The Developmental Systems Perspective: Organism-environment systems as units of development and evolution*

Paul E. Griffiths
Department of History and Philosophy of Science,
University of Pittsburgh

Russell D. Gray
Department of Psychology,
University of Auckland

1. Introduction

Undergraduate textbooks typically define evolution as change in gene frequency[1]. This reflects the conventional view of natural selection and the conventional view of heredity. Natural selection occurs because individuals vary, some of these variations are linked to differences in fitness, and some of those variants are heritable (Lewontin 1970). Because variants that are not heritable cannot play a role in natural selection, and because the mechanism of inheritance is presumed to be genetic, evolution is defined as change in gene frequencies. In the 1960s and 1970s this gene-centered vision of inheritance was extended to yield a gene-centered view of selection (Williams 1966, Dawkins 1976). According to gene-selectionism, the fact that individual genes are integrated into larger units, from genetic modules to entire phenotypes, is merely a special case of the fact that the fitness of any evolutionary unit is a function of the environment in which it happens to find itself (Sterelny and Kitcher, 1988). The study of development and the study of how phenotypes are integrated are thus doubly divorced from the study of evolution. First, all causal factors in the development of the phenotype other than genes are excluded as potential sources of evolutionary change. Second, the study of development and phenotypic integration cease to be possible sources of theoretical insight into the evolutionary process. The phenotypes to which an individual gene contributes and the developmental processes by which it makes that contribution are simply environmental factors like rainfall or predator density. The distribution of each individual allele across these environmental parameters determines the fitness of that allele. As far a theoretical population genetics is concerned, developmental biology and the nature of complex phenotypes are part of ecology and can be adequately represented by the varying fitness values of competing alleles. Insights into how organisms develop and how their phenotypes decompose into meaningful units do not yield any general insight into evolutionary dynamics, although, naturally, to understand the particular selective pressures on particular gene-lineages it will be necessary to study their 'ecology'.

The rapid advance of molecular developmental biology and the emergence of the new field of evolutionary developmental biology (EDB) has done a great deal to counter the atomistic approach to organisms and their evolution represented by gene-selectionism. It is now widely accepted that a meaningful decomposition of the organism – or its genome - into parts that can be considered to have their own evolutionary history must reflect an understanding of the developmental biology of the

organism. This has led to renewed attention to the concept of homology and extensive research on the newer concept of developmental modularity (Hall 1992; Hall 1994; Raff 1996; Arthur 1997; Wagner 2001). However, most evolutionary developmental biologists still accept that the developmental systems they study emerge from combinations of genes and genes alone. Jason Robert, Brian Hall and Wendy Olson have noted that, "EBD… continues to show a tendency toward reductionism and gene-centrism; developmental mechanisms are ultimately genetic…and there is no such thing as epigenetic inheritance (Robert, et al 2000, 959). In contrast, Developmental Systems Theory (DST)[2] questions both elements of the gene-centered perspective, integrating an emphasis on the relevance of development to evolution with an emphasis on the evolutionary potential of extra-genetic inheritance. The result is an account of evolution in which the fundamental unit that undergoes natural selection is neither the individual gene nor the phenotype, but the life cycle generated through the interaction of a developing organism with its environment. In our usage, the 'developmental system' is the whole matrix of resources that interacts to reconstruct that life cycle.

2. Inheritance

An organism inherits more than its nuclear DNA. A viable egg cell must contain a variety of membranes, both for its own viability as a cell and to act as templates for the assembly of proteins synthesized from the DNA into new membrane. A eukaryote cell must contain a number of organelles, such as mitochondria, with their own distinctive DNA. But the full variety of the contents of the cell is only now being uncovered. For normal gene transcription to occur, DNA must be accompanied by the elements of the chromatin marking system. For normal differentiation of the embryo, initial cytoplasmic chemical gradients must be set up within the cell. The essential role of still further parts of the package, such as microtubule organizing centers is becoming apparent. But unpacking the inherited resources in the cell is not the end of unpacking inheritance. In multi-cellular organisms the parental generation typically contributes extra-cellular resources. An ant in a brood cell is exposed to a variety of chemical influences that lead it to develop as a worker, a queen or a soldier. A termite inherits a population of gut endosymbionts by coprophagy. In viviparous organisms the environment of the womb provides not only nutrition but a range of stimulation essential for the normal development of the nervous system (for examples, see Gottlieb 1992, 1997, 2001). This stimulation continues after birth. The effects of severe deprivation of conspecific stimulation in infant primates, including humans, has been well documented (Harlow 1962, Money 1992). Nor are these effects confined to animals. Many eucalypt species have seeds that cannot germinate until they have been scorched by a bushfire. For eucalypts to increase the frequency of bushfires to the point where this system works reliably, local populations of trees must create forests scattered with resinous litter and hung with bark ribbons. These are carried aloft by the updraft as blazing torches and spread the fire to new areas (Mount 1964). Even after the resources created by the population as a whole are added in, a range of other factors must be present before the sum of the available resources adds up to a viable package. Development frequently requires gravity or sunlight or, for a hermit crab, a supply of discarded shells. These factors are unaffected by the activities of past generations of the species that rely on them. Nevertheless, the organism must position itself so that these factors interact with it and play their usual role in development.

While the evolving lineage cannot make these resources, it can still make them part of its developmental system.

It is uncontroversial to describe all these resources as playing a role in development. But it is highly controversial to say that these same resources are 'inherited'. With the exception of genes, and more recently the chromatin marking system, their roles are not supposed to extend to the intergenerational processes of evolution. Non-genetic factors, it is generally supposed, do not have the capacity for replication through many generations, and lack the potential to produce the kind of variation upon which natural selection can act: "The special status of genetic factors is deserved for one reason only: genetic factors replicate themselves, blemishes and all, but non-genetic factors do not." (Dawkins 1982, p. 99). Or, more bluntly: "Differences due to nature are likely to be inherited whereas those due to nurture are not; evolutionary changes are changes in nature, not nurture." (Maynard Smith 2000). The continued popularity of this argument is puzzling. Many non-genetic resources are reliably passed on across the generations. Variations in these resources can be passed on, causing changes in the life cycle of the next generation (Jablonka and Lamb 1995; Avital and Jablonka 2001). The concept of inheritance is used to explain the stability of biological form from one generation to the next. In line with this theoretical role, DST applies the concept of inheritance to any resource that is reliably present in successive generations, and is part of the explanation of why each generation resembles the last. This seems to us a *principled* definition of inheritance. It allows us to assess the evolutionary potential of various forms of inheritance empirically, rather than immediately excluding everything but genes and a few fashionable extras.

3. Natural selection
Armed with a thoroughly epigenetic view of development and an expanded view of inheritance, let us now turn to the concept of natural selection. In principle, there seems no reason why this concept should not be de-coupled from gene-centered theories of development and evolution. After all, Darwin developed the theory of natural selection prior to the mechanisms of inheritance being discovered. The three requirements for natural selection (variation, fitness differences, heritability) are agnostic about the details of inheritance. In Daniel Lehrman's classic phrase, 'Nature selects for outcomes' (Lehrman 1970, p. 28) and the developmental routes by which differences are produced do not matter as long as the differences reliably reoccur. Consider the following two cases: Newcomb et al. (1997) found that a single nucleotide change in blowflies can change the amino acid at an active site of an enzyme (carboxylesterase). This change produced a qualitatively different enzyme (organophosphorous hydrolase), which conferred resistance against certain insecticides. This case fulfills the three requirements for natural selection. There are phenotypic differences in insecticide resistance, these differences are likely to produce differences in fitness, and these differences are heritable. Moran and Baumann (1994) discuss a similar, fascinating example of evolution in action. Certain aphid species reliably pass on their endosymbiotic *Buchnera* bacteria from the maternal symbiont mass to either the eggs or developing embryo. The bacteria enable their aphid hosts to utilize what would otherwise be nutritionally unsuitable host plants. Aphids that have been treated with antibiotics to eliminate the bacteria are stunted in growth, reproductively sterile, and die prematurely. A lineage that inherits bacteria is clearly at

an advantage over one that does not. Once again there is variation (lineages with either different *Buchnera* bacteria or without *Buchnera*), these differences confer differences in fitness, and they are heritable. All biologists would recognize the first case as an example of natural selection in action, but they would probably balk at categorizing the aphid/bacteria system in the same way. Yet why should these cases be treated differently when both meet the three criteria for natural selection?

An obvious response would be to claim that if there is selection in this case then it can be reduced to selection of genetic differences. Aphids with genes for passing on their endosymbionts have evolved by outcompeting aphids with genes for not passing on endosymbionts. However, it is possible to have differential reproduction of the aphid/bacteria system without any genetic difference between the two lineages involved. An aphid lineage that loses its bacteria will produce offspring without bacteria. These offspring remains genetically identical to the lineages with which they compete, but have a lower expected reproductive output. A naturally occurring instance of this sort of selectively relevant non-genetic variation is found in the North American fire ant *Solenopsis invicta* (Keller & Ross 1993). Colonies containing large, monogynous queens and colonies containing small, polygynous queens were shown to have no significant genetic differences. Differences between queens are induced by the type of colony in which they have been raised, as shown by cross-fostering experiments. Exposure of eggs from either type of colony to the pheremonal 'culture' of a polygynous colony produces small queens who found polygynous colonies, leading to more small queens, and so forth. Exposure of eggs from either type of colony to the pheremonal 'culture' of a monogynous colony produces large queens who found monogynous colonies, leading to more large queens, and so forth. What appears to happen here is that a 'mutation' in a non-genetic element of the developmental matrix can induce a new self-replicating variant of the system that may differ in fitness from the original.

The moral that proponents of DST draw from the comparison of these cases is that the power of selective explanations need not be limited to genetic changes. The range of phenomena that can be given selective explanation should be expanded to include differences dependent upon chromatin marking systems (Jablonka, 2001), prions (Lindquist 1997, Lansbury 1997), dietary cues in maternal milk, cultural traditions and ecological inheritance (Gray 1992, Laland et al. 2001). Selection for differences in one of these heritable developmental resources is likely to have consequences for other aspects of the developmental system. Whitehead (1998) has argued that cultural selection has led to genetic changes in this way. He observed that in species of whales with matrilineal social systems mitochondrial DNA diversity is ten times lower than in those with non matrilineal social systems. He suggested that differences in maternally transmitted cultural traits, such as vocalizations and feeding methods, have conferred a sufficient advantage to lead to the spread of some maternal lineages, and thus their mtDNA. The mtDNA that exists today remains because it hitchhiked along with the cultural traits that were selected for.

At this point orthodox gene-centered biologists might concede that natural selection can be indeed be generalized to cover cases of expanded inheritance. Having made this concession they might then attempt to minimize its significance. We now turn to

discuss some well-known strategies for marginalizing the role of expanded inheritance in evolution and argue that they are unsuccessful.

3.1 Only genes contain developmental information

Genes are widely believed to contain a program that guides development and to contain information about the evolved traits of the organism. Perhaps the best known-aspect of DST is the rejection of this claim in Susan Oyama's book *The Ontogeny of Information* (Oyama 1985/2001). The obvious way to explicate information talk in biology is via information theory. In the mathematical theory of information as a quantity (Shannon & Weaver 1949) and its semantic relatives (Dretske 1981), a signal sender conveys information to a receiver when the state of the receiver is correlated with the state of the sender. The conditions under which this correlation exists constitute a 'channel' between sender and receiver. Changes in the channel affect which state of the receiver corresponds to which state of the sender. The information conveyed by a particular state of the receiver is as much a function of the channel, the context, as it is of the sender. In the case of development, the genes are normally taken to be the source, the life cycle of the organism is the signal and the channel conditions are all the other developmental resources needed for the life-cycle to unfold. But it is a fundamental feature of information theory that the role of source and channel condition can be reversed. A source/channel distinction is imposed on a causal system by an observer. The source is merely the channel condition whose current state the signal is being used to investigate. If all other resources are held constant, a life cycle can give us information about the genes, but if the genes are held constant, a life cycle can give us information about whichever other resource we decided to let vary. This fact is exploited whenever a biologist uses a clonal population to measure the effects of some aspect of the environment. Thus, so far as information theory and its relatives are concerned, every resource whose state affects development is a source of developmental information (Gray 1992, 2001; Griffiths & Gray 1994; Griffiths 2001; Johnston 1987).

A common response to the fact that genes and other physical causes are equally good sources of developmental information has been to look for a more demanding notion of information that allows the traditional distinction to be drawn. Several biologists and philosophers have suggested that 'teleosemantic' information can play this role. Teoelosemantics is a proposal originating in the philosophy of language to find a place in the material world for 'meaning' in the sense that human thoughts and utterances have meaning. The teleosemantic approach reduces meaning to teleology and then reduces teleology to natural selection in the usual manner: the purpose of a biological entity is the outcome for which it is an adaptation (Pittendrigh 1958). John Maynard Smith has offered one such teleosemantic account of biological information (Maynard-Smith 2001). He compares natural selection to computer programming using the 'genetic algorithm' technique. The genetic algorithm programmer randomly varies the code of a computer program and selects variants for their performance. In the same way, natural selection randomly varies the genes of organisms and selects those organisms for their fitness. Just as the purpose of the final computer program is to perform the task for which it was selected, the biological purpose of successful genes is to produce the developmental outcomes in virtue of which they were selected. This biological purpose constitutes the teleosemantic meaning of the gene. For example, the

defective haemoglobin gene in some human populations that has been selected because it confers resistance to malaria, carries teleosemantic information about malaria resistance.

Unfortunately, teleosemantic information is fundamentally unsuited to the aim of avoiding parity between genes and other developmental causes. Extra-genetic inheritance systems of the various kinds discussed above are designed by natural selection to cause developmental outcomes in offsprings. So all forms of extra-genetic inheritance transmit teleosemantic information about development. The most fully developed teleosemantic account of developmental information is the 'extended replicator theory' (Sterelny, Dickison et al. 1996; Sterelny 2000), which recognizes from the outset that teleosemantic information exists in both genetic replicators and in at least some extra-genetic replicators. Griffiths and Gray (1997) have argued that teleosemantic information is carried by all the material traces that play a role in inheritance in the extended sense defined above.

In conclusion, while many concepts of information can be applied to the role of genes in development, it appears unlikely that any of these captures the intuition that genes supply information and other developmental causes do not. The various senses in which genes 'code for' phenotypic traits, 'program' development, or contain developmental 'information' can be equally well applied to other factors required for development. This is not to say, of course, that there is no difference between the actual role of genes in development and the roles of membrane templates or host imprinting. Genes play a unique role in templating for proteins and a distinct role as nodes in the causal networks regulating cell metabolism. The point is that these empirical differences between the role of DNA and that of other inherited developmental factors do not imply the metaphysical distinction between 'form' and 'matter' that is often inferred from them (Griffiths and Knight 1998). The concept of information does not supply the missing link between these empirical differences and the conclusion that only genetic change is of evolutionary significance

3.2 Extragenetic inheritance systems have limited evolutionary potential

Maynard Smith and Szathmary have introduced a distinction between 'limited' and 'unlimited' systems of heredity (Maynard Smith & Szathmary 1995). They argue that it distinguishes genes and languages from all other forms of heredity. Most non-genetic inheritance systems, they argue, can only mutate between a limited number of states. In contrast, they note that the genome and language both have recursive, hierarchical structures, and hence an indefinite number of possible heritable states. This unlimited range of combinatorial possibilities enables microevolutionary change and cumulative selection to take place. These points are all perfectly legitimate, but from a developmental systems perspective the significance of unlimited inheritance should not be oversold for three reasons.

First, the unlimited nature of an inheritance system is a property of the developmental system as a whole, not only of the resource in which we find the recursive structure. The vast coding potential of genes, language and perhaps pheromones is created by the way in which combinations of these factors 'mean something' to the rest of the

developmental system. Asking if a system is limited or unlimited holds the current developmental system fixed, and asks what can be achieved by ringing the changes on one of the existing developmental resources. But the lesson of the major evolutionary transitions - the introduction of whole new levels of biological order such as multicellularity - is that evolution can change developmental systems so as to massively expand the possible significance of existing developmental resources. A base pair substitution in a multi-cellular organism has potentials that it lacked in a unicellular ancestor. If it occurs in a regulatory gene it could mean a new body plan. The role of systems of 'limited heredity' in these evolutionary transitions is considerable, as Maynard-Smith and Szathmary themselves have made clear.

Second, from a selectionist viewpoint the combinatorial richness of an inheritance system must be measured in terms of the number of different phenotypic effects, not just the number of combinations of components. If the rest of the developmental system were such that the indefinitely many base-pair combinations of DNA collapsed into only a few developmental outcomes, then for all its combinatorial structure DNA would not be an unlimited heredity system. It not hard to imagine cellular machinery with this result, as the existing genetic code is substantially redundant in just this way: several codons produce the same amino acid. Hence 'unlimitedness' is a property of the developmental system as a whole, not of one of its components.

A third and final reason not to place too much emphasis on the limited/unlimited distinction is that it treats genetic and extragenetic inheritance as if they acted separately. This is manifestly not the case. Adding one form of inheritance to another causes a *multiplication* of evolutionary possibilities, not just an *addition* to them. Extragenetic inheritance expands the set of possible heritable combinations, rather than merely offering a supplement to it set. Moreover, it makes accessible possibilities that would not be accessible to genetic inheritance acting alone. One of the distorting effects of gene-centrism is that it forces biologists who are interested in the evolutionary potential of extra-genetic inheritance to focus on the rare cases in which extra-genetic inheritance is relatively decoupled from genetic inheritance (as in the case of *Solenposis invicta* described above). This is because when genetic and extra-genetic inheritance act in conjunction with one another, the extra-genetic element is inevitably treated as a mere agent or assistant of the genetic element. But it is evident that the real importance of extra-genetic inheritance lies in the contribution it makes to the multi-faceted system which, as a whole, generates the heritable variation on which evolution acts.

3.3 Epigenetic Potential and Epigenetic Processes

As noted above, current work in evolutionary developmental biology (EDB) retains the traditional idea that the developmental system of an organism emerges from its genes, with the environment acting only as some kind of background or enabling cause. In a recent comparison of the ideas of EDB and DST, Jason Robert, Brian Hall and Wendy Olson use a distinction between the actual units of inheritance with epigenetic potential and the epigenetic processes to which these in an attempt to explain why EBD remains more focused on the genetic material (Robert et al 2001). They suggest that, at least one, 'hard' version of EDB 'identifies the gene (defined as the actual genetic material) as the sole unit of inheritance' (p 960). The difference

between EDB and DST, they suggest, is that EDB regards development as the expression of *epigenetic potentials* of genes in an environment, whereas DST regards development itself - *epigenetic processes* - as if they were passed on from one generation to the next: 'Developmental systems theorists...define inheritance as the reliable reconstruction of interactive causal networks' (p 961). Robert et al also suggest that, where DST sees aspects of the environment being passed on from one generation to the next, EBD sees the control of development in the next generation by genes from the previous generation which act via those aspects of the environment - a sort of 'extended genotype' (p 961).

As one might expect in an article entitled 'Bridging the gap between Developmental Systems Theory and Evolutionary Developmental Biology', Robert et al are concerned to show that the two views of inheritance just described are often only two ways to describe the very same biological phenomena. We do not think that DST and EDB are best compared in this way. DST is not an alternative way of conceptualizing the same phenomenon, but a challenge to different aspects of conventional, gene-centered thought. DST accepts the important theoretical advances of EBD but calls for other changes to theory that have not to date been part of EDB. Robert et al are on the right track, we think, when they compare DST to Scott Gilbert's call for EDB to embrace the role of the environment in development and forge an 'ecological developmental biology' (Gilbert 2000, and see fn. 2).

Understandably, Robert et al's attempt to treat DST as an alternative approach to the focal questions of EDB leads them to misinterpret DST. The alternative picture of inheritance they identify is an interesting one, but it is not the view outlined in canonical presentations of DST (e.g. Oyama et al 2001). The units of inheritance in DST are entities with epigenetic potential and not epigenetic processes, just like those of EDB. The units of inheritance are developmental resources that reliably reoccur in each generation and interact with the other resources to reproduce the life cycle. The difference is that DST identifies more things with epigenetic potential than does (hard) EBD. Some of these were briefly described above: membrane templates, chemical gradients in the egg, microtubule organizing centers, embosymbionts, hosts and habitats on which organisms are imprinted or with which they are passively biogeographically associated, the environment of the hive in insects with castes, cultural traditions, and constructed features of a niche such the acidity of the soil in a pine forest or the periodicity of fire in a eucalypt forest. There are important distinctions between these developmental resources. Some, but not all, are the immediate causal consequence of the expression of maternal genes. Some, but not all, are actively reproduced, either by the parents of the developing organism or by the wider population. The property all these resources share, and in terms of which we defined inheritance above, is that they are reliably present in each generation and causally necessary for the production of the life cycle of the evolutionary lineage. It is an important empirical question whether and to what extent the inheritance of *variation* in each of these resources has the potential to drive evolutionary change (for a overview of this question, see Sterelny 2001). A broad, principled definition of inheritance leaves this empirical question open for investigation, rather than prejudging it. Eva Jablonka and Marion Lamb make the same comment in their recent reply to Robert, Hall and Olson: "It seems to us that refusing to call the transmission of non-

DNA variations inheritance precludes a discussion of the evolutionary effects of the consequences of such transmission." (Jablonka and Lamb 2002, p. 291)

4. Adaptation and niche construction

The broadest form of extragenetic inheritance is the effect of niche construction on future generations. The idea of niche construction finds its ultimate origin in three seminal papers in which Richard Lewontin criticized the metaphors that have traditionally used to represent the process of adaptation by natural selection (Lewontin, 1982; Lewontin, 1983a; Lewontin, 1983b). The metaphorical conception that Lewontin criticized is the so-called 'lock and key' model of adaptation. Adaptations are solutions (keys) to the problems posed by the environment (locks). Organisms are said to be adapted to their ways of life because they were made to fit those ways of life. In place of the traditional metaphor of adaptation as 'fit' Lewontin suggested a metaphor of construction. Organisms and their ecological niches are co-constructing and co-defining. Organism's both physically shape their environments and determine which factors in the external environment are relevant to their evolution, thus assembling such factors into what we describe as their niche. Organisms are adapted to their ways of life because organisms and their way of life were made for (and by) each other. Lewontin also revised the popular metaphor of a 'fitness landscape'. In this image, populations occupy a rugged landscape with many fitness peaks and evolve by always trying to walk uphill. But because organisms construct their niches, the landscape is actually much like the surface of a trampoline. As organisms climb the hills they change the shape of the landscape. Lewontin's metaphor of construction is not merely a new way to describe the same evolutionary process. It is the public face of a substantially revised model of the actual process of natural selection, redefining the causal relationships that ecology and evolutionary biology must seek to model.

The most detailed attempt to develop the new metaphor of construction is that of F. J. Odling-Smee and his collaborators (for a brief overview, see Laland et al. 2001). The current prominence of the term 'niche-construction' is due to this group. The first two columns in Table 1 give the traditional model of adaptation as 'fit' and the model of adaptation as construction as these two models are described by Lewontin. In the conventional picture, change in organisms over time is a function of the state of the organism and its environment at each the previous instant. The environment acts on the existing state of organisms by selecting from the pool of variation those individuals best fitted to the environment. The environment itself changes over time too, but as the bottom equation shows, these changes are not a function of what organisms are doing at each previous instant. In Lewontin's alternative picture, shown in the center column of Table 1., organisms and their environments play reciprocal roles in each other's change. Change in the environment over time is a function of the state at each previous instant of both the environment and the organisms evolving in that environment.

Traditional neo-Darwinism	Lewontin's constructionism	Odling-Smee's general coevolution
$dO/dt = f(O,E)$ $dE/dt = g(E)$	$dO/dt = f(O,E)$ $dE/dt = g(O,E)$	$dO_{pop}/dt = f(O_{pop},E_{pop})$ $dE_{pop}/dt = g(O_{pop},E_{pop})$ $d(O_{pop},E_{pop})/dt = h(O_{pop},E)$

Table 1. Three pictures of the dynamical equations for evolution. E = Environment, O = organism, E_{pop} = organism-referent environment of a population. O_{pop} = population of organisms. These variables are related by functions f,g,h. See text for explanation.

The right hand column of Table 1 shows Odling-Smee's model of evolution as the co-construction of organism and environment (Odling-Smee 1988). Odling-Smee's 'general coevolutionary model' differs from Lewontin's in two ways. First, Odling-Smee hoped to generate a common framework in which to represent both development and evolution. This explains why the terms E_{pop} and O_{pop} occur in the equations in Table 1. Evolution is a process in which *populations* and their environments co-construct one another over time. If the terms were E_i and O_i then in Odling-Smee's notation the equations would describe the co-construction of an individual organism and it's developmental environment as the organism's life cycle unfolds. By introducing these indices Odling-Smee is making explicit what was already implicit in the explanation of Lewontin's equations given in the last paragraph - the term O in those equations refers to populations of organisms, not to some individual organism. Earlier versions of DST (e.g: Oyama 2000, Gray 1992) and some of Lewontin's writings are sympathetic to this idea that there is a significant parallelism between the way populations of organisms and their environments reciprocally influence one another and way in which individual organisms and their developmental environments do so. But this is not the place to give this idea the attention it deserves.

The second way in which Odling-Smee's treatment differs from Lewontin's is that he is concerned not to represent the organism-environment system as a closed system, as the equations in the center column would seem to imply. Although the eucalypt-bushfire relationship, for example, is one of mutual construction, the change in this system over time is externally driven by the progressive drying of the Australian continental climate. Organisms feel the impact of changes in the environment in it's traditional sense of their total biotic and abiotic surroundings - but they experience these impacts via the environment as it appears in relation to them, and thus different lineages experience 'the same changes' quite differently. Odling-Smee tries to respect this situation by assigning separate roles to the environment of a particular lineage of organisms and what he calls the 'universal physical environment'. The former, organism-referent

description of the environment is the source of evolutionary pressures on that organism, and the organism is the source of niche-constructing forces on that environment. The latter, the universal physical environment, is a source of exogenous change in the organism's environment (See Brandon 1990 for a similar treatment of the concept of environment).

The developmental systems model of evolution (Gray 1992; Griffiths & Gray 1994, 1997) can be clarified and improved by the insights of Odling-Smee and his collaborators. In particular, the insight that exogenous factors can affect the availability of developmental resources has not been sufficiently stressed in previous presentations. There remains, however, one major difference between DST and work on niche-construction up to and including the present time. Niche-construction is still a fundamentally dichotomous account of evolution (and, indeed, of development). There are two systems of heredity - genetic inheritance and environmental inheritance. There are, correspondingly, two causal processes in evolution - natural selection of the organism by the niche and construction of the niche by the organism. The niche-construction model could be modified to take account of recent work on narrow epigenetic inheritance, with a category like 'intra-cellular inheritance' taking the place of genetic inheritance. This, however, would seem to merely substitute one rigid boundary for another. A central theme of the DST research tradition has been that distinctions between classes of developmental resource should be fluid and justified by particular research interests, rather than built into the basic framework of biological thought. Fundamentally, the unit of both development and evolution is the developmental system, the entire matrix of interactants involved in a life cycle. The developmental system is not two things, but one, albeit one that it can be divided up in many ways for different theoretical purposes. Hence we would interpret niche-construction models 'tactically', as a method for rendering tractable some aspects of evolution. We would not interpret them 'strategically' as a fundamental representation of the nature of the evolutionary process.

The DST model of evolution can be represented in such a way as to make it directly comparable with the models in Table 1. We can aptly represent the developmental system with the symbol Œ. We retain OdlingSmee's insight that evolutionary change in organism-environment systems is often exogenously driven by using E to represent the universal physical (external) environment. We end up with the equation:

$$d\text{Œ}_{pop}/dt = f\,(\text{Œ}_{pop}, E)$$

Evolution is change in the nature of populations of developmental systems. This change is driven both endogenously, by the modification by each generation of developmental systems of the resources inherited by future generations, and exogenously, by modifications of these resources by factors outside the developmental system.

5. Fitness and adaptation
This representation of developmental systems evolution allows us to answer a persistent objection to DST. Since we claim that there is no distinction between

organism and environment, where do evolutionary pressures on the developmental system come from? What causes adaptation?[3] To give a clear answer we must go back to the definition of the developmental system given in Griffiths & Gray (1994). The developmental system of an individual organism contains all the unique events that are responsible for individual differences, deformities, and so forth. Just as a traditional model of evolution abstracts away from the unique features of individual phenotypes, developmental systems theory must abstract away from these features in order to tackle evolutionary questions. In evolutionary terms the developmental system contains all those features which reliably recur in each generation and which help to reconstruct the normal life cycle of the evolving lineage. Of course, many species have more than one normal life cycle, either because there are different types of organism in a single evolving population, each reproducing its own differences (polymorphism) or because there are variations in the developmental matrix from one generation to the next (facultative development). For example, there are tall and short human families and heights also vary from one generation to another due to nutrition. These features are handled in the same way as in characterizations of 'the' phenotype of an evolving lineage (Griffiths & Gray 1997). The resultant description of the idealized developmental system of a particular lineage at some stage in its evolution is highly self-contained. Because the focus is on how the complete life cycle is achieved, everything needed for that life cycle is assumed to be present. So everything that impinges on the process is an element of the system itself. It is this that creates the impression that all change in the system must be endogenously driven and creates the apparent puzzle about the source of selection pressures.

The puzzle is only apparent, because to think about evolution we need to switch from describing the developmental system characteristic of an evolving lineage at a time to describing an evolving population of individual developmental systems. We need to look at the causes of variation, as well as how the characteristics of the lineage are reliably reconstructed. Hence we need to look at the causes of idiosyncratic development in particular individuals. These causes lie 'outside' the description we have constructed of the typical developmental system of the lineage. A population of individual developmental systems will exhibit variation and differential reproduction for a number of reasons. Parental life cycles may fail to generate the full system of resources required to reconstruct the life cycle. Resources generated by the activities of an entire population (such as bushfires in eucalypt forest) may also be scarce, or patchily distributed, so that some individuals lack an important element of their developmental system. Finally, persistent resources - those developmental factors whose abundance is independent of the activities of the lineage, may be scarce or patchy and so some individuals may be unable to reestablish the relationship to these resources that is part of their life cycle. The external environment (E) can impinge on developmental systems by any of these routes. But this does not mean that we can go back to thinking of evolution as a response to the demands of the external environment. The effect of changes in the external environment on the evolution of a lineage can only be understood when those changes are described in terms of how they change the organism-referent environment (E_{pop}). 'Changes' in parameters of the external environment which are developmentally equivalent are not changes from the point of view of the evolving system. People in different regions of Britain experience substantially different quantities of dissolved limestone in their drinking water, but this

is generally of no ecological significance. Conversely, apparently trivial changes may seem momentous when described in terms of a particular developmental system. Far smaller changes in the concentration of lead from one region to another would have momentous consequences. This is, of course, the point already made by Lewontin, Odling-Smee and collaborators and Brandon (1990).

So far we have concentrated on how failures of development can lead to evolutionarily significant variation. But positive innovations are possible as well. An individual difference in the system of developmental resources may allow some individuals to cope better when both are deprived of some developmental resource because of exogenous change. Alternatively, an individual difference may simply alter the life cycle in such a way that it gives rise to a greater number of descendants. The source of novelty can be a mutation in any of the developmental resources -parentally generated, population generated or independently persistent. To make this discussion more concrete, imagine a typical population of hermit crabs. A key component of the developmental system in this lineage is a succession of discarded shells of other species. A dearth of shells would be an exogenous cause of selective pressure on the lineage. Variants with a beneficial set of behaviors or a beneficial habitat association that allowed them to continue to reliably reestablish their relationships to shells would be favored by selection. Shells will typically be an independently persistent resource and the case in which an independently persistent developmental resource acts as a limiting resource has obvious resonance with traditional ideas of selection of the organism by an independent environment. But, to fictionalize the example slightly, suppose the crab life cycle includes disturbing the soil in such a way as to expose a greater supply of discarded shells. That would make shells a population-generated resource, but they might still act as a limiting resource. Or suppose a lineage evolves behaviors that allows crabs to bequeath shells to their offspring when they themselves seek a larger home. Shells would then be parentally generated, but exogenous change in the availability of shells might still leave some offspring without them, just as a shortage of a trace element in the parental diet may lead to a birth defect in a viviparous species.

One factor that really is missing from this picture is the idea that the external (universal physical) environment poses definite problems that lineages must seek to solve. Instead, the lineage helps to define what the problems are. A dearth of shells is a feature of the ecological environment of a hermit crab and a problem for the hermit crab, but it is completely invisible to a blue-swimmer crab. The number of discarded shells per square meter is a feature of the external environment of both species, but it is only a feature of the ecological environment of one of them. So it is true that the developmental systems treatment of evolution does not incorporate Darwin's original, intuitive idea of fitness as a measure of the match between an organism and an independent environment (e.g: Darwin 1859/1964, p. 472). But this is a feature that the developmental systems treatment shares with conventional neo-Darwinism. Adaptation is no longer defined intuitively, as the sort of organism-environment relationship that a natural theologian would see as a sign of God's beneficent plan. Darwin set out to explain the fact that the biological world is full of adaptations in this sense, but as so often happens in science, the phenomenon to be explained got redefined in the process of explaining it. In modern usage, an adaptation is whatever

results from natural selection, even when what results is intuitively perverse and 'inefficient'.

We hope it is now clear how DST can explain adaptation, in the modern sense of that term. Change over time in the developmental system of a lineage is driven by the differing capacity of variant developmental systems to reconstruct themselves, or, in a word, differential fitness. What is fitness? In contemporary evolutionary theory fitness is a measure of the capacity of a unit of evolution to reproduce itself (Mills & Beatty 1979). Fitness differences are caused by physical and behavioral differences between the individuals in the population. So fitness can be translated on a case-by-case basis into a detailed causal explanation of evolutionary success. Fitness in general, however, does not correspond to any single physical property (Rosenberg 1978). The only general account of fitness describes its role as a parameter in population dynamic equations. It is clear that this orthodox account of fitness applies equally well to the developmental systems theory. There is no puzzle about how developmental systems that incorporate the whole range of resources that reconstruct the life cycle could come to vary in their success in reconstructing themselves and be selected on that basis.

6. Individuals, lineages and the units of evolution

A coherent theory of evolution requires an accurate conception of its fundamental units. According to DST an evolutionary individual is one cycle of a complete developmental process - a life cycle. We have shown that natural selection can act on populations of developmental systems and give rise to adaptation, but in doing so we have assumed that developmental systems are the sort of things that can be counted, that they have clear boundaries and that they do not overlap so much that they cannot be distinguished from one another. We now turn to justifying this assumption. Developmental systems include much that is outside the traditional phenotype. This raises the question of where one developmental system and one life cycle ends and the next begins There is an enormous amount of cyclical structure in most biological lineages. As well as the life cycles associated with traditional physiological individuals there are 'repeated assemblies' (Caporael 1995) within a single individual, such as cells or morphological parts like the leaves of a tree. There are also repeated assemblies of whole individual organisms, such as lichens or ant-acacia symbioses. In previous publications we have tried to identify what makes a repeated assembly a developmental system in its own right, as opposed to a part of such a system or an aggregate of several different systems (see especially Griffiths & Gray 1997). While we still see some merit in our previous suggestions, we have learnt a great deal from the work of David Sloan Wilson and Elliott Sober on trait-group selection, and also from Kim Sterelny's work on higher level selection (Sober & Wilson 1994, 1998; Sterelny 1996; Wilson 1997; Wilson & Sober 1994; 1998).

Wilson and Sober's work centers on the idea of a trait group - a set of organisms relative to which some adaptation is, in economic terms, a public good. The beavers that share a lodge form a trait group with respect to dam-building adaptations because it is not possible for one beaver to increase its fitness by dam building without increasing the fitness of its lodge mates. Wilson and Sober argue that trait groups are units of evolution. That is to say, it makes sense to assign fitnesses to trait groups and

to track the evolution of adaptations due to the differential reproduction of their associated replicators. But the emergence of a new level of evolutionary individuality seems to require more than this. The emergence of communal living in the beaver lineage, or of a symbiotic association between ant lineages and acacia lineages does not mark the same sort of fundamental transition as occurred with the origin of the eukaryote cell, the emergence of multicellularity or the evolution of eusociality in social insects. Not every trait group is a 'superorganism'. There are a number of features that seem to mark the difference between mere trait groups and superorganisms, such as the functional differentiation of parts and the dependence of parts on the whole for their viability. Sterelny and Griffiths have argued that the fundamental feature of a superorganism is that many traits of the component organisms are selected with respect to the very same trait group (Sterelny & Griffiths 1999, pp. 172-177; see also Wilson 1997). The ants in a nest and the cells in a human body have a shared fate not just with respect to one part of their activities, but with respect to all of them. A liver cell does not have some adaptations with respect to the whole body and other with respect to the liver alone. This is because the only way the liver cell can reproduce itself is via the success of the whole organism. Similarly, the only way an ant can contribute to its own reproduction is via the success of the nest as a whole. This broad congruence of interests results from evolved features that suppress competition between the component parts of the superorganism. The best known of these is the segregation of the germ line. However, it is easy to overstate the importance of this particular mechanism. Plants typically do not have germ-line segregation, so it cannot be a prerequisite for complex multicellular life. Leo Buss has explored some of the very different mechanisms that are used to bind the interests of cell-lineages together in plants and fungi (Buss 1987). Again, in bee nests, the queen marks her eggs with a pheromone that inhibits workers from eating them. Eggs laid by workers are eaten by other workers, so the only realistic way for workers to bring about the reconstruction of their life cycle is via the larger, colony life cycle (Ratnieks & Visscher 1989). The worker bee is reduced to a part of a larger cycle as effectively as a metazoan cell is reduced to a part by segregation of the germ line.

We suggest, then, that a repeated assembly is a developmental system in its own right, as opposed to a part of such a system or an aggregate of several different systems when specific adaptations exist, presumably due to trait group selection, which suppress competition between the separate components of the assembly. This account of the evolution of individuality can actually explain why the distinction between a colony of organisms or a symbiotic association and an individual organism is not a sharp one. The mechanisms that bind the trait group together can be more or less effective. They may also keep the evolutionary interests of the same group aligned across a wider or narrower range of traits. The metazoan organism and the unicellular eukaryotic cell are clearly individuals. Jellyfish, lichens, eusocial insect colonies and the ant-acacia symbiosis are progressively less clearly individuals. Each has a life cycle and a developmental system that feeds into its development. But in most of these latter cases, it is possible to describe evolutionary pressures with respect to which the smaller life cycles nested within the larger cycle do not form a trait group. The more forced and implausible these scenarios, the less theoretical role there is for a description in which these cycles are treated as independent and not as parts.

7. Building Bridges: The complementary programs of DST and EDB
At the end of a well-known paper on adaptation, Lewontin (1978) notes that adaptive evolution requires quasi-independence: selection must be able to act on a trait without causing deleterious changes in other aspects of the organism. If all the features of an organism were so closely developmentally integrated that quasi-independent variation did not exist, then "organisms as we know them could not exist because adaptive evolution would have been impossible" (Lewontin 1978, p.169). The requirement for quasi-independence means that we must add a caveat to the slogan that "Nature selects for outcomes" and not for how those outcomes are produced (Lehrman 1970, p. 28). The reliable reoccurrence of an advantageous variant is not enough. The developmental process that produces the variation must be quasi-independent (modular) if it is to be the basis for cumulative selection. There has been considerable recent interest in the extent to which the organization of development really is modular. Günther Wagner and Lee Altenberg (1996) suggest that directional selection might act on developmental systems to reduce pleiotropic effects between characters with different functions, thereby enhancing the modularity and evolvability of these developmental systems. They speculate that there should be evolutionary trends towards increased modularity. Brandon (1999) goes so far as to suggest that developmental modules at each level of in the evolutionary hierarchy and are the units of selection at that level. The study of developmental modularity is still in its infancy and the extent of that modularity far from resolved. However, it is clear that understanding the extent and nature of developmental modularity is an essential to understanding how evolution actually unfolds - and has unfolded - in practice.

The modularity issue is at the heart of the new discipline of developmental evolutionary biology (EDB), so it is striking that DST has had little to say about the issue of modularity, or the older, related issue of the extent of developmental constraints (Maynard Smith et al 1985, for an exception to this remark, see Oyama 1992). What, one might ask, is *developmental* about developmental systems theory? The answer is that the term 'developmental' in this context stands in contrast to 'innate'. To think developmentally is to focus on the many factors that must be present for a fertilized egg to give rise to a normal life cycle and on the process - development - in which those factors interact. Whereas EDB stems from the impact of the molecular revolution on developmental biology and comparative morphology, DST grew out of the continued efforts of developmental psychobiologists to resist the idea that evolved features of mind and behavior are outside the sphere of developmental psychology because they are programmed in the genes and so do not *have* a developmental psychology. Most developmental systems theorists trace their intellectual ancestry to Daniel S. Lehrman's 1953 'Critique of Konrad Lorenz's theory of instinctive behavior' and to the work in comparative psychology reflected in that critique (Johnston 2001; Gottlieb 2001). Research in the developmental systems tradition has thus had a strong emphasis on demonstrating the contingency of developmental outcomes on extra-genetic factors and, latterly, demonstrating the evolutionary potential of those factors. From this perspective, to understand their development is to understand how each stage of the developing organism interacts with its environment to give rise to the next. DST, with its emphasis on the life cycle in place of the adult phenotype and on the role of extra-genetic inheritance is an attempt to provide a general conception of

development and evolution in the spirit of this research tradition of developmental psychobiology[4].

In stark contrast, much of the criticism directed by developmental morphologists at conventional neo-Darwinism has emphasized, not the contingency of developmental, but its fixity. The literature on 'developmental constraints' suggests that some aspects of phenotypes are too strongly integrated to be altered by natural selection acting on the genes, let alone by natural selection manipulating non-genetic developmental parameters! In recent years, however, EBD has been able to move beyond treating development as a set of constraints on selection, in part because of conceptual advances and in part because technical advances have made it possible to elucidate developmental 'constraints' mechanistically and not merely describe them phenomenologically on the basis of gaps in the comparative data

In our view, these two critiques of earlier evolutionary thought are essentially complimentary. DST does not provide a theory of phenotypic integration and modular evolution, but rather stands in need of one, and EDB is beginning to supply such a theory. Conversely, nothing in the fundamental ideas of EDB excludes applying that theory to a wider conception of the developmental system, not as emerging from interactions between genes, but as emerging from interactions between the whole matrix of resources that are required for development. In fact, the need to extend the research agenda of EBD in this manner has been recognized in recent calls for greater attention to the ecological context of development and the developmental basis of phenotypic plasticity (Sultan, 1992; Schlichting and Pigliucci 1998; Gilbert 2000; this volume). Research under the banner of 'phenotypic plasticity' has emphasized the fact that the environment plays an informative, not merely a supporting, role in development. For understandable reasons, however, the emphasis of research on phenotypic plasticity has been on *adaptive* plasticity. Organisms have evolved to use the environment as a source of information for the deployment of facultative adaptations. DST can enrich this perspective by emphasizing that the dependence of development on the ecological context is a fundamental feature, not a last flourish of adapted complexity. EBD recognizes that the nature of development explains the nature of evolution as much as evolution explains the nature of development. In the same way, the fact that what changes over evolutionary time are organism-environment systems is an essential part of any adequate theory of adaptive evolution. 'Ecological developmental biology' is not merely a framework for studying adaptive plasticity, it is a fundamentally better, more inclusive way of approaching the evolution of development and the implications of development for evolutionary theory.

The ubiquity of environmental effects on development can be nicely illustrated using neuroscientist Terence Deacon's concept of 'addiction to the environment' (Deacon 1997). During primate evolution, an abundance of dietary vitamin C caused the loss of the normal mammalian pathway for ascorbic acid synthesis (Jukes and King 1975). Because this vital developmental resource could be inherited passively, rather than via the genes previously involved in its synthesis, the primate lineage became dependent on ('addicted to') this form of extra-genetic inheritance. In the same way, hermit crabs are 'addicted' to discarded shells and almost all large organisms are 'addicted' to the earth's gravity. In fact, evolved lineages are 'addicted' to innumerable aspects of the

environment with which they have coevolved, although most of these aspects are reproduced so reliably that this does not give rise to significant variation, and so is overlooked. Nevertheless, any account of how organisms develop that neglects these factors, and the evolutionary processes that led to their incorporation in development, is seriously incomplete.

8. Conclusion

DST yields a representation of evolution that is quite capable of accommodating the traditional themes of natural selection and also the new results that are emerging from evolutionary developmental biology. But it adds something unique - a framework for thinking about development and evolution without the distorting dichotomization of biological processes into gene and non-gene and the vestiges of the 'black-boxing' of developmental processes in the modern synthesis, such as the asymmetric use of the concept of information. Phenomena that are marginalized in current gene-centric conceptions, such as extra-genetic inheritance, niche construction and phenotypic plasticity are placed center stage.

Endnotes

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1. Here is a random selection: "Evolution 1. Process by which organisms come to differ from generation to generation. 2. Change in the gene pool of a population from generation to generation." (Arms & Camp 1987, p. 1121). "Evolution is the result of accumulated changes in the composition of the gene pool." (Curtis & Barnes 1989, p. 989).

2. DST is an attempt to sum up the ideas of a research tradition in developmental psychobiology that goes back at least to Daniel Lehrman's work in the 1950s (Johnson 2001, Gottlieb 2001). Robert, Hall and Olson (2001) set out to compare DST with the more gene-centered ideas of contemporary evolutionary developmental biology (EBD) but they miss the fact that DST has its roots in developmental psychobiology. They note that "EBD has yet to draw extensively from behavior/psychology" (p 958) and cite the work of Gilbert Gottlieb as an exception. But Gottlieb, of course, is one of the seminal figures in DST and his 'developmental-psychobiological systems view' is quite unlike most work in EBD because it stresses the roles in development of highly structured, species-specific environments and of extra-genetic inheritance. As developmental psychologists David Bjorklund and Anthony Pellegrini state in their recent book on evolutionary developmental psychology, "In this book we adopt a specific model, the developmental systems approach (Gottlieb 2000; Oyama 2000a)... strengthening considerably, we believe, evolutionary psychologists' arguments that genes are not necessarily destiny" (Bjorklund & Pellegrini 2002). It is encouraging to see that the tradition represented by Gottlieb and Oyama has received increased attention in the last few years. It has been embodied in a textbook by George Michel and Celia Moore (1995) and popularized by authors like David Moore (2001; see also Bateson and Martin 1999). Much of our own work has been designed to demonstrate

the relevance of DST concepts outside their original home in the study of behavioral development. DST may still be 'virtually unknown among biologists' (Robert et al 954), if this means biologists working on the evolutionary developmental biology of morphological structures, but as calls for an 'ecological developmental biology' suggest, those biologists could learn much from the tradition of developmental psychobiology.

3. We are not aware of any published version of this criticism, but it was first suggested to Griffiths in conversation by Lindley Darden in 1994 and has also been raised by Alexander Rosenberg (personal communication).

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