

Replicator II – Judgement Day

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Abstract. The Developmental Systems approach to evolution is defended against the alternative ‘extended replicator’ approach of Sterelny, Smith and Dickison (1996). A precise definition is provided of the spatial and temporal boundaries of the ‘life-cycle’ that DST claims is the unit of evolution. Pacé Sterelny et al., the extended replicator theory is not a bulwark against excessive holism. Everything which DST claims is replicated in evolution can be shown to be an ‘extended replicator’ on Sterelny et al.’s definition. Reasons are given for scepticism about the heuristic value claimed for the extended replicator concept. For every competitive, individualistic insight the replicator theorist has a cooperative, systematic blindspot.

Key words: gene, replicator, unit of selection, individuality, development

At some point a particularly remarkable molecule was formed. We will call it the *Replicator*. (Dawkins 1976, p. 16. Italics in original.)

1. Replicator I and Replicator II

In our ‘Developmental Systems and Evolutionary Explanation’ (1994) we attempted to sum up the current dissatisfaction with gene centered accounts of development and evolution. In our view, the replication of genes is simply one aspect of the replication of a life cycle. Many other elements of that process are replicated. Genes, methylation patterns, membrane templates, cytoplasmic gradients, centrioles, nests, parental care, habitats and cultures are all constructed by past generations, and interact to construct future generations. There is a lot of replication going on, much of which has been overlooked in the past, but there is no privileged class of replicators.

Kim Sterelny, Kelly Smith and Michael Dickison (1996) accept many of our arguments against a gene centered account of evolution and development. But they are unwilling to give up the idea that there are some developmen-

tal resources which occupy a privileged role in these processes. Their new 'extended replicator' comes in many forms. In one context it is a gene, in another a nest, in another a social tradition. In Dawkin's vision the 'immortal' replicators were locked away in cells 'sealed off from the outside world, communicating with it by tortuous, indirect routes, manipulating it by remote control' (Dawkins 1976: p. 21). In this newer theory, the very burrow an organism lives in may be a ruthless replicator manipulating the creature for its own selfish ends! We humans may be the 'survival machines' not only of our genes, not only of our methylation patterns, but even of our cultural artifacts.

In this paper we examine the relationship between the developmental systems account of development and evolution and this 'extended replicator' account. We show that to a very large extent, the two theoretical frameworks are inter-translatable, although it can be a little complex to describe some elements of the evolutionary process in the extended replicator framework. Finally, we look at the heuristic value of the two frameworks.

2. Developmental Systems Theory

According to DST the stability of biological form can be explained by the recurrence of the same system of developmental resources in each generation (Oyama 1985). The idea that developmental information resides in the genes is a shorthand for the idea that if all other elements of the developmental matrix are held constant, changes in the genes are reflected in changes in the phenotype. But it is equally true that if everything including the genes is held constant, changes in other elements of the matrix are reflected in changes in the phenotype (Johnston 1987). It is sometimes assumed that these latter changes must be uninteresting failures (Konrad Lorenz's 'bad rearing') rather than the interesting changes in design produced by altering the genes. In fact, developmentalists since T.D. Schneirla and D.S. Lehrman have documented in fascinating detail the dependence of the evolved phenotype on a rich and informative developmental context (Lehrman 1953). An infant primate inherits a social context without which it will not develop a typical adult mentality. Specific forms of social deprivation in the infancy of Rhesus monkeys can eliminate typical play and maternal care from the behavioural phenotype or create inability to successfully complete copulation. An even more striking example occurs in the fire ant *solenopsis invicta*. This species has two types of colonies: monogynous colonies with single, large queens and polygynous colonies with multiple, smaller queens. The 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 polygynous colony produces small queens who found new polygynous colonies. Exposure of eggs from either type of colony to the pheromonal 'culture' of a monogynous colony produces large queens who found new monogynous colonies (Keller and Ross 1993). This is not the outcome of a 'disjunctive genetic program' because the two types breed true. Under natural conditions offspring of monogynous queens do not get raised in the pheromonal environment of polygynous colonies or vice-versa. Without the experimental intervention most workers would have assumed that the two sub-species were genetically distinct. But the few genetic differences between the two types seem to be responses to the different selection pressures in the two nest types. What appears to have happened here is that a 'mutation' in the non-genetic elements of the developmental system has induced a new, self-replicating variant.

DST takes to its logical conclusion the slow unravelling of the idea that genes are the sole evolutionary replicators. This picture has broken down most spectacularly at the cellular level. Workers in the developmental tradition had drawn attention to the large class of structures which are inherited in parallel with the genes and play an essential role in development at the cellular level. These structures include basal bodies and microtubule organising centres, DNA methylation patterns, membranes and organelles (Moss 1992; Smith 1992, 1994; Griesemer 1994; Jablonka and Lamb 1995). These intracellular elements of the developmental matrix are essential for the replication of DNA and are not themselves constructed on the basis of DNA sequences. Changes in these epigenetic elements cause heritable variation in the cellular phenotype. They constitute an additional 'epigenetic inheritance system' (Jablonka and Szathmáry 1995). In more popular presentations these intracellular developments have caused a move from talk of a genetic program to talk of 'the genes along with the developmental machinery as one integrated suite of adaptations – the developmental programs' (Cosmides and Tooby 1992: p. 78).

DST extends the 'developmental program' beyond the walls of the cell. The characteristics that cause intra-cellular entities to be recognised as an epigenetic inheritance system are shared by many extra-cellular entities. The literature on habitat and host imprinting shows how critical many elements of the traditional 'environment' are to development. Parasitic bird species are adapted to their particular host species, but the association between parasite and host is often maintained by imprinting on the foster parent (Immelmann 1975). The use of imprinting as a mechanism of inheritance creates rich opportunities for evolutionary innovation by mutations in the 'environmental' elements of the developmental matrix. The social and hunting behaviours

of the European Barn Owl have been shown to be a function of environmental variables. Birds from the UK population moved to Malaysia produce a totally different, but highly functional, behavioural phenotype (Lenton 1983). The most principled response of these facts is the conception of 'extended inheritance' associated with DST (Gray 1992). Every element of the developmental matrix which is replicated in each generation and which plays a role in the production of the evolved life-cycle of the organism is inherited. The 'remarkable Replicator' is neither the genome nor the zygotic package, but the entire developmental system.

The prime focus of a DST account of evolution is the life-cycle, the series of events that occurs in each generation of a lineage. The development of an individual (ontogeny) is the reconstruction of a new life cycle from the resources left by previous life cycles. The process of evolution is the differential reproduction of variant life-cycles. The end of one life-cycle and the beginning of the next is marked by the reconstruction of the various complex devices which allow the life-cycle to reproduce itself from relatively simple resources. As Dawkins (1982 Ch. 14) has argued, this sort of cyclical reconstruction is required for the evolution of any complex, adapted organism. Adaptation requires cumulative selection on successive variations. So there must be a point in the life-cycle where small, undirected changes can restructure the organism.

The move to a process view of the unit of evolution is in line with G.C. Williams recent preference for a view of the organism as a structured stretch of space-time – in other words, a process (Williams 1992). For Williams, what is passed from one generation to another is not any physical essence, but disembodied information which then induces organisation in a stretch of space time. DST does without this ghostly organiser by emphasising the self-organising properties of the system of physical resources which occupy that stretch of space-time as a result of the activities of past generations. This self-organisation reconstructs the life-cycle. In this way the evolutionary version of DST keeps faith with a central element of the developmental systems tradition – the demand for a materialistic account of development. Explanations of ontogeny in terms of a program or organising centre are promissory notes redeemable against developmental biology.

3. Some Supposed Problems with DST – The Boundaries of the Developmental System

The strategy of Sterelny, Smith and Dickison's critique of DST is twofold. First, they argue that DST has failed to give a precise account of its proposed unit of evolution, and that there may be hidden difficulties in giving these

details. Second, they argue that the replicator concept has an heuristic value that should give it a place in any new, non-gene centered account of evolution. Hence biologists moved by the developmental systems critique of genocentric biology should extend the class of replicators, rather than embracing the developmental system as the unit of evolution. We confront the first element of this critique in this section and the next, simply by providing more detail on each of the specific points Sterelny et al. raise. We confront the second element of the critique by examining the relative heuristic values of the two approaches in section six. The most rhetorically powerful element of Sterelny et al.'s critique, however is the repeated insinuation that DST's concern with non-genetic developmental resources will lead to an unmanageable holism. They recommend their view as a way to honour the importance of non-genetic resources without having to study the whole organism as complex system. We confront this line of argument in section five by showing that the class of 'extended replicators' defined by Sterelny et al. is identical to the class of 'replicated developmental resources' defined by DST. Neither theory can be more holistic than the other. In any case, the accusation of unmanageable holism is misguided. It rests on the mistaken idea that because a wide class of resources may be of evolutionary significance, adherents of DST cannot make strategic research decisions about which of these resources to study at one time.

We discern five specific concerns about DST in sections 2.1 and 2.2 of Sterelny et al.'s paper: a basic request for a definition of the developmental system; some related concerns about the description of developmental resources; a concern about defining generations of developmental systems; a concern about distinguishing separate individuals in symbioses; and a pseudo-problem about the transitivity of causation.

Sterelny et al.'s first concern is that innumerable factors affect an organism during its development. How can this be reduced to a manageable 'developmental system'? In our article (1994) we solved this problem by an appeal to history. The way to describe a manageable developmental system is by distinguishing events which occur regularly in each generation from events which are unique to an individual. Sterelny et al.'s 'boundary problem' is solved by:

distinguishing developmental outcomes that have evolutionary explanations from those which do not. . . . There is an evolutionary explanation of the fact that the authors of this paper have a thumb on each hand. We have thumbs because of the replication of thumbed ancestors. The thumb is an evolved trait. But the fact that one of us has a scar on their left hand has no such explanation. The scar is an individual trait (We are referring, of course, to the trait of having a scar just thus and so, not the general

ability to scar). The resources that produced the thumbs are part of the developmental system. Some of those that produced the scar, such as the surgeon's knife, are not (1996: p. 287).

We do not claim that this is the only legitimate way to define a developmental system. This definition defines a developmental unit of evolution. A different definition would be needed, for example, in a study of the development of autism. There is nothing surprising in the fact that an account of pathological development must include different factors in the developmental system. The conventional phenotype concept does not encompass non-heritable pathologies either.

Sterelny et al.'s second worry is closely related to the first. They have 'doubts about the robustness' (p. 384) of the distinction between evolved and individual traits. Their doubts arise because of phenotypic plasticity: 'The Lyrebird's song is unique to each bird, for they are famous mimics. . . . Yet this does not seem to be an "individual" trait in the same sense that a scarred hand is' (p. 384). But the Lyrebirds' song is an individual trait in *exactly* the same sense as the scarred hand. There is an explanation of the general ability to form scars in terms of adaptation and history. There is no further explanation of my individual scar in terms of adaptation and history. The location and size of the scar must be explained in terms of surgical experiences unique to me. In just the same way, there is an explanation of the Lyrebird's general ability to form songs in terms of adaptation and history. There is no further explanation in terms of adaptation and history of Larry the Lyrebird's song including snatches from Tricky's album 'Maxinquaye'. This fact is explained by the personal history of Larry, not the evolutionary history of his lineage.¹

We find it reassuring that all of Sterelny et al.'s worries about boundaries are equally problems for the traditional phenotype concept. Life-cycles, like traditional phenotypes, can be polytypic. A lineage may contain a number of variant forms, each of which can give rise to the others. These different forms can be discontinuous, as happens with seasonal colour morphs in some butterflies (Smith 1993). They can also be continuous, as happens with quantitative characters like human height. All human heights within a certain range are equally the outcome of human evolution. No one height is the 'intended' outcome, with other heights being defects. Both these forms of variation, discontinuous and continuous are built into a full description of the developmental process. Like any other post-Darwinian approach to the organism, DST embraces variation as an essential feature of the evolutionary process rather than trying to dismiss it as noise. Another common form of variation, however, is abstracted away from in an evolutionary description of the developmental process. This is where the surgery scar on Griffiths'

left wrist fits in. It is not ignored because of any developmental difference – individual traits develop in just the same way as evolved traits. It is ignored in a description of the *evolutionary* developmental system because this trait (as opposed to the conditional trait of which it is a manifestation) is not heritable. Until some variation in the developmental system makes specific scars heritable, they are not part of the evolutionary process. Only heritable traits can be subject to selection and drift, or be bound together by the developmental process.

4. More Supposed Problems – Defining Life-Cycles

Sterelny et al.'s third concern is the 'cycle problem' This is the question of where one generation ends and another begins. In a traditional view of evolution generations begin and end with the phenotypic individual. In a view where the unit of evolution is the individual gene, generations begin and end with meiosis. But the developmental system has many elements, which need not all be replicated at one time. Sterelny et al. worry that 'on inspection, the developmental system replicating itself generation by generation seems perhaps a congerie of associated and perhaps co-evolving but still independent lineages' (1996: p. 383). Sterelny et al. would presumably be equally worried by Dawkin's proposal that the individual is defined by the 'single cell bottleneck' of the zygote. Although the nuclear DNA is all replicated together at meiosis, the DNA in each mitochondrion replicates itself by simple division with a quite different periodicity. Dawkins defines the individual by finding a cyclical pattern in the activities of this 'congerie of associated and perhaps co-evolving but still independent lineages'. Developmental systems theory does the same. The life-cycle is a series of events, possibly polytypic, which recurs reliably to make up a lineage. Its periodicity is unrelated to the periods of the various resources on which it draws. Some resources, like the contents of a pine nut, are used up in the construction of a single life-cycle. Others, like the modified soil conditions produced by a pine forest are drawn on and maintained by many generations. These differences do not obscure the regular series of events that constitutes the life and death of a tree.

There is a second 'cycle problem' which Sterelny et al. do not comment upon. As well as the cycles associated with traditional physiological individuals there are 'repeated assemblies' (Caporeal 1995) within a single individual, such as the leaves of a tree. There are also repeated assemblies of individual organisms, such as human groups and annual clonal populations of aphids. We embrace these larger and smaller cycles as potential units of evolution in the same way as authors working within the traditional replicator/interactor framework (Brandon 1988; Brandon 1990; Sober and Wilson 1994). Where

large cycles such as clonal populations or social groups have heritable differences in their ability to initiate new cycles of themselves, they may be units of evolution. Some smaller cycles within the organismic life-cycle may also be units of evolution. The evolutionary dynamics of meiotic drive genes are different from those of the organisms that contain them. They could be treated as life-cycles in whose developmental system the containing organism plays the role of a 'persistent' resource. We will not discuss these ideas here except to point out that any problems concerning these higher-level units of evolution should be no more intractable than those associated with current hierarchical models of the levels of selection.

There is yet another 'cycle problem' which requires work by the developmental systems theorist. This is Sterelny et al.'s fourth concern about DST. They ask how DST can distinguish between separate evolutionary lineages linked by ecological relationships and the parts of a single evolutionary lineage. In both cases, it would seem, we have a collection of cycles coupled together in characteristic ways. Like the other cycle problems this one has its correlate in discussions of the traditional phenotype concept. It is now widely recognised that intimate ecological relationships *do* sometimes cause the coevolving members of that relationship to merge into a single lineage. The eukaryotic cell descends from a symbiotic association of previously free-living organisms (Margulis 1970; 1981). The descendants of these organisms, the cell-nucleus and the cell organelles, are replicated with different periodicities and have different patterns of inheritance. Mitochondria, for example, are inherited only in the female line. Nevertheless, eukaryotes are usually regarded as individuals, not symbiotic associations. 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 symbioses like this one should be regarded as a single evolutionary lineage. A strongly obligate mutualism creates the same sort of merger in the tokogenetic tree – the pattern of relationships between individuals – as a hybridisation event does in the phylogenetic tree – the pattern of relationships between species. Two lineages whose evolutionary fates were previously separable (though interacting) are now inseparably bound together. In a more traditional treatment of the same cases, John Maynard-Smith and Eörs Szathmary (1995) refer to this as the 'contingent irreversibility' of the transition to a new unit of evolution.

A definition of the individual lineage as a set of coupled cycles for whom 'de-coupling' is not an evolutionary option is a principled one, but like the traditional phenotype concept it does not generate a sharp boundary between single lineages and intimately coupled ecological associations. It is an objective fact about the natural world that slime moulds and other colonial

organisms represent intermediate cases between a well-defined individual and a mutualistic ecological association. Leo Buss (1987) and others have used these organisms as models for the evolution of genuine multi-cellular individuals. Sterelny et al. mention ant-plant mutualisms as another class of problem cases. We think the details of this case make it fairly clear that these associations are not 'contingently irreversible'. Either partner could evolve out of their association with the other. Acacias can, for example, recruit a new ant colony if they lose their original partner. If eukaryotic cells could survive the loss of their mitochondria and recruit a new population of symbionts they would look a great deal less like a single evolutionary lineage. A class of symbioses closer to lineage merger may be those lichens in which the algal component is from a clade which is not found living free. Free life seems only the most distant possibility for both algal and fungal components of this association. Once again, we find it puzzling that this continuum of cases is regarded by Sterelny et al. as a consequence of DST's supposed holistic excesses, when the continuum is equally apparent with the traditional phenotype concept.

The criteria we have used to distinguish symbioses from mergers can also be used to distinguish a part of a life-cycle from a whole cycle. Can the constituent cycle become a separate, free-living entity within the (vague) bounds of biological possibility?² A leaf of a vascular plant is an unproblematic part. Mutation in the developmental resources creating the leaf are heritable via vegetative reproduction, but they lead to an entire variant plant not a free-living variant leaf. A single slime mould is an individual, since common mutations lead to the abandonment of the collective phase of the life-cycle in favour of a completely free-living existence. It is illuminating to contrast the slime mould to a traditional, phenotypic individual in an eusocial insect colony. This 'individual' approaches far closer to a mere part than the individual slime mould, because it is further in the space of biological possibility from any free-living form. Another interesting case is presented by species in which individuals go through metamorphic stages. The period between stages, when the complex structures of the organism must be assembled from relatively unstructured resources, are an obvious opportunity for small changes in the resources to induce substantial re-organisation of the life-cycle. They might therefore be thought of as the end of one, polytypic life cycle and the beginning of another. In our article (1994) we suggested that this interpretation is not appropriate because biologically plausible variants of one metamorphic stage recapitulate at least the earlier stages in the life-cycle.

Sterelny et al.'s final concern is the effect of the transitivity of causation on the definition of the developmental system. Causation is transitive in the

sense that if A causes B and B causes C, then A also causes C. DST defines a developmental system by looking at the typical causal interactions which create the life-cycle. But if causes form a chain stretching back indefinitely into the past, then isn't DST saying that the developmental system of a modern frog includes events ten million years ago? Once again, Sterelny et al. raise the spectre of unmanageable holism! This spectre is easily dismissed, however. DST claims that the unit of evolution is the life-cycle, a series of events that forms a unit of repetition in a lineage. The events that feed into this process can be characterised at a greater or lesser causal remove, but this does not impinge on the definition of the life-cycle. The events that lead to a fire can be described at a greater or lesser causal remove – the striking of the match, the upbringing of the arsonist and even the 'big bang' – but this does not make it hard to describe the sequence of events that make up a fire. The transitivity of causation may create general philosophical problems in enumerating 'the causes' of an event, but it raises no special problems for DST.

5. The Extended Replicator Theory

Sterelny et al. (1996) propose an alternative response to the developmental critique of gene-centered biology. Their 'extended replicator theory' (ERT) claims that the genes do have a special, informational role in development, although they are not the only things that have that role. ERT admits that the causal relationship between the genes and developmental outcomes is no different from the relationship between those outcomes and many other developmental resources. They base the special status of the genes and other replicators on the special biological functions of these resources. According to ERT, developmental resources are only replicators if they are adaptations for (have been selected for) their role in development.

The background to ERT is the modern etiological theory of biological function. An item's biological functions are those effects for which it is an adaptation. It is possible to explain a trait in terms of its functions because those functions are precisely those effects of the trait which are mentioned in a selective explanation of its current prevalence (Millikan 1989; Neander 1991a,b; Griffiths 1993). Karen Neander (1995) has shown that a trait typically has a whole series of functions, produced by more or less abstract representations of the selection process that gave rise to the trait. We can describe the functions of a particular state S of the frog's visual system as follows. The state S:

contribute/s to fitness

\wedge \vee
 so as to by
 \wedge \vee

occur/ing in response to food

\wedge \vee
 so as to by
 \wedge \vee

occur/ing in response to flies

\wedge \vee
 so as to by
 \wedge \vee

occur/ing in response to small dark moving things

(Goode and Griffiths 1995: p. 101).

The functions ascribed in this hierarchy of descriptions can be more or less specific to the trait under examination. Every adapted trait of an organism has the function of enhancing its fitness, but only some have the function of detecting flies. Sterelny et al. hope to use this idea of the specific function of a trait to distinguish a smaller class of replicators amongst the overall class of developmental resources. While all adapted traits have as their ultimate function helping to reproduce the organism's life-cycle, only some have this as their *specific* function. Sterelny et al. predict that the genes will be amongst this smaller class of 'developmental traits':

The genome is one of the designed mechanisms in virtue of which phenotypes and genotypes duplicate themselves. Adaptation is seen in the proof-reading and repair mechanisms of the genes, but not only there. . . . This idea of a designed copying mechanism is the key to understanding the privileged role of the replicators in the total developmental matrix. Some parent-offspring similarities result from elements of the developmental matrix that have been selected to produce those similarities. Replicators exist because of those selection histories, and that distinguishes their role in development (1996: p. 387).

At this point the reader is supposed to sink back in her seat and relax as the spectre of unmanageable holism recedes. The effects of the developmental critique have been contained. The genes must accept some companions – the intra-cellular elements described above and a few odd extras like gut endosymbionts with a direct role in producing growth spurts. But most factors

which play a role in development can be relegated to their traditional role as a passive background against which the developmental programs unfold:

Garbage cans are part of the developmental matrix of suburban-adapted Australian possums, but possum behavior does not result in the flow of new cans. Only some elements of the developmental matrix are adapted for their role in development (1996: p. 393).

In reality, however, the rhetoric of conservatism, containment and manageability with which ERT is presented is entirely at odds with the substance of the theory. We have already demonstrated that DST does not lead to unmanageable holism, but if it did then so would ERT. A principled application of Sterelny et al.'s definition of a replicator shows that everything which DST claims is replicated in development is also a replicator according to ERT. According to Sterelny et al., a component of a developmental system is a replicator if the component has an adaptive history as part of a mechanism causing similarities between parent and offspring:

Some developmental factors do not just cause similarities between one developmental cycle and its successor. They have the form they do because they cause those similarities. These are the replicators (p. 384).

Let us apply this definition to the developmental system as defined by DST, which starts with the developmental process or life-cycle. The life-cycle draws on a whole class of developmental resources, many of which have some causal dependence on previous generations of the life-cycle. Some resources are produced by the immediate parents of the developing individual. Others, like soil conditions or micro-climates, are produced by activities of many individuals or many generations. Other resources, like sunlight or gravity, persist independently of the activities of the lineage. DST says that all developmental resources except these persistent resources are replicated in development. DST also claims that the relationships which individuals establish with persistent resources in order to reconstruct their life-cycle are replicated in development. It is immediately apparent that both the replicated resources and the replicated relationships fit the ERT definition of a replicator. Life-cycles proliferate or decline because of their differing ability to replicate themselves. The form of existing life-cycles is explained by this differential replication of variants. The form of a life cycle is a result of the particular resources and relationships that construct it. The resources and relationships which we find constructing organisms today can therefore be explained as the results of a process of differential replication and as having the adaptive function of producing the existing life-cycle. So all these resources and relationships meet the ERT requirements for replicators. The only elements of the developmental matrix which don't qualify as replicators on Sterelny et

al.'s definition are the persistent resources. Our (1994) presentation of DST already clearly stated that these are not replicated in development.

We have argued that all actively replicated developmental resources and all relationships to persistent resources are replicators in the sense defined by Sterelny et al., because developmental outcomes have evolved through the differential replication of the variant life-cycles which depend on them. But it is not enough for Sterelny et al. that something *does* play a role in the development of an evolved feature. It must have the *adaptive function* of playing that role. Here ERT might hope to find grounds to make a stand upon. Sterelny et al. might say that many developmental resources are not *adaptations* for development in the strong sense that they require. Perhaps there has not been enough variation in some of the key elements of the developmental matrix for a selective explanation to be illuminating. Perhaps several elements of the developmental matrix are so strongly linked together by anatomy or physiology that the preservation of some of them in evolution should be construed as a side-effect of the preservation of others. By strengthening the requirement that developmental resources be adaptations Sterelny et al. might hope to live up to their aim of characterising a more restricted class of replicators. But this would be a very dangerous road for them to travel. Key elements of the machinery of cell replication, like the specific genetic codes of nuclear or mitochondrial DNA, are probably good candidates for things locked in place long ago in evolutionary time and strongly linked together by physiology. Some of the most apparently unproblematic replication machinery might fail the adaptive test while some of the most controversial, like habitat and host imprinting, passes it with flying colours.

Although ERT is not actually any more narrowly focused than DST, it is easy to think that it is. This impression is produced in two ways. First, Sterelny et al. focus on the physical components of the organism, rather than events in the organism's life-cycle. They ask of each physical part whether it is basically developmental or basically non-developmental in function. But most components of an organism have many different biofunctions, some of which, at some time in an organism's life-cycle, are developmental. For example, Sterelny et al. claim that: 'Not every reliably recurring factor is a replicator. The human hand is not a replicator. The hand's biofunction is economic, not developmental' (1996: p. 389). But the hand is regularly used in providing childcare, which is presumably an evolved developmental mechanism. Biological functions attach to structures in virtue of the role those structures play in the ecologically significant activities of the organism. Like many other complex structures the hand is used for a whole range of such activities, each of which partly explains its continued importance to the organism. Sterelny et al. might argue that the hand's role in childcare is an

exaptation and has contributed nothing to its evolution, but this would be *ad hoc* speculation. Primate forelimbs have been used in childcare (and in the child's case for hanging onto mum) for as long as they have been used for anything beyond locomotion. Similar remarks apply to more extended features like the speech stream. Language is a device for communication, but the fact that exposure to language helps children to learn the local conventions of communication cannot be dismissed a fortuitous side-effect. It is a key evolutionary property of languages that they are learnable by human infants. Because it has an evolved role in shaping the minds of infants, the speech stream has developmental biofunctions. Even the general claim that 'not every reliably recurring factor is a replicator' is misleading. It implies that DST says that every reliably recurring factor *is* a part of the developmental system. DST does not claim this. It does claim that every event which is part of the evolved life-cycle is an *outcome* of development. That is surely a truism. But DST does not claim that everything that regularly occurs in the life-cycle is an *input* to development. The inputs to development are the developmental resources. These are the things which must be produced by previous generations in order for the next generation to develop. This description will capture all those products of the life-cycle which have, in Sterelny's sense, specifically developmental biofunctions.

The second main way in which ERT gives the impression that it is more disciplined and narrowly focused than DST is by resisting the idea that an organism's relationship to a persistent resource such as a habitat can be the subject of an evolutionary explanation. This is important, because the only class of developmental resources that clearly is excluded by ERT is the class of persistent resources. Any class of resources such which owes its existence to the life-cycles which use it as a resource can be a replicator as defined in ERT. A rainforest microclimate may be a replicator. Only the persistent resources, which have no causal dependence on the life-cycles they help to generate, are excluded from being the products of evolution and hence from being replicators. Unfortunately for ERT, DST does not claim that persistent resources are replicated in development, or that their existence can be given evolutionary explanations. They are highly important for understanding development, but they are not part of the unit of evolution. What DST does claim, however, is that the relationship which is forged with a persistent resource in each generation is replicated in development and can receive an evolutionary explanation. By excluding relationships from evolutionary narratives ERT could claim to be narrower than DST and make good its anti-holistic rhetoric. But ERT is not in fact in a position to exclude these relationships from the evolutionary story. There are well-founded evolutionary narratives in which relationships proliferate or are extinguished by differential replication of variants. These

cannot be excluded without reducing the explanatory power of evolutionary theory.

In many parts of their paper Sterelny et al. show a clear grasp of just how much can be explained by the differential replication of variants, and just how far the replicator extends:

Nesting burrows are replicators. The causal relations between burrows and burrowers is like that between genes and their interactors. No gene makes an organism. But variance explains variance: a variable oystercatcher may be black rather than pied because it has one gene complex rather than another, even though no gene complex makes a colour pattern. Similarly, a variation in a burrow can cause a variation in a burrower: a particular penguin chick may be healthy and safe because its burrow has one site rather than another, even though no burrow features make penguin flesh (1996: p. 397).

This is exactly what DST means by a relationship to a persistent resource. In Sterelny's own habitat (Wellington, New Zealand) Soames Island is a better place for burrows of the Little Blue Penguin than the Eastbourne foreshore, with its cars, cats and houses. If a lineage of penguins has a habitat association with one location rather than the other, it will have more descendants. The composition of the population at some later date can be explained by the differential replication of island penguins over foreshore penguins. In this particular case this explanation may not be wildly exciting. In cases of host imprinting in parasitic insects or cuckoos, however, much of the rest of the parasite group's evolution may result from the success of lineages with one relationship rather than another.

Despite these examples, Sterelny et al. try to exclude relationships from the class of replicators. The penguin burrow can be a replicator, but the relationship between the penguin and its habitat cannot, because it is not 'part of a copying and interaction cycle' (1996: p. 397). We do not think this position can be sustained. The strategy Sterelny et al. use to exclude relationships is the same that Sterelny and Phillip Kitcher (1988) used successfully to deflate Dawkins' (1982) concept of the extended phenotype. In that earlier debate, Sterelny and Kitcher argued that an extended phenotypic trait can always be reduced to the more proximate activity of the organism that brings the extended trait into existence. The evolution of beaver dams can be reduced to the evolution of dam-building behavior. In this new debate Sterelny et al. argue that when a relationship between a lineage and a persistent resource appears to have evolved, this can always be reduced to the evolution of the mechanisms that sustain the relationship. The evolution of habitat associations can be reduced to the evolution of habitat imprinting. We have already shown in our article (1994) why this reduction will not work. There are

many cases in which the particular association found in nature is the result of differential reproduction, as well as the general mechanism by which all variant associations are reproduced. Some specific examples will make this point more clear. Hermit crabs are dependent on the discarded shells of other species for survival. The crab's activity usually has no impact on the fate of the other species, so the shells constitute a persistent resource with respect to the crab. We have argued with Sterelny in personal communications that although the shells are not part of the same unit of evolution as the crab, the relationship of the crab to the shells is part of that unit. Hermit crabs presumably gained an adaptive edge over relatives by forging this relationship and have proliferated in virtue of their continued replication of the relationship. We tried to block the reduction of this evolutionary narrative to one about the evolution of shell-using behavior by pointing to crab lineages which are going extinct because they rely on a supply of fossil shells which is running out. These lineages are less successful than their rivals because they have forged an inferior relationship. Their evolutionary achilles heel is the character state 'related to *this* shell species'.

Although the hermit crab is a striking example, it is probably not the best one for our purpose because there is likely to be a specific mechanism producing the preference for one shell type. In many cases of habitat and host imprinting, however, exactly the same physiological mechanism produces stable preferences for many different hosts/habitats. These mechanisms include habitat/host imprinting and the purely passive 'mechanism' of biogeographic association. Immelmann (1975) cites a study of European mistle-thrushes which illustrates the importance of habitat imprinting. This species expanded its range from forest to parkland in France and Germany. The expansion proceeded not by the spread of several local populations from local forests to local parklands, but by the spread of a single population which had become habitat imprinted on parkland. The fate of different thrush lineages will depend on their interaction with the particular habitat with which they are reliably associated, and the fate of that habitat. Another of Immelmann's examples demonstrates the importance of host imprinting. Cuckoo-style parasitic viduine finches have developed morphological sub-species and species because of their association with different parasitised species. These associations are sustained by host-imprinting. Being associated with a successful host species, and one that has not developed anti-parasitic adaptations is a critical factor in success for the parasitic species.

Sterelny et al. reject all these evolutionary narratives on the grounds that persistent resources are not replicated by the lineages that rely on them:

The crab-fossil shell relationship is not a replicator, precisely because the hermit crab is unable to influence the availability of a critical resource

in the next generation. There are no mechanisms in this developmental matrix that have the biofunction of shelter making. . . . So while this relationship may be of evolutionary interest, it is not copied, though shell hunting and occupying behavior may be. The hermit crab shell relationship is thus quite unlike that between penguins and their burrows (1996: p. 397).

This argument seems to be a non-sequitur. The relationship between crab and shell *is* replicated in every generation of the lineage. It is not automatic that hermit crabs crawl into the very same species of shell or that organisms which use sunlight to synthesise metabolic products spend enough time in the sun. Lineages evolve into and out of these relationships. The rest of the developmental system must be structured in such a way as to recreate the relationship. We think Sterelny et al. have something like this argument in mind: replications of relationships are not ‘copying and interaction cycles’ because the activity of the organism (interaction) does not create the conditions for its own replication (copying) – ‘the hermit crab is unable to influence the availability of a critical resource in the next generation’ (p. 397). But this argument excludes either too much or too little. If Sterelny et al. deny that the activity of the organism creates *some* of the conditions for its own replication, they are clearly wrong. Parents shape offspring in a way that allows them to replicate the right relationships. A mutant hermit crab could leave children which do not seek out shells. If, however, Sterelny et al. merely deny that the activity of the organism creates *all* the conditions for its own replication, then they have set a test for being a replicator which *genes* cannot pass! A major element of the developmental critique has been to reveal the myth that genes ‘replicate themselves’. Genes cannot replicate without an independent inheritance of membranes, centrioles, endoplasmic reticulum and so forth. ‘Prime movers themselves unmoved’ occur in theology, not biology.

We conclude that ERT has no real grounds for rejecting relationships as replicators. The only elements of the developmental system that are not ERT replicators are the persistent resources, elements which DST has already said are not replicated in development and are not part of the unit of evolution. The rhetoric of manageability and containment that ERT deploys against DST is not justified by any reduction in the complexity of the picture of evolution from one theory to the other.

6. The Debate over Heuristic Value

There is one other way in which ERT tries to live up to its anti-holistic rhetoric. First, Sterelny et al. suggest that ERT allows the study of evolution

in a manageable way by focusing on one replicator at a time while holding the others fixed as a background. DST, however, forces us to study the evolution of the whole complex system involved in development. Second, they suggest that ERT saves the heuristic value of earlier 'selfish replicator' theories. These theories draw attention to the continual struggle between individual replicators, and the way that the need to guard against subversion from within has shaped evolution. 'No doubt it is possible to formulate these problems in that (DST) language, but they are not "in your face"' (1996: p. 395).

In this section we rebut these arguments from heuristic value. The first works by comparing a complete account of developmental system evolution with a simplified, operational version of the evolution of a replicator. The replicator theorist can, indeed, focus on one replicator and regard all the others as a constant background. This is often a sensible way to think of a more complex reality. But a nest design, for example, does not really evolve against a constant background of genes, preferred nest site and so forth. These 'background conditions' change over evolutionary time. This changing background changes which nest design will confer the maximum replicating power on the life-cycle as a whole. The evolutionary dynamics of nests are therefore a function of the dynamics of the other developmental resources. In general, a complete 'replicator and background' account of the evolutionary process must describe the coupled co-evolution of organism and environment, as outlined by Robert Brandon and Janis Antonovics (Brandon and Antonovics 1996). This account will be at least as complex as DST. The equations describing the evolutionary dynamics of certain alleles as a function of habitat factors will be coupled to equations describing the evolution of those habitat factors as a function of the prevalent alleles, and so forth until the entire co-evolving system has been described.

The point we want to make is not that a replicator and background account must actually construct such a complete set of coupled equations in order to study any actual biological system. The point is that when a replicator and background theory which fails to do so is contrasted with a full-blown theoretical account of developmental systems a completely unfair contrast is being drawn. A practical, operational simplification of one theory is contrasted with a full, theoretical representation of the other, and the latter is condemned as impractical and holistic! In fact, pragmatic, local simplifications for the purpose of actually doing experiments are equally open to the developmental systems theorist. The developmental systems theorist can study the evolution of particular elements of the life-cycle while assuming that many other elements play a more or less constant role in reconstructing the life-cycle over the relevant stretches of evolutionary time (although sometimes this assumption will prove misleading).

The heuristic insights offered by the ‘selfish replicator’ perspective are also overrated. It is interesting to compare Sterelny et al.’s response to Leo Buss’ (1987) work on the evolution of individuality to our own. Buss argues that major transitions in the history of life have occurred with the evolution of mechanisms that suppress competition between individuals at an existing level of organisation. These mechanisms create new units of evolution. Examples of such major transitions are the emergence of eukaryotic cells and the emergence of multicellularity. Sterelny et al. see the significance of Buss’ work as its highlighting the potential for subversion of larger systems by their components:

From the perspective of the germline cells, the construction of the body is an enormous investment of resources that might instead be directed to replication. Why is it worth it? Why is this investment not inevitably subverted by cell-line rebellion (1996: p. 395).

We see the significance of Buss’ work rather differently. It reveals some of the ways in which developmental systems are structured so as to reduce what were previously individuals to components to parts of a single evolutionary unit. Our discussion of the nature of individuality (above) owes a great deal to the insights derived from this source.

The replicator theorist focuses on the potential of the system to break down, and how its components might then evolve as free-living systems. The developmental systems theorist focuses on the integration of living systems and the evolutionary potential that result. We would claim that the heuristic advantages of this perspective are just as great. For every individualistic, competitive insight the replicator theorist has a cooperative, systematic blindspot. The negative heuristic effect of the replicator perspective is well exemplified in Richard Dawkins’ (1982) discussion of the evolution of individuality. Dawkins sees the segregation of the germ line as the only possible barrier to ‘subversion’ of the individual by its selfish components. If somatic cells were not restricted to reproduction via their germ line relatives the adaptive structure of the organism would inevitably break down as cell lines devoted their entire resources to reproduction. Dawkins suggests reproduction via multicellular propagules could never lead to the evolution of complex, adapted bodies (1982: p. 260). But Buss has described in some detail how the nature of plant cells has allowed retention of vegetative reproduction as a major means of reproduction. The existence of entire fields of grass grown from stolons and rhododendron forests grown from rooted branches testifies to the reliability with which form can be reconstructed by this method of propagation. Buss’ discussion of fungi reveals that the segregation of the germ line can be replaced by alternative complex organisational properties as well as by the fundamental properties of cell physiology that replace it in plants.

If the selfish replicator perspective has focused attention productively on questions like the origins of sex, it has equally distracted attention from the existence of phenomena involving integration at higher levels of organisation. The recent work of David Sloan Wilson and Elliott Sober (1994a; 1994b) has shown how the stress on unstable alliances of warring replicators blinded people to the evolutionary potential of aggregations of physiological individuals. Mutualisms, symbioses and various forms of societies represent the evolution of diverse mechanisms whereby physiological individuals are forged into new units of evolution. The fact that levels of organisation sometimes break down need not be given more prominence than the fact that they work well enough to evolve interesting properties. Cancers are not more central to physiology than normal cell differentiation.

7. Conclusion

We hope we have calmed fears that DST is a form of woolly holism. We have provided grounds for scepticism about the purported heuristic value of the alternative, selfish replicator perspective. The positive reasons to adopt DST remain what they have always been. DST provides the right framework for the re-integration of developmental and evolutionary biology that has been called for repeatedly since the foundation of neo-Darwinism. As Susan Oyama (1985) has argued, no other perspective will finally lay to rest the confusions about development represented by the nature/nurture debate and current formulations of the relationship between genes and environment.

Notes

¹ There is a sense of 'adaptation' found in psychology and physiology in which Larry's song is an 'adaptation'. This is the sense in which adventurers become 'cold-adapted' after some months in the antarctic. Larry is 'rock-adapted'. This sense is quite distinct from the idea of an evolutionary adaptation.

² A search through the literature on possible world semantics would likely reveal some interesting findings about notions of possibility defined over fuzzy sets of possible worlds. We have not yet had time to investigate this possibility.

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