



Extending the Extended Phenotype

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The mid to late 1970s witnessed an insurrection within evolutionary biology: Starting within the field of animal behaviour, it was the driving force behind the sociobiological revolution, central to the emergence of behavioural ecology and evolutionary psychology, and revitalized population genetics. Labelled 'gene-selectionism' or 'the gene's-eye view', it was a powerful new way of thinking about the process of natural selection. If we wish to understand what phenomena ought to have evolved, we should consider the problem from the perspective of the gene and ask which properties would be most likely to increase its frequency. From this new standpoint, life evolves through the differential survival of replicating entities, with the gene the archetypal replicator. The much-vaunted organism is a mere tool by which genes ensure their propagation. Bodies are battle grounds in which rival genes fight out conflicts, while the behaviour of one party is manipulated by the genetic interests of another.

Pioneers of the gene-selectionist perspective included some of the greats of modern evolutionary biology: Bill Hamilton, John Maynard-Smith, Robert Trivers and George Williams. But nobody, before or since, has expressed gene-selectionism with the clarity and rigor of Richard Dawkins, particularly in his two most influential books *The Selfish Gene* and *The Extended Phenotype*. The 'individual-as-unit-of-selection' establishment may have responded to Dawkins' writings with a hostile rearguard, but the younger generation were wowed by the sheer persuasiveness of Dawkins' argument. For most readers, there simply was no other way to think.

In the preface, Dawkins describes *The Extended Phenotype* as a sequel to *The Selfish Gene*, although geared to an audience of professional biologists. In many respects, *The Extended Phenotype* can be viewed as a defense of Dawkins' earlier tome: If Hamilton, Williams, Maynard-Smith and Trivers were the heroes of *The Selfish Gene*, Gould, Lewontin, the Cambridge ethologists and other critics, were the villains of the follow-up. But *The Extended Phenotype* was much more than a re-iteration of an earlier position.

It was a more sophisticated account of gene selectionism than any preceding text, and it contained a host of new insights. In *The Extended Phenotype* Dawkins took gene selectionism to what appeared its logical conclusion. If genes are regarded as propagating themselves through the construction of 'lumbering robot' vehicles, it makes sense to see them as expressed in artefacts, or in the behaviour of heterospecifics:

The phenotypic effects of a gene are the tools by which it levers itself into the next generation, and these tools may 'extend' far outside the body in which the gene sits, even reaching deep into the nervous systems of other organisms (Dawkins 1982: vi).

As in all his books, Dawkins' writings are brought to life through compelling examples. When reed warblers feed cuckoo chicks, cuckoo genes are being expressed. Those genes were favoured by selection because, more effectively than their alleles, they 'exert their developmental power over host phenotypes' to ensure their own replication. Genes even exert their influence outside of the living world. No matter that they are abiotic, beaver's dams and caddis fly larvae' houses have evolved by Darwinian processes, under the control of naturally selected genes.

The Extended Phenotype has a genuinely radical quality and, in my opinion, history will judge it as the clearest exposition of a conceptual revolution. At the heart is Dawkins' attempt to challenge the then orthodox position that organisms behave in such a way as to maximize their own fitness. In Dawkins' world, behaviour, like any aspect of the phenotype, is not there 'for the good of' the organism, it is 'for the good of' genes, and frequently someone else's genes. In 1982 this message seemed seditious, even fanatical. Yet as *The Extended Phenotype* rolled off the press, Dawkins was able to point to early signs that gene-selectionism was beginning to take over. Twenty-one years on, Dawkins' position is now pretty much the orthodoxy. Certainly, Dawkins still has his critics. But whether he is maligned for his 'confrontational' writing style, his 'adaptationist' stance, his treatment of religion, the (wrongful) accusations of genetic determinism, or merely as the face of 'sociobiology' (a dirty word to thousands), in professional circles at least, it is not for his gene selectionism. Currently, no undergraduate course on evolutionary biology is complete without Hamilton's kin selection, Maynard-Smith's evolutionary game theory or Trivers' conflict theories; there is legions of theory and data on parasites manipulating host behaviour (Moore 2002), and gene-selectionist theory continues to throw up new insights (Haig 1997). The gene's-eye view has proved its value. Whether we like it or not, we now live in Dawkins' world.

To my mind, *The Extended Phenotype* is Dawkins' best book, a judgement with which many professional biologists concur (including, I have heard

rumored, Dawkins himself). I regard it as one of the most influential scientific books of recent years, a book with big ideas, and implications that are still not yet fully appreciated. Dawkins is not just a talented communicator but a savant, and there is no doubt that he has been instrumental in changing the way that people think about evolution.

There is also a sense in which *The Extended Phenotype* is a profoundly conservative book, and it is on this aspect that I will concentrate the remainder of this article. Two-thirds of the way through the book, Dawkins gently reproaches his colleague Hamilton for not ‘following his ideas through to their logical conclusion’ (p. 194). In the same spirit, I would like to suggest that Dawkins too has held back from teasing out the full implications of the extended phenotype concept; that he has wavered on the cusp of another revolution, and let caution steady his hand.

I will begin by drawing a distinction between two kinds of causation that may be instrumental within biology, *linear* and *cyclical*. Linear causation is exemplified by the hammer and nail. Appropriate use of a hammer drives the nail into some substrate such as wood, but nails do not reciprocate by propelling hammers. Here, for clarity, I am ignoring the force exerted by the nail on the hammer. Most people would feel comfortable with the description of the hammer as *causing* the nail to enter the wood. Chickens and eggs, on the other hand, represent cyclical causation. Chickens produce eggs, and eggs hatch into chickens. Neither could exist without the other.

The conventional view of the evolutionary process is closer to the linear than the cyclical notion of causation. Hot climates select for heat dispending adaptations, such as sweat glands or large ears. But no matter how much an animal sweats it is not regarded as affecting the local temperature to any significant degree. As a result of natural selection, the properties of environments shape the properties of organisms, but not the other way around (except in cases such as co-evolution where other organisms are the environment). A gene-selectionist perspective does not change this relationship – it merely switches the focus from organisms to genes. The properties of the selective environments favour certain genes over others, according to the utility of their phenotypic effects. As Dawkins puts it:

the genes that exist today are a selected set, and the qualities that made them survive reflect the qualities of the environments in which they survived (p. 94).

Conversely, with the above caveat, the properties of genes are not generally regarded as producing the selective environment. Adaptation is regarded as a process by which natural selection, stemming from an external environment, gradually molds organisms to be well suited to their environments (Godfrey-

Smith 1998). Despite recognition that processes independent of organisms often change the world to which populations adapt, the changes that organisms themselves bring about in their environments are rarely considered in evolutionary analyses.

Yet all living creatures, through their metabolism, their activities, and their choices, partly create and partly destroy their own, and each other's, niches, on scales ranging from the local to the global. Organisms choose habitats and resources, construct nests, holes, burrows, webs, dams, pupal cases, and a chemical milieu, and choose, protect and provision nursery environments for their offspring. They also take energy and resources from environments, emit detritus and die in environments, and by doing all these things, modify at least some of the natural selection pressures present in their own, and in each other's, local environments.

After Odling-Smee (1988), this process of organism-driven environmental modification is known as "niche construction". For a number of years my colleagues John Odling-Smee, Marc Feldman and I have argued that niche construction has a number of important, but hitherto neglected implications for evolutionary biology and related disciplines. Due recognition of niche construction changes the evolutionary process from a linear to a cyclical conception of causality (Odling-Smee et al. 2003). We regard ourselves as part of a growing movement that has sought a re-conceptualization of the process of adaptation by placing emphasis on niche construction (Brandon and Antonovics 1996; Griffiths and Gray 2001; Jablonka 2001; Lewontin 1982, 1983; Oyama et al. 2001).

Niche construction is not the exclusive prerogative of large populations, keystone species or clever animals; it is a fact of life (Odling-Smee et al. 2003). Organisms across the breadth of all known taxonomic groups construct important components of their local environments. Niche construction is, after natural selection, a second major participant in evolution. The properties of environments *cause* (some of) the properties of organisms through the action of natural selection, but equally the properties of organisms *cause* (some of) the properties of selective environments through niche construction.

At first sight, Dawkins' extended phenotype concept seems to capture the essential features of niche construction, and hints at cyclical causation. Genes manufacture environmental states to their own ends, reaching out of bodies to be expressed in the construction of webs, mounds and bowers.

an animal artefact . . . can be regarded as a phenotypic tool by which that gene could potentially lever itself into the next generation (p. 199).

But for Dawkins, the only relevant feedback from extended phenotypes is to the genes that produce them. Consequently, the only role for phenotypes, be

they ‘conventional’ or ‘extended’, is to survive and reproduce and ensure that the genes responsible are replicated. When beavers build dams they ensure the propagation of ‘genes for’ dam building, and that is all. Linear causation is maintained.

Conversely, we emphasize the fact that, through its niche construction, a beaver radically alters its environment, modifying many selection pressures that affect the fitness of genes that are expressed in quite different traits, such as beaver teeth, tails, feeding behaviour, susceptibility to predation, diseases, and life history. Niche construction feeds back to modify natural selection, which changes niche construction, and so forth, in endless cycles.

Dawkins is aware of this feedback, but does not dwell on it:

if the gene-pool is dominated by genes that make animals seek dry places, this will set up selection pressures in favour of genes for an impermeable skin. But alleles for a more permeable skin will be favoured if the gene-pool happens to be dominated by genes for seeking damp places. . . . An important aspect of the environment which selects between alleles at any one locus will be the genes that already dominate the gene-pool at other loci (p. 111).

For Dawkins niche construction is regarded as the product of naturally selected genes, but not part of the process. Indeed, Dawkins says as much:

There are causal arrows leading from genes to body. But there is no causal arrow leading from body to genes (p. 97).

I am quoting Dawkins out of context here, since he was making a point about the non-inheritance of acquired characteristics, but I suspect he would not have written this if he regarded niche-constructing organisms as modifying selective environments and *causing* alternative genes at other loci to be favoured.

The conventional perspective might be more justifiable if the feedback from niche construction was inconsequential, but we have carried out mathematical analyses using population genetics models that suggest this is not the case (Laland et al. 1996, 1999, 2001; Odling-Smee et al. 2003). The effects of niche construction can override external sources of selection to create new evolutionary trajectories, which leads to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected, and the elimination of what would otherwise be stable polymorphisms. Even small amounts of niche construction, or niche construction that only weakly affects resource dynamics, can significantly alter both ecological and evolutionary patterns. Mathematical models of maternal inheritance and indirect genetic effects are drawing similar conclusions (Mousseau and Fox 1998; Wolf et al. 1998, 2000). Collectively, this body of theory suggests that niche construction changes the dynamics of the evolutionary process.

The extended phenotype represents one of several ways that contemporary biology deals with niche construction, which include ecological and demographic models (e.g. of resource depletion), and population genetic models of frequency- and density-dependent selection, habitat selection, co-evolution, maternal inheritance and indirect genetic effects. These models may constitute a satisfactory and comprehensive theoretical foundation for their own topics of interest but, even collectively, they provide only a limited foundation for understanding the ramifications of niche construction. Interestingly, much of this theory explicitly models niche construction as a process in its own right. Yet in conceptual and verbal accounts of evolutionary events the reciprocity explicit in the models is lost, and niche construction is relegated from the status of an evolutionary process to being merely a product of prior selection.

Philosopher, Peter Godfrey-Smith (1996) distinguishes between a variety of different types of explanation for the relationships between organisms and environments. 'Externalist' explanations account for the internal properties of organic systems in terms of environmental properties, while 'internalist' explanations describe one set of internal properties in a system in terms of another set of internal properties in the same system. The conventional view is that niche construction should not be regarded as a distinct process in evolution because the manner in which organisms modify their environments does not redirect the pressures of natural selection in any significant way. Hence, the ultimate cause of niche construction is the natural selection of genotypes in environments, Godfrey-Smith's 'externalist' explanation. However, the properties of environments are usually only accounted for in terms of 'internalist' explanations in the environments themselves. Lewontin (1982, 1983) made the same point.

This is a distortion for at least two reasons. The first reason is that no aspect of the phenotype can be regarded as fully determined by naturally selected genotypes, which means that niche construction is not reducible to prior natural selection. Genes may be regarded as determining proteins, but their influence on phenotypes is more diffuse. Besides, not all of the genes that influence niche construction are likely to have been subjected to prior selection. The pattern of alleles at these loci could be due to other causes, for instance, mutation, drift or selection of linked genes. In addition, the information that is expressed by niche-constructing organisms could be non genetic in origin. For instance, individual animals may learn appropriate niche-constructing behaviour either as a result of their own independent experience, such as the Galapagos woodpecker finch that learns to use a cactus spine to peck for insects under bark (Tebbich et al. 2001) or as a result of social interaction, such as the British birds that learned from each

other to peck open the foil tops of milk bottles and drink the cream (Fisher and Hinde 1949). New evolutionary episodes could be initiated by changes in the activities of organisms rather than by autonomous changes in natural selection pressures.

Dawkins seemingly accepts these points with respect to development but not evolution. For instance, in accounting for an apparent disagreement with fellow ethologist Patrick Bateson (pp. 98–99), Dawkins distinguishes between the study of development and the study of natural selection, and seems to agree with Bateson that there is a need to take account of ‘the Great Nexus of complex causal factors interacting in development’. But if non-genetic factors are important to development they are important to niche construction, which is an outcome of such developmental processes, and hence they are important to all of the selection pressures modified by niche construction and all of the genetic replicators selected as a consequence.

The second and perhaps more fundamental reason is that the selective environments of organisms are not independent of organisms but are themselves partly products of the prior niche-constructing activities of organisms. The argument that niche construction can be disregarded because it is partly a product of natural selection makes no more sense than would the counter proposal that natural selection can be disregarded because it is partly a product of niche construction. One cannot assume that the ultimate cause of niche construction is the environment that selected genes for niche-constructing, if prior niche construction had partly caused the state of the selective environments. Ultimately, such recursions would regress back to the beginning of life, and as niche construction is one of the defining features of life, there is no stage at which we could say natural selection preceded niche construction, or that selective environments preceded niche-constructing organisms. From the beginning of life, all organisms have, in part, modified their selective environments, and their ability to do so was, in part, a consequence of their naturally selected genes. Dawkins seems to be thinking along similar lines when he emphasizes that the only kinds of replicators that are important in evolution are *active* germ-line replicators, those with effects on the world.

Other weaknesses in the conventional perspective can be illustrated by two examples. The first was brought to the attention of biologists by Charles Darwin (1881). Through their burrowing activities, their dragging organic material into the soil, their mixing it up with inorganic material and their casting, which serves as the basis for microbial activity, earthworms dramatically change the structure and chemistry of the soils in which they live, often on a huge scale. As a result of their industry, earthworms affect ecosystems by contributing to soil genesis, to the stability of soil aggregates, and to soil

porosity, aeration and drainage. Because their casts contain more organic carbon, nitrogen and polysaccharides than the parent soil, earthworms can affect plant growth by ensuring the rapid recycling of many plant nutrients. In return, the earthworms probably benefit from the extra plant growth they induce by gaining an enhanced supply of plant litter (Lee 1985).

Here the 'long reach of the gene' stretches through several ecosystem components, further than Dawkins ever described. Many of these effects of earthworm niche construction typically depend on multiple generations, leading only gradually to cumulative improvements in the soil. It follows that most contemporary earthworms inhabit local selective environments that have been radically altered by many generations of ancestors. It is likely that some earthworm phenotypes, such as epidermis structure, or the amount of mucus secreted, co-evolved with earthworm niche construction over many generations. Here then is another ramification on which Dawkins does not dwell; some extended phenotypes are 'heritable'. Organisms not only acquire genes from their ancestors but also an *ecological inheritance*, that is, a legacy of natural selection pressures that have been modified by the niche construction of their genetic or ecological ancestors (Odling-Smee 1988). Ecological inheritance does not depend on the presence of any environmental replicators, but merely on the persistence, between generations, of whatever physical changes are caused by ancestral organisms in the local selective environments of their descendants. Thus ecological inheritance more closely resembles the inheritance of territory or property than it does the inheritance of genes.

There can be little doubt that ecological inheritance is likely to be ubiquitous, particularly when the widespread evidence for maternal inheritance is taken into account (Mousseau and Fox 1998). Consider, for instance, the observation that most species of insects are oviparous, with the female depositing eggs on or near the food required by the offspring upon hatching (Gullan and Cranston 1994). These offspring inherit from their mother the legacy of a readily available, nutritious larval food and a nursery environment. When one considers that careful selection of appropriate sites by ovipositing females is found in the vast majority of insects, and that estimates of the number of insect species range from 5 to 80 million, the pervasiveness of ecological inheritance becomes clear.

Furthermore, mathematical analyses suggest that ecological inheritance cannot be ignored. Theoretical population genetic analyses have established that processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number

of generations), opposite responses to selection, and sudden catastrophic responses to selection (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989; Laland et al. 1996, 1999, 2001; Odling-Smee et al. 2003; Robertson 1991; Wolf et al. 1998, 2000).

Returning to the earthworms, because these originally aquatic creatures are able to solve their water- and salt-balance problems through tunnelling, exuding mucus, eliminating calcite, and dragging leaf litter below ground, that is, through their niche construction, earthworms have retained the ancestral freshwater kidneys (or nephridia) and have evolved few of the structural adaptations one would expect to see in an animal living on land (Turner 2000). For instance, earthworms produce the high volumes of urine characteristic of freshwater rather than terrestrial animals. As a consequence, if high-school students were asked to classify an earthworm using standard classificatory methods they would probably conclude that the earthworm has no business living in soil. Earthworms are structurally very poorly adapted to cope with physiological problems such as water and salt balance on land, and they would seem to belong in a freshwater habitat (Turner 2000). They can only survive in a terrestrial environment by co-opting the soils that they inhabit and the tunnels they build to serve as accessory kidneys that compensate for their poor structural adaptation. For instance, by producing well-aggregated soils the worms weaken matric potentials, and make it easier for them to draw water into their bodies (Turner 2000). However, in the process, earthworms dramatically change their environments. All of this earthworm activity highlights a problem with the concept of “adaptation”. In this case it is the soil that does the changing, rather than the worm, to meet the demands of the worm’s freshwater physiology. So what is adapting to what?

This kind of phenomenon explains why, for so many years, one of Dawkins’ arch critics, Richard Lewontin has been arguing that there is something wrong with the concept of adaptation (Lewontin 1982, 1983). Standard evolutionary theory short-changes the active role of organisms in constructing their environments, generating explanations that are sometimes misleading. Without ancestral niche construction by many organisms, including earthworms, topsoil would not exist. The ancestors of contemporary earthworms must have chosen and partly constructed the soil environments to which they are now adapted. There are two logically distinct routes to the complementary match between organisms and their environments. Either organisms can change to suit their environments, or environments can be changed by organisms to suit themselves. In the earthworm case, there is no denying that in contemporary populations the match between earthworms and their soil environment is brought about at least in part by the second route, that is through earthworm-induced changes in the soil. The problem is that in

invoking standard evolutionary theory the contribution of this second route to the complementary “adaptive” match between organisms and environments is downplayed.

In parallel to those researchers stressing niche construction, within ecosystem ecology can be found a like-minded group of workers stressing ‘ecosystem engineering’. For instance, Jones et al. (1994, 1997) point to several ecosystem phenomena that cannot be understood exclusively in terms of conventional energy and matter flows. They stress the critical role played by the creation of physical structures and other modifications of their environments by organisms that partly control the distribution of resources for other species. Niche construction establishes “engineering webs” or “control webs” in ecosystems.

Such webs are not well explained by conventional ecological theory, largely because ecosystem engineers are not necessarily part of the flows or cycles they control. For instance, it is generally assumed that trophic relations must conform to the principles of mass flow and conservation of energy. But to coin one of Dawkins’ examples, the amount of mass or energy put into a beaver (minus its wastes and the energy it uses to build its dam) does not equal the mass of the dam or the water it holds, nor the magnitude of the varied ecosystem effects that flow from dam construction (Jones et al. 1997). Standard evolutionary theory is of little utility to ecosystem ecologists, who seek to understand how whole ecosystems work, including their abiotic components (O’Neill et al. 1986). However, if niche-constructing organisms pump abiota into modified states, with knock-on effects on downstream biotic components, it becomes possible to envisage how control webs might begin to emerge in ecosystems, threaded by ‘environmentally mediated genotypic associations’ (*EMGAs*) between sometimes distant components (Odling-Smee et al. 2003). Dawkins writes

The living world can be seen as a network of interlocking fields of replicator power (p. 247).

– if the extended phenotype is taken to what I see as its logical conclusion, then so can the non-living world (Odling-Smee et al. 2003).

Consider a second example. Around the world, both the proportion of the adult population able to consume milk and dairy products without becoming sick, and the frequency of genes for lactose absorption covary strongly with current and historical use of dairy products (Feldman and Cavalli-Sforza 1989; Holden and Mace 1997). Societies with a history of dairying, but not other societies, have high frequencies of genes facilitating lactose tolerance. A recent comparative analysis by Holden and Mace (1997) revealed that dairy farming emerged some 6000 years ago, *prior to* the spread of genes for adult lactose absorption. Dairy farming almost certainly created the selection

pressures that favoured the genes for adult lactose absorption found at high frequency in many human populations, not the other way around.

Now would want to describe dairy farming and associated technologies as ‘an effect of human genes’. Certainly human genes are expressed in these activities, in the rather trite sense that genes are expressed in everything that humans do, but there are no ‘genes for’ herding, I doubt that dairying has been fashioned by natural selection, and the manufacture of cheese is no adaptation. Rather humans exploit a more general and flexible adaptation, namely the capacity to learn, to develop the skills necessary to exploit dairy products in an adaptive manner. Farmers did not become farmers because of the presence of relevant genes. One could depict the capacity of some adult humans to enjoy cheese as an indirect effect of genes that direct learning, but that provides a distorted explanation that doesn’t really capture the causal processes.

Now in spite of endless facile charges to the contrary, Dawkins is clearly no genetic determinist, and his meme concept implies that he is at least open to the idea that genes are not the only replicator guiding human behaviour. But for biologists, it is no more satisfactory to describe dairy farming as a phenotypic effect of ‘memes’ than genes, since culturally transmitted information is only part of the causal story. As Dawkins says, we need to take account of that ‘Great Nexus of complex causal factors interacting in development’.

In contrast, to describe niche construction as a ‘process’ immediately gives due recognition to the fact that there is much more to (human) behaviour than the expression of naturally selected genes, that developmental processes including learning impose a structure on (human) niche construction that goes well beyond what could ever be pre-specified by any replicator, and that there are non-Lamarckian forms of feedback in evolution from phenotypes to genotypes that invalidate evolutionary biologists treating of embryonic development as irrelevant. The claim that human dairying and milk use is a consequence of complex developmental processes incorporating individual and social learning, as well as a myriad of influences from related cultural practices and institutions is a far more reasonable and compelling account than that it is an ‘effect’ of our genes. Perhaps human culture is a special case, but the general point remains, that to describe any organism’s behaviour as ‘an effect of its genes’ assigns an unmerited pre-eminence to the role of genes over other causal factors and downplays the processes of development (Jablonka 2001).

The Extended Phenotype ends with a chapter that seeks to ‘rediscover the organism’, in which Dawkins sets out to explain the function of organisms from a replicator perspective. While he confesses that his answers are not completely satisfactory, Dawkins suggestion that ‘it has paid replicators

to behave gregariously' is intuitive enough. Earlier Dawkins describes the organism as 'a unit of behavioural action', which 'takes decisions as a unit'. I am sympathetic to the view that the organism functions to coordinate and enhance the power of replicator's phenotypic effects. In my terms, there are two processes in evolution, natural selection and niche construction. There is a power and utility to regarding the gene as the unit of selection, but equally there is value to seeing the organism as the unit of niche construction. I suspect that if we truly wish to rediscover the organism we will have to extend the extended phenotype.

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