Open almost any biology textbook and you will find the following definition: Evolution is change in gene frequency. This definition 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.

Developmental systems theory (DST) is a radical challenge to dichotomous accounts of development—accounts centered on a dichotomy between genes on the one hand and every other causal factor on the other. Proponents of DST argue that the empirical evidence does not support the view that each developmental process is specified by different genes, and that of other developmental resources do not justify the metaphysical distinctions currently built upon them. In particular, any sense in which genes code for phenotypic traits or program development or contain developmental information can be equally well applied to other factors required for development (Gray 1992, 2001; Griffiths and Gray 1994a; Johnston 1987). In this paper we explore the implications of this “parity thesis” (Griffiths and Knight 1998) for the orthodox picture of evolution by natural selection. It is generally accepted that the neo-Darwinian synthesis marginalized developmental biology (Depew and Weber 1995; Gilbert, Opitz, and Raff 1996). Attempts to reintroduce developmental considerations have often been framed as attacks on (neo-) Darwinian (Goodwin 1984). We think this is a mistake. Here we explore how the traditional Darwinian concepts of inheritance, selection, adaptation, and lineage can be reworked from a developmental systems perspective. Rather than diminish the power of natural selection, in the spirit of Darwin’s original insight this approach expands the range of phenomena that can be given adaptive-historical explanations.

Inheritance

What does an organism inherit? Certainly more than the 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 eukaryotic 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 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 multicellular organisms the parental generation typically contributes extracellular 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 also a range of stimulation essential for the normal development of the nervous system (for examples, see chapter 4 this volume). This stimulation continues after birth. The effects of severe deprivation of conspecific stimulation in infants has been documented in many tragic “experiments” (Harlow and 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. To increase the frequency of bushfires...
to the point where this system works reliably, local populations of eucalyptus 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. 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 from other species. 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. Nongenetic 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 nongenetic factors do not" (Dawkins 1982: 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 nongenetic 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. It is still more puzzling to find many of these very phenomena discussed, and their evolutionary significance recognized, in John Maynard Smith's own work (Maynard Smith and Szathmáry 1995). 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, developmental systems theory 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, rather than immediately excluding everything but genes and a few fashionable extras.

One way to conceptualize the role of extragenetic inheritance is as a number of separate ("parallel") channels for the transmission of developmental information. The most traditional multiple channel model has two systems of heredity: genes and culture. In recent years more biologically sophisticated models, with their roots in actual empirical work on inheritance, have emerged (see chapters 9, 10, and 23 of this volume). Multiple channel models are an effective way to draw attention to the phenomena overlooked by a purely genocentric account of heredity. However, we have strong reservations about multiple inheritance or "extended replicator" (Sterelny, Dickson, and Smith 1996) models. We believe that it is both more biologically realistic and, in the long run, more productive to think of the life cycle being reconstructed by a system of resources. Let's start with issues of biological realism. So-called channels are not generally independent of one another. Many "channels" are so strongly intertwined that they cannot affect development unless other channels develop in a way that is automatically "epistatic" with the first channel. The chromatin marking system, often described as a "parallel" inheritance mechanism, modifies the pattern of gene expression. It can be useful to treat DNA sequences and chromatin marks separately in some modeling exercises, but this is an idealization akin to leaving out linkage...
in a genetic model. It should not be built into the basic way we conceive the system. Furthermore, the developmental system as we conceive it includes not only the "channels" of the other formulations, but also developmental resources which are not easily represented as "channels" or "replicators." It is hard to think of germination in eucalypts as a character transmitted via the bushfire channel, but it would be necessary to think this way to make a multiple channel model complete. The extended replicator theory handles this case by treating it as the replication of selfish bushfires which use eucalypt trees to achieve their goals. Whether or not that is adequate, the extended replicator theory also has to model the standing features of the physical world which form part of most developmental systems. Sunlight, gravity, mineral concentrations in the local soil, and many other factors must be present if "channels" are to convey and "replicators" to replicate. There are a number of ways in which evolving lineages can ensure the inheritance of these factors. These range from highly active methods, such as habitat and host imprinting, to entirely passive methods such as the biogeographic association between a lineage and a region. It is clear that evolving lineages can do better or worse than one another because of fitness differences caused by these developmental factors. As we have argued elsewhere (Griffiths and Gray 1997), the idea that developmental systems can be reduced to a collection of independent replicators is either inadequate or has to recognize relationships to persistent features of the environment as an addition to the cost of replicators. The "selfish standing-biogeographic-association-with-a-low-rainfall-region" is unlikely to appeal.

We would also argue that a developmental systems conceptualization is more heuristically valuable than a multiple channel or multiple replicator model. Holding most of the developmental system constant in order to tease out the roles of a single factor is a valuable technique, and much research in the developmental systems tradition makes use of it (see, for example, chapter 4 of this volume). However, describing this work in the way we have just done keeps the context-dependence of causation in development in the center of the stage. One of the main motivations of developmental systems theory is to draw attention to fact that developmental causes do not have their effects in isolation, but as part of a wider system of causes. Causation in development is thus intrinsically likely to be context-dependent. The very idea of "developmental information" runs some risk of disguising this fact. Susan Oyama (1985) points out that once information is localized in, for example, a sequence of DNA, it is all too easy to forget that the developmental effect of this sequence is a function of context. The same DNA sequence in a different time or place might convey quite different information. "Information" here is being used in the statistical sense, that of correlation between developmental input and developmental outcome. But the associations of the vernacular concept of information are often present when the statistical concept is applied. In the vernacular sense, information is "intentional", it is the meaning conferred on a symbol or a message by its creator. This meaning can be misinterpreted by the recipient of a message, but the meaning of the message is not thereby changed. Hence thinking of developmental causation as the expression of information carries the association that the significance of a cause is independent of the context in which it acts. The idea of dual (or multiple) inheritance systems runs a similar risk of pushing context dependency into the background. Consider, for example, the methylation inheritance system (Jablonka and Szathmáry 1995). The developmental significance of a methylation pattern depends on the gene whose transcription it modifies, and on much else. It is, of course, possible to identify predictive relationships between patterns of methylation and developmental outcomes. However, the idea that these developmental outcomes are transmitted down the methylation inheritance channel obscures the way in which the
relationship between methylation pattern and outcome depend on what is happening in numerous “other” channels. Eva Jablonka recognizes this difficulty when she says that the different inheritance systems cannot be treated as autonomous. However, the very idea of separate systems suggests autonomy and it would be desirable to find a formulation that avoids this.

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 decoupled 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: 28). The developmental routes by which fitness differences are produced do not matter as long as they 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 hydrolyase), 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 and Ross 1999). Colonies containing large, monogynous queens and colonies containing small, polygyrous 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 pheromonal “culture” of a polygyrous colony produces small queens who found polygyrous colonies, leading to more small queens, and so forth. Exposure of eggs from either type of
colony to the pheromonal "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 which may differ in fitness from the original.

The moral that proponents of developmental systems theory 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 (chapter 9), prions (Lindquist 1997; Lansbury 1997), dietary cues in maternal milk, cultural traditions and ecological inheritance (Gray 1992; chapter 10). 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 recently 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 nonmatrilineal 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 indeed be generalized to cover cases of expanded inheritance. Having made this concession they might then attempt to minimize its significance. Genic selectionists, for example, might be tempted to reduce cases of expanded inheritance to a dual inheritance model—genes and their cultural equivalent (memes). But many of the examples of extragenetic inheritance discussed in this book do not fit this dichotomy (e.g., chromatin marking systems, chemical traces from the maternal diet passed on via fetal olfactory conditioning or in maternal milk, the inheritance of gut symbionts, and the inheritance of fire ant colony type). A division of these cases into those that are "sort of genetic" and those that are "sort of cultural" will be largely arbitrary. A somewhat more insightful response to the challenge of expanded inheritance has been outlined by Kim Sterelny (chapter 23). Following Richard Dawkins's well-worn track up Mt. Improbable (Dawkins 1996), Sterelny argues that only cumulative selection can produce complex adaptive structures. Sterelny then outlines some of the requirements an inheritance system would need to make cumulative selection possible (e.g., a large range of possible phenotypes, longevity, high fidelity replication, vertical transmission, and developmental modularity). According to Sterelny, extended forms of inheritance like cultural traditions and ecological inheritance are unlikely to satisfy these requirements; they are inheritance systems, but not highly evolvable inheritance systems. In contrast, however, he argues that symbiont transmission might score quite highly on his criteria for evolvability.

While there is much that we agree with in Sterelny's analysis, there are two important conceptual differences between our views. First, Sterelny adopts a particularly Dawkinsian view of what is important in evolution (i.e., cumulative selection leading to adaptation). While we do not deny that cumulative selection is an important part of evolution, there is a lot more to be explained than just this. Our Darwinian mission is, after all, to explain the diversity of life—the myriad fascinating changes in shape, size, physiology, behavior, and ecology. Extended forms of inheritance can play important roles in evolution without providing the heritable basis for cumulative selection. For example, Maynard Smith and his collaborator Eörs Szathmáry (1995) argue that
epigenetic inheritance has played a crucial role in some of the major evolutionary transitions. Sterelny is sympathetic to this view. He notes that symbiosis might be of considerable significance in the generation of evolutionary novelty. After all, the eukaryotic cell is probably an example of frozen symbiosis. Not only might expanded forms of inheritance play an important role in the generation of evolutionary novelty they could also significantly alter the dynamics of evolutionary change. Pal and Miklos (1999) recently modeled the impact of epigenetic inheritance, such as chromatin marking, on the evolutionary trajectory of a population through an adaptive landscape. Their results suggest that this expanded inheritance can facilitate transitions from suboptimal to higher peaks, thus creating more effective evolutionary dynamics than would be possible under strict genes-only conceptions. Expanded forms of inheritance may also be the cause of reproductive isolation and hence of speciation. Parasitic Wolbachia bacteria infect up to 20 percent of insect species, and it has been suggested that this cytoplasmically inherited microorganism may be a major cause of speciation in insects. In many species, individuals infected with one strain of the bacteria cannot successfully fertilize individuals infected with another strain. Some clearly separate species also become interfertile when "cured" of their Wolbachia infections (Vines 1999). In all these ways, epigenetic inheritance can be a major factor in evolution.

Our second point of departure from Sterelny's position is that we do not divide expanded inheritance into separate inheritance systems or multiple replicators. As we argued above, these factors are physically and functionally linked. The effects of differences in these factors are likely to be context sensitive, and should be seen as part of a system of causes rather than as separate information channels or replicators. Putting these conceptual differences aside, there is still a great deal that can be gained by examining Sterelny's criteria for an evolvable inheritance system (i.e., the range of possible phenotypes, longevity, fidelity, vertical transmission, and developmental modularity). We will now address each of these criteria in turn.

Natural Selection and the Range of Possible Phenotypes

Maynard Smith and Szathmáry have introduced a distinction between limited and unlimited systems of heredity (Maynard Smith and Szathmáry 1995; Szathmáry and Maynard Smith 1997). They argue that most non-genetic inheritance systems 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 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 unicellular organism has potentials that it lacked in a unicellular ancestor. If the substitution 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 Szathmáry make 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 (chapter 23). 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 because the existing genetic code is substantially redundant in just this way. Several codons produce the same amino acid.

A third and final reason not to place too much emphasis on the limited/unlimited distinction is that it treats genetic and extragenetic inheritance separately. From a developmental systems perspective these sources of heritable variation should viewed as acting together. Adding one form of inheritance to another causes a multiplication of evolutionary possibilities, not just an addition to them. The greater the range of possibilities the more scope there is for cumulative selection and microevolution.

Natural Selection, Longevity, and Fidelity

Another strategy that could be used to minimize the evolutionary significance of expanded forms of inheritance is to argue that they lack sufficient longevity and high fidelity replication to be the targets of cumulative selection. Sterelny (chapter 23) claims that this is likely to be the case with cultural inheritance. Following Tomasello, Kruger, and Ratner (1993) he argues that high fidelity cultural inheritance requires genuine imitative learning, and this is rare outside humans. Other forms of social learning, like local enhancement and emulation, are unlikely to result in faithful reproduction of the same motor patterns. Thus, in the words of Boyd and Richerson (1996), culture is common but cultural evolution is rare.

Although this is certainly a possibility, evolutionary biologists know remarkably little about the longevity of cultural traditions in animals and the degree to which they have involved cumulative changes. Research on these questions, while exciting, is in its infancy. For example, Whiten et al. (1999) have documented substantial cultural variation in tool use, grooming, and courtship behaviors between populations of wild chimpanzees (Pan troglodytes). However, there is little evidence that these variations have persisted for long periods of time, nor that they are a product of cumulative cultural change. It is possible that sensitive periods and social and ecological scaffolding may facilitate reliable cultural inheritance. One example is the reliability of human linguistic inheritance. If the controversial claim that human language relationships are congruent with our evolutionary history is correct, then linguistic inheritance has tracked genetic divergence for as long as 200,000 years (Cavalli-Sforza et al. 1988; Penny, Watson, and Steel 1993). In nonhumans we know much less. However, a study on chaffinches on Atlantic islands by Lynch and Baker (1986) found substantial congruence between a tree based on morphology and a tree constructed from song syllables, indicating a common evolutionary history going back one to two million years. Whitehead’s (1998) study on the possible effect of cultural selection on mtDNA diversity in whales suggests that cultural inheritance has exhibited considerable longevity and fidelity in the species with matrilineal social systems. The results of his computer simulations indicate that, assuming a 10 percent reproductive advantage is culturally transmitted down maternal lineages, it would take more than two hundred generations to produce the observed tenfold reduction in mtDNA diversity.

While the cases both for and against cultural inheritance are limited by a lack of evidence, the
same cannot be said for some other forms of extended inheritance. Perhaps the most impressive involves the aphid/bacteria symbiosis analyzed by Moran and Baumann (1994) and discussed earlier. Phylogenetic trees of the bacteria and their aphid hosts are perfectly congruent. This suggests that speciation of the aphids has lead to speciation of the bacteria—they have co-speciated. Molecular and fossil evidence suggests that this association is incredibly ancient—between 160 and 280 million years. The *Buchnera* bacteria are thus a vital and remarkably reliably inherited developmental resource.

**Vertical Transmission**

The lack of strict vertical (parent to offspring) inheritance is another potential problem for the ability of certain forms of extended inheritance to lead to cumulative selection. Again Sterelny (chapter 23) has discussed the problem with considerable insight:

Transmission of ecological and cultural differences is not vertical. Indeed, it is not even individual. It is diffuse. Groups of trees engineer their soil structures or a fire-prone understory; individual trees do not make their microenvironments for themselves and their descendants. In most cases groups of animals make warrens, trackways, track-and-bowl systems, beaver lodges, termite mounds and other structures ultimately taken over by the next generation. If this is transmission at all, it is diffuse and development is holistic (p. 344).

It is likely that even quite small departures from 100 percent vertical transmission could undermine the evolutionary coherence of some forms of extended inheritance with the rest of the developmental system. For example, in Whitehead’s (1998) simulation of the effects of cultural selection on mtDNA diversity in whales, if horizontal transmission was much greater than 0.5 percent, then there was little reduction in genetic diversity. One possibility is that ecological and cultural inheritance, while diffuse and horizontal at the individual level, might be vertically inherited in larger units such as families and local populations. Linguistic inheritance may operate like this (Gray and Jordan 2000). The inheritance of species-specific strains of *Wolbachia* bacteria in some species is also extremely unreliable for individuals while being highly reliable for the species as a whole. Ecological and cultural inheritance could then play an important evolutionary role by providing the basis for higher level trait groups (see Wilson 1997 and the discussion on lineages that follows). In fact, a group selective explanation has been offered for the individually unreliable nature of transmission in *Wolbachia* (Vines 1999: 47). However, as Sterelny notes, the conditions that allow group selection are quite restrictive. An alternative possibility is that although changes in ecological and cultural inheritance might not provide the heritable basis for cumulative selection, they could play important evolutionary roles both in opening up new sets of adaptive possibilities and by facilitating the dynamics of evolutionary change. It should also be emphasized that the problem of diffuse horizontal inheritance does not apply to all forms of expanded inheritance. Sterelny notes that cytoplasmic factors, symbiont systems, and ant nest types are all likely to be inherited in a highly vertical fashion.

**Modularity and One Reason Why Selectionists Cannot Ignore Development**

At the end of his classic paper on adaptation, Lewontin (1978) notes that adaptive evolution requires quasi-independence. By quasi-independence he means that 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: 169). This means that we must add a caveat to Lehrman’s slogan “Nature selects for outcomes” (Lehrman 1970: 28). Development does matter.
The reliable reoccurrence of an advantageous variant is not enough. The developmental route which produces the variation must be quasi-independent if it is to be the basis for cumulative selection. A common finding in artificial selection experiments is that although many traits initially respond rapidly to selection, the response will often slow and reach a plateau (Lerner 1970). One interpretation of these results is that developmental links mean that many traits can only be changed to a certain degree without having deleterious effects on other aspects of the phenotype. Further directional change would thus require some kind of developmental reorganization.

There has been considerable recent interest in the extent to which the organization of development really is modular. For example, Halder, Callerts, and Gehring (1995) demonstrated the modularity of eye formation in *Drosophila* by successfully inducing eyes on the antennae, wings, and legs of *Drosophila*. The targeted mis-expression of the "eyeless" gene produced structures in these unusual locations that contained a cornea, bristles, and photoreceptors and were responsive to light. Wagner and 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 are the units of selection. The study of developmental modularity is still in its infancy and the extent of modularity far from resolved. However, from a DST perspective the exact extent of modularity is not a pivotal concern. DST is agnostic on this question (Sterelny in press). Instead, we would emphasize three general implications that arise from the modularity issue. First, analyzing development itself is the key to understanding the ability of selection of act in a cumulative manner. Second, there is no reason to think that extended forms of inheritance such as symbiont transmission or cultural traditions will be any less modular in their developmental consequences than genetic factors, and thus extended forms of inheritance cannot be brushed off as lacking an essential requirement for cumulative selection. Third, because extended inheritance must be taken seriously rather than brushed aside, the range of phenomena that can and should be given selectionist explanations is considerably increased. This is something that we as Darwinian biologists should be excited about. DST expands the scope of Darwinian explanation, and that is exactly the general conclusion of this section on natural selection. From a DST perspective there is lots more work to be done—there are exciting new questions that we have, at best, only partial answers to. As students of cumulative selection, we really need to know the extent to which extended forms of inheritance fulfill the requirements of longevity, fidelity, and vertical inheritance, and we really need to investigate the modularity and evolvability of developmental systems.

### Adaptation and Niche Construction

In three seminal papers Richard Lewontin criticized the metaphors that have traditionally been 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 codefining. Organisms both physically shape their environments and determine which factors in the external environment are relevant to their evolution, thus assembling
such factors into what biologists describe as a 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 which ecology and evolutionary biology must seek to model.

Lewontin’s ideas challenge one of the central elements of contemporary neo-Darwinism, the idea that the source of the selective pressures that explain adaptive evolution can be sought in a relatively independent science of ecology. Darwin himself was well aware of the reciprocal influence of organism and environment, and conducted pioneering studies on the role of earthworms in the formation of soils (Darwin 1881). Despite this, many presentations of Darwinism treat the environment as a source of fixed problems which every organism must solve or die. Environments for which there is no fossil or other direct evidence can be reconstructed by “reverse engineering” the organisms that those environments shaped to fit themselves. Some even suggest that evolutionary research can proceed by first identifying the niches in an environment and then predicting how organisms will evolve to fill them—so-called adaptive thinking. But as Lewontin has pointed out, there are indefinitely many overlapping niches in an unoccupied physical landscape. Until the organisms that occupy the niches are specified, the concept of the niche is completely unhelpful. Of course, there is a sense in which every possible niche that an organism could construct in an area of space and time “exists.” This sense becomes still more tenuous, however, once it is recognized that occupied landscapes owe much of their physical structure to the activities of the organisms that occupy them. In this tenuous sense there were niches for species requiring high rainfall in the Amazon basin before the biota which make it a high-rainfall region had evolved. So a region of space and time contains not only the niches that can be defined using its existing features, but all those that could be defined using the features induced by the action of all the species that could evolve so as to make a niche in that region!

Sterelny and Griffiths have argued that the concept of a “vacant niche” makes sense only in an ecosystem that has already been structured by a collection of organisms which are part of it (Sterelny and Griffiths 1999). It may then be possible to determine that an organism of a specified type not present in that ecosystem could maintain itself were it introduced. The move from this idea to the idea of an unoccupied landscape with a determinate niche structure is an illicit idealization. It idealizes away from precisely those factors that create the possibility of identifying vacant niches. Similarly, the idea that knowing the “shape” of the vacant niches allows us to predict how organism will evolve to fit them ignores the fact that different organisms will construct different niches. Some eucalypt species can establish and sustain “islands” of dry sclerophyll forest in rainforest by facilitating bushfires. Once this process is understood it is possible to identify a vacant niche for these species in many other landscapes, despite the fact that they would not even germinate if simply planted there (Mount 1964). We would argue that the idea of a vacant niche for *E. delegatensis* in all non-Australian rainforests is simply perverse in comparison to the idea of niche construction.

The most detailed attempt to develop the new metaphor of construction is that of F. J. Odling-Smee and his collaborators (for an overview, see chapter 10 of this volume). The current prominence of the term *niche construction* is due to thi
The first two columns in Table 16.1 give the traditional neo-Darwinian model of adaptation as "fit" and the model of adaptation as construction as these two models are described by Lewontin (1982, 1983a). In the traditional picture, change in organisms over time is a function of the state of the organism and its environment at each 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 16.1, 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.

The right-hand column of Table 16.1 shows Odling-Smee's model of evolution as the co-construction of organism and environment. Odling-Smee's general coevolutionary model differs from Lewontin's in two ways (Odling-Smee 1988). First, Odling-Smee hoped to generate a common framework in which to represent both development and evolution. This explains why the terms $E_{\text{pop}}$ and $O_{\text{pop}}$ occur in the equations in Table 16.1. Evolution is a process in which populations and their environments co-construct one another over time. If the terms were $E$ and $O$, then in Odling-Smee's notation the equations would describe the co-construction of an individual organism and its 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 previous paragraph—the term $O$ in those equations refers to populations of organisms, not to some individual organism. Earlier versions of DST (e.g., Oyama 1985; Gray 1992) and some of Lewontin's writings are sympathetic to Odling-Smee's 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 changes in this system over time are externally driven by the progressive drying of the Australian continental climate. Organisms feel the impact of changes in the environment in the traditional sense of that term—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 environment."
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-constraining forces on that environment. The latter, the universal physical environment, is a source of exogenous change in the organism’s environment.

Robert Brandon’s theory of the role of the environment in adaptation is a useful complement to Odling-Smee’s ideas. Brandon distinguishes three different senses of “environment” (Brandon 1990, 1992). His “external environment” corresponds to Odling-Smee’s universal, physical environment. All organisms in a particular region of space and time share an external environment. The “ecological environment” must be described with reference to a particular evolving lineage. It consists of those environmental parameters whose value affects the reproductive output of members of the lineage. Finally, the “selective environment” is that part of the ecological environment which differentially affects the reproductive output of variant forms in the evolving lineage. It is this last which contains the sources of adaptive evolutionary pressures on the lineage. Brandon has used these ideas in the context of his own exploration of organism-environment coevolution (Brandon and Antonovics 1996). Organisms modify the selective and ecological environments in numerous ways. All these can potentially influence their evolution. Only some of these modifications of the selective and ecological environments also constitute modifications of the external environment, but whether they do or not is unimportant when determining their role in the future evolution of the organism-environment system. This point, which was touched on earlier, is one reason why the simple notion of (external) environment is inadequate. Many changes in the external environment do not constitute change from the point of view of the organism and, conversely, an organism can transform its environment without actually changing the universal physical environment (for example, by changing a habitat association). It is the organism-referent description of the environment—the ecological environment—which captures the aspects of the environment that are relevant to the organism and defines what counts as a “change.”

The developmental systems model of evolution (Gray 1992, 1997; Griffiths and Gray 1994a, 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 “intracelluar inheritance” taking the place of genetic inheritance. This, however, would seem merely to 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. This response
is closely related to the comments about "multiple channel" models of inheritance given above. The DST model of evolution can be represented in such a way as to make it directly comparable with the models in Table 16.1. We can aptly represent the developmental system with the symbol $\mathcal{E}$. We retain Odling-Smee'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:

$$\frac{dE_{pop}}{dt} = f(E_{pop}, E)$$

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.  

**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? To give a clear answer we must go back to the definition of the developmental system given in Griffiths and Gray (1994a). 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 and 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 be understood only when those changes are described in terms of how they change the organism-referent environment (E	ext{org}). “Changes” in parameters of the external environment that 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's, and Brandon's work and by the concepts of ecological environment and organism-referent description of the environment.

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 sand 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 allow crabs to bequest 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 idea that really is missing from this picture is the notion 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: 472). But this is a feature which the developmental systems treatment shares with conventional neo-Darwinism. Adaptation is no longer defined in-
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...tainly, 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. Gould and Lewontin once described a mutation in a bird which doubles clutch size when the population is at the limits of the carrying capacity of the environment. The mutation sweeps to fixation with a consequent doubling of chick mortality. They described this as a case of selection operating without producing adaptation (Gould and Lewontin 1978). They were using "adaptation" in its original sense and consequently swimming against the neo-Darwinian tide. To most of their critics it seemed obvious that this trait was a paradigmatic adaptation. The first example of this shift in the concept of adaptation is, of course, Darwin's own idea of sexual selection. In at least some of his moods Darwin still saw this as a separate force that could act in opposition to natural selection. That suggests that he was limiting the idea of natural selection to processes that produce adaptations in the sense of William Paley's "contrivances"—features that suggest the world was designed by a beneficent creator. But it has been a long time since sexual selection seemed anything other than one kind of natural selection. 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 and 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.

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 an 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 skin of 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 the characteristic mother/child dyad or the ephemeral dyad formed of a buyer and seller in a market. It has recently been suggested that repeated assemblies of human individuals like these can themselves be units of evolution (Wilson and
Sober 1994). 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 and Gray 1997). Our focus has been on identifying developmental systems that could be evolutionary individuals. We have also been concerned to examine the extent to which DST can support a hierarchical model of natural selection. On the one hand, there is no reason why natural selection should not operate at different levels of biological organization (Brandon 1988; Sober and Lewontin 1982). On the other hand, not every repeated assembly is the focus of a selection process. So we need criteria to identify which developmental systems count as evolutionary individuals. While we 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 the concept of a superorganism, and also from Kim Sterelny’s work on higher level selection (Sober and Wilson 1994, 1998; Sterelny 1996; Wilson 1997; Wilson and Sober 1994). In this section we revise our previous account of the individual in the light of this work.

In earlier work we suggested that an evolutionary individual was distinguished from a collection of such individuals by the strength of the evolutionary association between its components: “We argue that the eukaryotic cell should be seen as a single life-cycle because its constituents are obligate symbionts and there are strong barriers to their evolving back to free-living forms. Strongly obligate symbiotes like this one should be regarded as a single evolutionary lineage” (Griffiths and Gray 1997: 478). The inspiration for this idea was the now almost universal acceptance that symbiotic lineages sometimes merge into a single lineage, as in the origins of eukaryotic cells (Margulis 1970). The descendants of these symbiotic organisms, the cell nucleus and the cell organelles, are replicated with different periodicities and have different patterns of inheritance, just like the various developmental resources that go to make up the developmental system of an organism. Nevertheless, unicellular eukaryotes are regarded as individuals, not collections of individuals. In contrast, the ants and acacia trees of the ant/acacia symbiosis are normally regarded as two separate evolutionary lineages. We suggested that the distinction between one and many turns on whether one element of the symbiosis can give rise to new cycles of itself that are not coupled to the other members of the symbiosis in the characteristic way. The meaning of “cannot” here is that the free-living form is very distant in the space of biological possibility. There are strong barriers to the components of the eukaryotic cell evolving back to free-living forms. The barriers for the ant and the acacia tree are weaker. We defended the vagueness of this answer by arguing that there is no clear line on the continuum between strong symbioses, facultatively colonial organisms like slime-molds and obligate colonial organisms like sponges and metazoans at which individuality springs into existence. We suggested that Maynard-Smith and Szathmáry’s concept of “contingent irreversibility” of an evolutionary development in a lineage came close to the concept of biological (im)possibility we required (Maynard Smith and Szathmáry 1995). Our proposal was intended to assist in defining an evolutionary lineage, as well as an evolutionary individual. If two life cycles become coupled in a way that is contingently irreversible, then the evolutionary lineages of which they are representatives have also merged.

We now see these ideas as strongly convergent with Wilson and Sober’s idea of “shared evolutionary fate” (Wilson and Sober 1994). In our 1997 paper we wrote: “Two lineages whose evolutionary fates were previously separable (though interacting) are now inseparably bound together” (Griffiths and Gray 1997: 478). However, we had not really assimilated Wilson and Sober’s proposal, one of whose advantages is the substance it gains from its relationship to Wilson’s concept of trait-group selection (Wilson 1983). A trait group is a set of organisms relative to which some adap-
tation 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. The water will be 1 cm deeper for everyone. Trait group selection can occur when there is a correlation between having an adaptation and being part of the relevant trait group. If the beavers that share a dam are closely related, shared descent will produce such a correlation—a mechanism long recognized as kin selection. Another long-accepted evolutionary mechanism—reciprocal altruism—produces the same effect. If individuals differentially associate with those who return their favors, then there will be a correlation between giving and receiving favors. The advantage of the trait group-selection model is that it brings out the underlying unity of the various models for the evolution of cooperation and reveals the whole landscape, only a few peaks of which had previously poked up through the fog of the group-selection debate.

The general phenomenon of which kin selection and reciprocal altruism are special cases is population structured evolution. Organisms do not interact with equal probability with every other member of the population. Population structure creates opportunities for trait group selection. The most obvious form of population structure is geographic structure. Robert Trivers’s famous paper on the evolution of reciprocal altruism gives as an example a symbiotic relationship between small cleaner fish and the large predators whose parasites these fish remove (Trivers 1971). The larger fish do not eat the small cleaners after they have finished cleaning, as a simple game-theoretic model would suggest. Trivers argues that this is because the large fish find it hard to locate cleaners. They solve this problem by returning to the same cleaning site each time. By eating the cleaners they would reduce their probability of being cleaned next time. Trivers treats this as a case of reciprocal altruism, but it is more common to define reciprocal altruism as requiring recognition and memory of individuals. What matters is that both the cleaner-fish example and more standard cases of reciprocal altruism are examples of population structured evolution and trait group selection. In the case of the fish, it is the patchy distribution of cleaners on the reef that creates a correlation between not eating cleaners and getting cleaned. In reciprocal altruism, the source of population structure is refusal to associate with those who do not dispense benefits. There are many other possibilities. Richard Dawkins has described a bizarre fictional example. He imagines some people with green beards who are disposed to help anyone else with a green beard (Dawkins 1976: 96–97). Given suitable cost-benefit ratios, individuals with this trait complex could outcompete those who neither dispense nor receive benefits. Dawkins uses this example to demonstrate that it is not kinship that is important in kin-selection models, but shared genes. He postulates that his green-bearded people are unrelated but share a pleiotropic gene that confers the trait complex upon them. However, the example would work just as well if different green-bearded individuals had many different genes that produced the same effects. The different genes could all impair the same normal biochemical pathway—many “genetic diseases” work this way. Dawkins’s example would also work if the trait complex were produced by cultural inheritance—a subculture keen on hair dye and cooperation. The particular mechanism of inheritance is irrelevant. What the hypothetical green-beard example actually demonstrates is not that kin selection is a special case of gene selection, but that it is a special case of trait-group selection. It is not necessary that individuals who selectively benefit one another be related or that they share a gene. The essential feature needed to get models like this to work is population structure. Something has to create a statistical association between dispensing benefits and associating with other individuals who dispense benefits.

Wilson and Sober argue that trait groups are units of evolution. More specifically, trait groups are interactors sensu David Hull (Hull 1980).
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. In one respect, however, a trait group is very different from the kinds of evolutionary individuals we tried to define in previous work. Each trait potentially defines a different trait group. The beavers in a dam are not a trait group with respect to foraging behaviors. In humans, each cooperative behavior may define a different trait group. Paying for your shout in the bar does not benefit the same group as helping with the housework. This has caused Dawkins to deny that there is any room for the replicator/interactor distinction in the selection processes described by Wilson and Sober (Dawkins 1994). According to Dawkins, "vehicles" (interactors) only exist in a special subset of selection processes where the fate of a collection of replicators is strongly linked by their joint investment in a complex, physiologically interdependent collection of adaptations like organism. In other selection processes, there are only individual replicators and their impact on their own replication prospects. This criticism seems to us both right and wrong, and to point to the need to clearly distinguish the concept of an interactor as it figures in the replicator/interactor distinction from the interactor as a generalization of the concept of the organism. If we concentrate on the replicator/interactor framework for thinking about natural selection then Dawkins's criticism is clearly misguided. Replicator and interactor are two aspects of the process of selection. In classic cases of gene selection, such as meiotic drive, the replicator and the interactor are the same physical object—a stretch of DNA. Nevertheless, this object is playing two separate roles. The fact that it plays the replicator role is supposed to explain the stable replication of form from one generation to the next. The fact that the same stretch of DNA plays the interactor role explains the selection of those replicators associated with the most efficient interactors. In paradigm cases of phenotypic evolution, the two roles are played by different physical objects—traditionally one or more genes and one or more phenotypic traits. Proponents of the replicator/interactor framework believe that identifying the occupants of these two roles is essential to understanding how natural selection is operating in a domain. We think the replicator/interactor framework has fatal flaws as a representation of evolution, embodying as it does the gene/environment dichotomy rejected by developmental systems theory (Griffiths and Gray 1994a, 1994b). But be that as it may, the arguments in favor of the framework have as much application in the case of trait group selection as elsewhere. In this sense, Dawkins is wrong and there are interactors in the selection processes Wilson and Sober describe.

The concept of an interactor has a double life, however. It also serves to generalize the notion of an organism. Sometimes, when we look for the interactor in a potential domain for natural selection we are looking, not for something that can play the abstract role of interactor in selection theory, but for something that corresponds to the organism. In earlier group selection models a spatially cohesive local population of a species—a deme—was assumed to correspond to the organism. In that case the analogy with paradigm cases of individual selection seemed clear enough. The new trait-group selection models show that the interactor role can be fulfilled in such a piecemeal way that nothing at this new, higher level of selection corresponds to the organism in paradigm cases. In this sense, Dawkins was right that in some trait-group selection models there is no interactor. Sterelny and Griffiths have argued that trait-group selection sometimes gives rise to functionally organized units with many adapted traits and sometimes does not. The old term superorganism is a useful one to replace the ambiguous interactor for these higher-level evolutionary units.

What makes a group into a superorganism? At an intuitive level, an ant nest is a much more convincing superorganism that a lodge full of
beavers. There are a number of features that seem to underlie this intuition, such as the functional differentiation of parts and the dependence of parts on the whole for their viability. Sterelny and Griffiths argue that what is fundamental to a superorganism is that very many traits of its organisms are selected with respect to a single trait group. That trait group is the superorganism (Sterelny and Griffiths 1999: 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. The general phenomenon that we see in these cases is the existence of evolved features that suppress competition between the component parts of the superorganism. The best known of these is the segregation of the germ line. In most animals a particular cell lineage is physiologically isolated relatively early in development as the source of all future gametes. This means that other cell lines that do not contribute to successful functioning of the whole organism are, like cancer cell lineages, doomed to extinction. Segregation of the germ line is an important mechanism. Organisms that do not have this feature, such as slime-molds, rapidly lose their multicellularity when selection for it is relaxed and become once again a population of free-living individuals. One species of aphid seems to segregate a proportion of its inherited endosymbionts as the exclusive source of founder populations of endosymbionts for its offspring, presumably in order to keep the remaining endosymbionts at work (Frank 1996). However, it is easy to overstimate the importance of this particular mechanism. Plants typically do not have germline 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). 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 and Visscher 1989). The worker bee is reduced to a part of a larger cycle as effectively as the cell of a metazoan body is by segregation of the germ line or an equivalent mechanism.

The idea that evolutionary individuals are trait groups thus converges on our older idea that an individual is a life cycle whose components cannot reconstruct themselves when decoupled from the larger cycle. Much trait-group selection does not give rise to new levels of individuality, but only to transitory interactors. However, when new features evolve, presumably by trait-group selection, which link together the members of a group in a way that is contingently irreversible, a new kind of individual emerges. At this point, the population structure on which trait-group selection depends is no longer just a cause of trait-group selection, but an effect of trait-group selection. An individual is a system in which the parts form a trait group with respect to most future evolutionary processes. 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/acetia symbiosis are less clearly so. Each of these has a life cycle and a developmental system that feed 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.

Conclusion

The aim of this chapter is quite simple. The fear that DST will lead to wholesale rejection of current evolutionary theory is not well founded. DST is not anti-Darwinian, nor does it render the basic explanatory terms of evolutionary theory incoherent. To the contrary, DST expands the scope and power of adaptive/historical explanation. The core Darwinian concepts of inheritance, natural selection, adaptation, individual, and lineage can be productively reworked in DST terms as follows:

- Developmental system—the interactants and processes that produce a life cycle.
- Evolutionary developmental system—the interactants and processes that produce those developmental outcomes that are reliably reproduced in a lineage.
- Inheritance—the reliable reproduction of developmental resources down lineages.
- Natural selection—the differential reproduction of heritable variants of developmental systems due to relative improvements in their functioning.
- Adaptation—the product of natural selection.
- Individual—the most inclusive sequence of developmental events (life cycle) such that the smaller repeated cycles nested within it form a trait group with respect to most plausible evolutionary scenarios.
- Lineage—a causally connected sequence of similar individual life cycles.
- Evolution—change over time in the composition of populations of developmental systems.

The benefits of this reconceptualization of evolution in DST terms are considerable. Phenomena that are marginalized in current genocentric conceptions of evolution, like expanded inheritance, niche construction and developmental organization, are placed center stage. Here are some suggestions for the kind of research questions we think DST encourages.

1. Treat all claims about instincts, genetic programs and other black boxes as potential research questions for developmental analysis, that is, how does this trait actually develop, what resources does its reliable development depend upon, are there many developmental routes to this outcome or only one, over what range of parameters is this developmental outcome stable, how does the “environment” change as a function of initial development differences that produce this trait?

2. Study expanded forms of inheritance. Conduct studies to investigate the longevity and fidelity of extended inheritance. Are there physiological and developmental mechanisms that enable these forms of inheritance to be vertically reproduced down lineages with fidelity and longevity? If extragenetic inheritance is an adaptive developmental resource, then developmental systems that reliably and efficiently pass on that resource would be at an advantage. Test adaptive hypotheses about extended inheritance using comparative methods—for example, is species diversity greater or rates of evolution higher in lineages with certain forms of extragenetic inheritance? Develop mathematical models of the impact of different types of extragenetic inheritance and their coevolution with genetic change. How tightly coupled do different developmental resources have to be to influence each other’s evolutionary dynamics? What role have expanded forms of inheritance played in major evolutionary transitions?

3. Study “niche construction.” Conduct field experiments to assess the fitness impact of niche construction. Develop models to investigate the
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4. Investigate the extent and functional basis of developmental modularity. How modular is development? Are functionally linked traits also linked together in development? Are there evolutionary trends in the degree of modularity? Does the modularity only hold over a restricted range of parameters? Can these parameters be changed by selection? Are extended forms of inheritance more or less modular than genetic inheritance in their developmental consequences?

Neo-Darwinism was the result of the union of Darwin's theory of natural selection with a particular view of heredity. The new view of heredity transformed Darwin's vision and gave rise to a wide range of research questions. In rejecting the narrowly gene-centered view of heredity and bringing developmental processes back into our account of evolution, we are not rejecting the theory of natural selection but are attempting to unite it with the developmental systems account of heredity and thus to reveal new and promising research agendas.

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Notes


2. Although the definition of evolution as change in gene frequencies is widely accepted, its significance is disputed. In G. C. Williams's influential view, when we measure change in gene frequencies we are getting at the heart of the process of evolution. It is genes that compete and are selected (Williams 1966). In contrast, phenotypic or hierarchical views of evolution accept that evolution can be represented by change in gene frequencies, but locate the processes of competition and selection at higher levels of biological organization.

3. In the mathematical theory of information (Shannon and Weaver 1949) and its 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 the “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.

4. In local enhancement the model directs the subject's attention to salient features of environment and the subject then develops the appropriate behavior through individual trial-and-error learning. In emulation the subject learns about cause and effect relations rather than the behavior itself.

5. The traditional neo-Darwinian explanation of adaptation is an “externalist” explanation. Explanation flows from the environment to the organism and not vice versa. For a good discussion of “externalist,” “internalist,” and “constructionist” explanatory strategies in general, see Godfrey-Smith (1996).

6. For example, Dennett (1995) and Pinker (1997). The idea is popular in the evolutionary psychology movement (Barkow, Cosmides, and Tooby 1992). For an attempt to integrate the idea that each trait has its own selection of relevant environmental parameters into evolutionary psychology, see Irons (1988).

7. Susan Oyama (personal communication) is less happy than we are with the idea of the external or universal physical environment. The next section makes clear that our formulation actually preserves the DST insight that a full description of the developmental systems of an individual organism, as opposed to a description of the typical developmental system of a population, will include all the causal factors that influence that individual's development. Oyama is legitimately concerned that the need for a concept of endogenous sources of change in evolution will create the impression that there is a need for sources of change outside
the developmental system in the individual case. That would be exactly the sort of dichotomous account of development that DST seeks to avoid, albeit with the boundary in an unusual place.

8. 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).

References


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