisms do and how they function are causes of both phenotypic variation and natural selection. *Phenotypic accommodation* (West-Eberhard, 2003), *facilitated variation* (Gerhart & Kirschner, 2007), and *niche construction* (Odling-Smee et al., 2003) are all concepts that capture the goal-orientation of individual development and behaviour. By crediting the biological processes that underlie biological agency with the power to cause adaptive change, this perspective sets an alternative explanatory agenda for evolutionary biology (Love, 2008; Brigandt, 2011). This agenda is associated with a different set of explanatory standards compared to the standards of the traditional, genetic, representation of evolution by natural selection. These standards in turn motivate scientists to draw on different sets of knowledge, concepts and methods in their evolutionary analyses, including from fields that previously were considered largely irrelevant (e.g., from cell and developmental biology).

That proximate causes can be explanatory for adaptive evolution is a notion that has gained traction (see Uller & Laland, 2019a), but it remains a source of contention in the field.[6] Assigning explanatory responsibility in evolution to the organisms themselves may be controversial in part because it seems to reinstate internal drivers of adaptive evolution. These perspectives will tend to bring to

Lamarckism, orthogenesis and similar ideas that sometimes are considered very problematic and perhaps even inherently 'unscientific'. However, it is not the facts of developmental plasticity that are controversial, and few would claim that explanations for adaptive change that cite both developmental plasticity and natural selection do not adhere to the explanatory standards of the natural sciences more generally. It would have been much more controversial to claim that organismal goals themselves are explanatory. As it happens, there are some philosophers and biologists who do claim that something along those lines is an inevitable conclusion of taking biological agency seriously.

Biological Agency Could be Explanatory

It is extraordinary that the diversity of multicellular life evolved from single-celled organisms – what are the reasons for this impressive capacity for open-ended evolution? The answer cannot be that biological evolution occurs through natural selection, because any entities to which one can assign 'parents' and 'offspring' could in principle evolve through generation of heritable variation and selective retention. Perhaps the answer has more to do with what organisms are? Some biologists and philosophers suspect that biological evolution is special because organisms are agents (recent examples include Walsh, 2015; Jaeger, 2021; Sultan et al., 2021). Agency, in this context, refers to how living systems have the ability to initiate activity from within their own boundaries, and to sustain and transform themselves in ways that ensure their continued existence (Walsh, 2015). On this agential view, adaptive evolution is not something that happens to organisms, but a consequence of organisms' goal-oriented activities.

So far, this perspective seems very much in line with (perhaps even the same as) the perspective that motivated West-Eberhard and similar-minded biologists to rethink explanatory standards in evolutionary biology. However, according to philosopher of science Denis Walsh, those researchers have not gone far enough. Walsh argues that – if biological evolution happens because organisms are agents – there is a counterfactual relation between goals and organismal activities that can exploited to actually explain evolutionary events (Walsh, 2015; 2018; see also Jaeger, 2021).

To unpack this claim, it may be helpful to return to the hypothetical fish population adapting to a novel predator. Recall how keeping proximate causes out of evolutionary explanations implies that adaptive change is to be explained by fitness differences between individuals with alternative behaviours. A perspective that recognizes a role for development in evolution could motivate the search for additional explanans in how the fish responded behaviourally and physiologically to the risk of predation.[7] Referring to both behavioural plasticity and natural selection could be the more satisfactory explanation (Baedke et al., 2020; Uller et al., 2020), but perhaps it still leaves an explanatory gap? Specifically, the explanation seems unable to account for why those consistent biases imposed by the fishes' behaviours exist in the first place, and how they could impose an adaptive bias on evolution? One possible answer is that those developmental biases that facilitate adaptive evolution themselves are products of natural selection of unbiased genetic (and phenotypic) variation (see also footnote 7). However, on the agential view, natural selection underdetermines organismal responses to their environment: organisms are not agents because they carry a naturally selected genetic program but because living systems have a particular kind of organisation (Mossio & Bich, 2017; Jaeger, 2021). Moreover, it seems to be precisely because organisms can initiate action from within their own boundaries that their actions cannot be accounted for solely by referring to external factors, such as the past 'selection' of favourable characters by the environment (on the agential view, natural selection is an outcome of organismal agency rather than an external cause or force; Walsh, 2015). Walsh instead suggests that we should recognize the 'endogenous source of changes in form' (Walsh, 2018, p.181) as means conducive to the goal of survival. On this account, the goal of survival appears to be a legitimate difference maker for adaptive evolution. It would explain why the fish encountering a predator responded as they did by recognizing that those behavioural responses conduce on the fish's goal of survival. If these were not means to goals, the behavioural responses that caused adaptive evolutionary change would not have occurred, and the prey population would have

adapted in some different way, or not adapted at all.

While the case for naturalistic teleological explanation in evolutionary biology is likely to be met with scepticism by many scientists and philosophers, biologists do recognize that it matters to evolutionary dynamics whether or not organismal activities are oriented towards goals. For example, the niche construction literature emphasizes that organismal activities that are goal-oriented result in more consistent selective pressures than do other sources of selection (Laland et al., 2017; Clark et al., 2020). Similarly, it has been pointed out that the evolutionary consequences of developmental plasticity depend on whether or not plastic responses are adaptive (e.g., Ghalambor et al., 2007; Feiner et al., 2020). In fact, the explanatory agenda motivated by organismal agency, discussed in the previous section, largely seems predicated on the idea that it matters to evolution that organismal development and behaviour are goal-oriented processes. A challenge to the agential perspective is to demonstrate that reference to goals provide an additional layer of scientific understanding of evolutionary outcomes that are difficult to grasp by existing accounts. Analyses of when and why reference to (human) goals are explanatory in human (cultural) evolution may be helpful in this regard (Chellappoo, 2022).

Conclusion

Evolutionary biologists have a complicated relationship to organismal agency; seemingly undeniable, yet hard to accept as a difference maker for biological evolution. Agential concepts frequently function as metaphorical short-hand to communicate ideas and findings, but they can also be conceptual tools that make evolutionary theory intelligible to individual scientists. Neither the short-hand nor the conceptual tool functions of biological agency necessarily assign properties to biological systems themselves, but biologists do not usually deny that at least organisms can be considered agents. Historically, evolutionary biology has rather done away with biological agency by assuming that proximate causes be kept out of evolutionary explanations. However, the causal fabric of the world does not have to be cut this way. A representation of the evolutionary process that 'put[s] the flexible phenotype first' (West-Eberhard, 2003, p.3) recognizes as evolutionary causes what organisms do and how they work. As such, biological agency sets an explanatory agenda that differs from the traditional representation of evolution, which considers natural selection the only real difference-maker for adaptive change. A more radical claim is that biological agency implies that goals can be explanatory because of a counterfactual relation between organismal goals and the organismal activities that generate evolutionary change. Whether agency is considered something to be avoided or a fundamental driver of adaptation, organismal agency exercises an influence over the kinds of problems biologists address, what knowledge, concepts and methods they import from other disciplines, and what they consider a satisfactory explanation.

Notes

1. Sultan, Moczek and Walsh refer to biological agency as "the capacity of living systems at various levels to participate in their own development, maintenance, and function by regulating their structures and activities in response to conditions they encounter" (Sultan et al., 2022).

2. Not all evolution is adaptive, of course, and thus there are additional ultimate causes that directly change allele frequencies, such as migration and stochastic processes ('genetic drift').

3. By agential concepts, I roughly mean concepts that (at least seemingly) recognize goal-orientation in biological systems or entities. For example, a strategy implies that someone (for example, a gene or an organism) has a goal. Many concepts in biology seem to have built into them that development and behaviour are goal-oriented processes. For example, phenotypic accommodation is commonly used to refer to mutual adaptive adjustment of parts in development that ensures functionality of the phenotype as a whole (West-Eberhard, 2003).

4. West-Eberhard writes 'the proximate-ultimate distinction has given rise to a new confusion, namely, a belief that proximate causes of phenotypic variation have nothing to do with ultimate, evolutionary explanation. For evolutionary biology, proximate mechanisms represent more than just different levels of analysis or research styles. They are the causes of the variation upon which selection acts' (West-Eberhard, 2003, p. 11).

5. To be clear; this evolutionary scenario does not assume any inheritance of acquired characters. It simply recognizes that there are multiple different ways to adapt and that the phenotype that eventually evolves must first appear in some rudimentary form for selection to be able to refine it.

6. This is in part because of the argument that all the adaptively relevant consequences of development and behaviour in evolution are themselves best explained by natural selection in the past. This would keep the distinction between proximate (= non-explanatory) and ultimate (= explanatory) causes in evolutionary biology intact. On this account, evolutionary biologists may accept that the mutual adjustment of bone, muscles and tendons in response to movement on land could have facilitated adaptation to land. However, they would argue that citing developmental plasticity is an optional 'add-on', or even a misleading level of detail. In their view, a better explanation for the evolution of the proto-limb would replace reference to developmental plasticity with past natural selection for plasticity, on the logic that selection for plasticity is the only valid explanation for the mutual adjustment of bone, muscle and tendons (see Laland et al., 2014). The details of the refutations of this counterargument goes beyond the scope of the present paper, but include pragmatic considerations (e.g., replacing plasticity with past natural selection would not provide better insights; Baedke et al., 2020; Uller et al., 2020), arguments from general biology (e.g., biological systems exhibit some degree of adaptive organisation without natural selection; Newman & Müller, 2000), and evolutionary theory (e.g., the presence of adaptive plasticity does not imply past selection for plasticity; Rago et al., 2019), and the recognition that the explanatory preference for natural selection relies on a particular representation of the evolutionary process (e.g., it rests on the idea that the principles of evolution by natural selection are autonomous or separable; Walsh, 2015; Pocheville, 2019; Uller & Helanterä, 2019). See Uller & Laland (2019b) for an overview.

7. There is now good evidence that learning and plasticity structure the distribution of phenotypes, but when and why such effects are strong and persistent enough to shape patterns of phenotypic evolution remain poorly understood (see discussion in Feiner et al., 2020).

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