Natural Selection in Relation to Complexity

Stanley N. Salthe*
City University of New York
Binghamton University

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Abstract Structural complexity characterizes our representations of dissipative structures. As a mechanistic concept, when referred to natural systems it generates perplexity in the face of logically sound models. Natural selection is a simple mechanistic concept, whose logic is well exemplified in genetic algorithms. While biological traits and functions do appear to have been subjected to selective culling, current neo-Darwinian theory is unable to account for the evolution of traits or functions when many of these are taken as the separate objects of independent fitness functions. Soft selection, acting in a phenotypically holistic manner, does model selection acting upon structurally complex systems with many traits and functions, but does not account for the evolution of specific traits or functions. It is further suggested that selection cannot be other than a weak force in the early, generative stages of complex life histories, and that this is a good thing, preserving their generativity. I conclude that natural selection theory by itself cannot account for increases in structural complexity.

1 Introduction

This article will examine the question: Are the principles of natural selection as they are currently understood sufficient to explain the evolution of complexity in living systems? I will present some facts about selection acting in nature, that, because they point to weaknesses in selectionist thinking, should be of interest to those involved with artificial life. Natural selection was formulated in relation to living systems, which are widely understood to be emblematic of complex systems. But I note here that there is no strong opinion in evolutionary biology that complexity increase has evolved in living systems by way of natural selection [29, 30]. In the context of artificial life, it could be pointed out as well that selection occurs in the abiotic world [50], where, however, it lacks a fertility component [52] in addition to the viability component characterizing any kind of selection. Furthermore, abiotic systems are no less complex than biological ones when viewed as whole systems—for example, when taking into account an entire drainage system rather than just a single reach of a stream, or an entire storm front instead of a single tornado. Biological systems may seem to be especially complex mostly because their scale is close to our own observational scales, giving us a sense of many details with respect to a definite view of system boundaries. After pointing out that a common view of the natural selection of traits and functions does not fare well faced with the complexity of actual systems, I reintroduce a model of selection that can relate well to complex systems, even if not to increases in complexity.

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* 42 Laurel Bank Avenue, Deposit, New York, 13754. E-mail: ssalthe@binghamton.edu

2 Complexity

Definitions of complexity range from positive ones like Gell-Mann's [15] or Crutchfield's [10] "effective" or "structural" complexity, as a concise listing of the regularities shown by a system, to the negative one that complexity characterizes situations that generate perplexity [48]. Both kinds of definition are observer dependent. Gell-Mann and Crutchfield's view has complexity arising in situations intermediate between complete order and complete disorder. Collier and Hooker [8] gave a useful gloss of a similar view, which I give a version of in Figure 1. I would take dissipative structures generally to be complex. In 2006 [48] I suggested that there are two frameworks that are particularly prone to generating complexity, which I call the *scale hierarchy* and the *specification hierarchy* [45, 47]. These both exemplify the idea that complexity involves an inability to describe a system using only a single criterion or viewpoint [43]. This view could be summed up as "the more you look, the more you see"—that is to say that complex systems seem to be inexhaustibly productive of new information upon continued examination from new perspectives.

Systems describable using the scale hierarchy format (formally a compositional hierarchy) are complex—my [45] *extensional complexity*—in that more than one system occupies the same locale, ranging from macroscopic ones through mesoscopic to microscopic, and these transact in various indirect ways, frequently provoking chaotic dynamics. In this case changing the scale of observation delivers completely different information at the same locale [16, 62]. Extensional complexity exists wherever systems of different spatiotemporal scale influence each other without directly interacting. Systems describable using the specification hierarchy format (formally a subsumptive hierarchy) are complex—my [45] *intensional complexity*—in that any system at any scale exists at more than one integrative level, or [38] *level of reality*. For example, an organism could be viewed as a physical system, focusing on circulation, fluid dynamics, and diffusion. Or it could be viewed as a chemical system, considering metabolism. Again, it could be viewed as a biological system, looking at reproductive processes. Intensional complexity exists where systems of different kind (physical, biological) interact coherently. It is the complexity we face when we realize, for example, that leg muscles active in running consist of muscle cells powered by chemical energy.

From either hierarchical perspective, complexity can be seen to characterize any material system, and so neither is restricted to biological systems. It is, nevertheless, possible to consider the question of whether natural selection can work to increase any form of complexity, or to particularly support it, in living systems, as for example does Wilson [59, 60], who describes a model of ecosystem-level

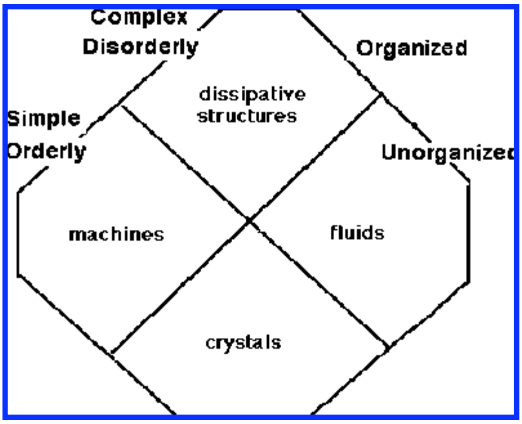

Figure 1. Contextualizing structural complexity (modified from Collier and Hooker [8]). Note that, while machines can be quite complicated and can generate complex output, they are conceptually simple in the sense that they can be explicitly described fully. Note as well the mapping of complexity to disorder. This reflects the perplex aspect of complexity.

selection promoting the coexistence of mutually beneficial species, which would increase the structural complexity of an ecosystem.

The definition of complexity is crucial when trying to determine whether selection can increase it. Lenski and colleagues [26] claim to have used the Avida platform to promote the evolution of complexity in "digital organisms." During evolution therein the digital organisms can construct logic functions, some of which allow them to replicate faster by way of garnering increased amounts of "energy" (CPU cycles) or by increasing replication efficiency. Logic functions may be acquired by way of random mutations. The authors claim that increased size and numbers of logic functions amounts to increased complexity. I think this can be questioned inasmuch as they have assigned the system two (what amount to phenotypic) components of fitness—one fertility function (replication efficiency) and one viability function (rate of energy capture)—neither of which can get to be more complex. The logic functions (nine possible ones) can be viewed as genes coding for the two functions, as this information is what is replicated. There is no increase in *organismic* complexity, but, rather, in my view, an increase in the number of *genes*. Admittedly, Gell-Mann and Crutchfield's definition of complexity might be used to defend the assignment of complexity here.

3 Natural Selection

Fisher's fundamental theorem of natural selection [12] encapsulates the basic logic of natural selection, which depends upon variation in fitness relative to biological functions, as carried by variation in phenotypic traits. In the simplest models of evolution by selection, this variation is reduced by selective culling of inferior types, being traded for adaptation as the current best type for any trait increases its representation in a population. The model implicitly focuses upon single traits. So, in this simplest model, selection would be a process of simplification, resulting in diminished numbers of genotypes and phenotypes as a consequence of a population becoming specialized in the currently most successfully reproducing type that it can generate.

Even this simple process could logically promote (but not create) a more complex habitat for selected populations, for example, as in the result of character displacement [4]. Here, niche space (sensu Hutchinson [20]—see [46]) gets progressively reduced within sympatric populations as they make room for each other's existence by way of selection acting separately in each population, culling types that waste energy in competing with another population. This has the effect of reducing niche overlap between the populations, therefore reducing interspecific competition. However, this process likely will destabilize relations with yet other species' populations, requiring further selective adjustments in connection with these—and so on, delivering in effect a "continual deterioration of the environment" [53] so that selective adjustment can never really settle down. Here we see a lowest level of selective percolation as the background to occasional episodes of secular evolutionary change. And here we also see selection entangled in a mesh of extensional complexity that it cannot be held responsible for having produced as a result of promoting the currently best organismic traits within the coexisting populations.

This perspective on selection would be sufficient to understand the preservation of adaptation if organisms were composed of just one or very few traits. But organisms, like their environments, are complex under any criterion (e.g., [13])—considerably more so, with their manifest intensional complexity, than other kinds of dissipative structures. They have at least as many traits as they have functions connecting them to their environment [42]. Any one or more of these functions might become challenged by environmental change, and so become the focus of selective maintenance or improvement. Then, viewing organisms as collections of traits, one might envision selection reviewing traits first in connection with one function, then another, and so on in unending concatenation, and more intensely during times of severe environmental deterioration.

This is the general picture of selection informing the technique of genetic algorithms, where some function is improved by simultaneously modifying many different traits until a targeted functional optimality is achieved after some generations of selection—or, in a selection experiment, honing some trait by simultaneously promoting various alleles at a number of different genetic loci. But this is really a form of artificial selection insofar as the function in question is anything other than enhanced success in reproduction (or—in applications—stability, satisfaction, promotion), which is the sole target of *natural* selection regardless of what particular challenges might face a population. While separate functions might be optimized, only differential reproductive success is maximized. In such a natural context the fitness function of a genetic algorithm might be, for example, "maximize corporate profits"—that is to say, something that cannot be determined in advance ("whatever works"), or even, necessarily, understood after the fact.

In nature, selection focused upon a single function might occur during an exceptionally severe environmental deterioration—a blizzard, firestorm, or flood—where such a function might become key to survival. However, studies of extreme deteriorations in nature (e.g., [6], and several such studies since then) show that what generally happens is that individuals fail with a likelihood scaled to the distance that their trait measurements (arbitrarily chosen by the observer) depart from the mean value of the population. Populations seem to be held in the grip of a central tendency. This would be like a genetic algorithm with a fitness function promoting a current average (i.e., established) type instead of culling variation with respect to a particular function that might contribute to survival. This centripetal mode of selection would characterize periods of evolutionary stasis in continually, as well as in episodically (periodic selection [37]), deteriorating environments. This maintenance of the status quo has been argued by some [3] to be the major role of natural selection in biology. Given a flow of small-effect mutations and recombinants, this selective tinkering [35] could occasionally be called upon to initiate secular change as a result of some punctuation in the routine, when culling might become biased away from an established trait mean.

This mode of natural selection as a holistic reviewing of the entire organism was specified by Wallace [56] as *soft selection* (see also Maynard Smith's [28] "threshold selection"), in contrast with the *hard selection* of particular traits or functions, as in Fisher's model or in artificial selection.[1] In hard selection global fitness over many independent traits would be viewed as multiplicative over the separate fitnesses for each trait, and would result in serious depletion of the population size if more than just a few traits were being selected at one time in a very large population. In soft selection only overall fitness is in view, with the overall worst kinds being eliminated first, and so on, until the carrying capacity of the environment for that population has been reached. In fact, this is nothing more than being explicit about the standard idea in evolutionary biology that natural selection maximizes population fitness, or its overall fertility, rather than improving any trait or function that might contribute to that variational tendency. And this, of course, is the source of the charge that natural selection merely states a tautology—the survival of those that best survive.

Soft selection raises the issue of what fitness is (for some views on this problem see [21, 32, 33, 51]). Looking again at character displacement in this light, suppose we find two species of bird with beak sizes significantly differentiated, feeding on significantly different food sizes, but otherwise having large niche overlap. Given the viewpoint taken here, it seems unlikely that these beaks can have been other than one trait among many that have been episodically modified in a past period of coevolution of these populations. It would be misleading, then, to state that beak size here "has evolved" in the sense of "the evolution of beaks" being the label of an actual process that took place in nature. As mediated by natural selection, nothing in particular evolves other than as a byproduct of a more general process of population survival from generation to generation.

Looking again at Fisher's fundamental theorem—which implicitly views a single trait or function—a forward-looking perspective would predict that traits having the greatest variability, which therefore could be associated with the greatest variation in fitness, would be most likely to experience the greatest selective intensity during the next environmental deterioration (rather than

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[1] It has been pointed out to me that Ridley [41] has a discussion of soft and hard selection that seems quite different from mine. However, it seems to me that we are just emphasizing different aspects of it. My view is that soft selection is the mode of selection focused only on overall fitness, without regard to particular traits or functions, thereby avoiding the need for multiplicative global fitness, wherein no more than a few traits in very large populations could undergo selective change at significant rates.

particular traits that seemingly could be most affected by the particular bearing selective pressures). But, looking back the other way after selection has occurred, we expect that traits that have been subjected to the greatest selection pressures will be those now having the least variability. This last was tested using traits of frogs' legs [49]. An earlier study had identified particular ratios of leg measurements that were found in experiments to be most important for jumping. We compared the variability of these trait ratios in populations of frogs that regularly jump, and found that, in fact, they were significantly less variable than arbitrarily chosen ratios of leg measurements. Furthermore, these ratios were not less variable in species of frogs that do not jump.

But, surely, jumping is only one of many functions we could identify that frogs must carry out successfully! If all of these functions had been under selection simultaneously, then important traits for other functions would also show less variability than arbitrarily chosen ones. And all these traits would seem to have been selected simultaneously as independent traits. But this supposition raises the issue of the limitation on the number of individuals available to be culled by (hard) selection for each separate trait in actual populations of finite size. Considering how many important functions an organism must carry out, the genetic load on the population, with so many independent traits being simultaneously selected, would be unbearable, even with individuals overlapping in reasons for failure [18]. It has been suggested that selective neutrality of most genetic loci [22] would obviate this cost-of-adaptation argument, but it is difficult to imagine that most traits or functions could be selectively neutral even if most genetic loci are—or that functions, if not traits, are not independent as selective targets.

Here again we can invoke soft selection, where individuals fail in each generation in rank order according to how many of their traits have a currently less favorable condition, culling first the worst and working up into increasingly fitter types until the environmental carrying capacity of the population has been reached. In this concept, if a given generation of selective culling were to be repeated, a partially different group of individuals would be found to fail, showing that traits, as such, cannot logically be taken to be under individual selective scrutiny, and many different (therefore nearly selectively neutral) genotypes can produce an adequate phenotype. Good jumping proportions would be among many traits of importance to frogs, any and all of which would statistically tend, generation after generation, to sometimes be among those having prominence in the activities leading up to reproduction. Then no particular trait will have been selected as such—an uncanny situation, given that we can actually identify traits and clearly associate them with important functions, and ones that, in addition, do appear to have been subjected to selective culling. So the phenotype, as we perceive it as being composed of many traits, is effectively or structurally complex, while concepts of natural selection are simple abstractions.

Here the observer becomes liminal as a bearer of complexity. It is biologists, as mechanists, who identify different functions (e.g., [13])—jumping, eating, seeing, and so on—as unarguably conceptually separate functions, and who map these to genetic loci in the DNA information storage. The latter supposed representation relation—genes for this or that—has long been known to be an oversimplification. For example, messenger RNA is often a pastiche of pieces from different genetic loci, and/or is manipulated in different ways by the products of other genes, whose final gene product must interact with the products of several loci in order to inform some function. As well, traits are widely polygenic, and any one genetic locus can be widely pleiotropic, carrying information used in more than a single trait. Clearly the relationship between genetic information and functional traits is complex [27, 61]. Mitton [34] found plentiful evidence of selection distinguishing different allelic forms of proteins. But, as I pointed out [44], the properties allowing detection of such molecular differences have no necessary connection to a protein's functionality. This does not stop biologists from pinpointing ever finer discrimination of traits, as can be seen in Abzhanov et al. [1], who suggest "a mechanistic explanation for the independence of beak evolution along different axes." They claim to show that a biochemical pathway that mediates calcium signaling is expressed at higher levels in Darwin's finch species with long, pointed beaks than in those with more robust beaks.

Concerning traits, there is a further complexifying issue concerning what they actually are [44, 54]. Taxonomists can be satisfied with whatever can be discriminated, but it seems that evolutionary biologists ought to be concerned about the relation of traits to functions—and, indeed, that they do in fact relate in some way to functions, and that they do therefore, in whatever uncanny way, get subjected to selective pressures [14]. There is also the more general question "What is a part?" [31]. The same problem appears with functions as well. Physiological functions show some interesting relations in this context. In experiments with several kinds of animals reviewed in [44], various regimes were imposed to force animals to exert progressively more work. For example, fishes can be made to swim faster in a "wind" tunnel. It was found that as the animals worked harder their heart rates increased. Comparing statistics across different work loads shows that the standard deviation of heart rate among individuals declines as the animals work harder. So in peak performance the animals get to be increasingly more alike in important functions. At the same time, functions unrelated to that work (e.g., in the swimming case, blood flow rate in veins leaving the intestines) become more variable during faster swimming. The implication is that selection has been reviewing heart rate mostly (or only?) under conditions of stress. So, while a fish is slowly poking about picking up morsels here and there in a leisurely manner, selection would not see its heart rate (unless it is grossly deficient, in which case it would have been eliminated long before anyway).

So we see that traits need to be viewed as aspects of performance, and these need to be viewed—or even, perhaps, defined—during periods of intensified function (on the issue of functions, see [5, 55]). Corning's [9] arguments about widespread synergetic effects during functioning could be taken into consideration here as well. These considerations feed as well into Crutchfield's [10] call for a theory of biological structure. Quoting: "Functionality…comes equally from the context of a given form—something much harder to detect than form itself." Regarding his concept of "epochal evolution" (as the cause of punctuated equilibrium), biological functioning during periods of reduced stress on a given function could be the nexus from which functional innovations might self-organize, inasmuch as selection's stern gaze is then focused elsewhere (see also [40]).

Taking stock, let us note that, while selection theory (e.g., Fisher, Haldane, Wallace, and almost all since them) has been concerned with selective improvement of functions leading to the evolution of various traits, the indirect evidence cited above relating to selection in nature concerns entirely the process of selection (periodic and soft) during periods of stasis. This, of course, is necessarily so given the time frame of observations in nature now compared with the number of observer generations it would take to substitute alleles [34].

Here we can note three reviews of many studies of natural selection in natural populations [11, 23, 34]. They all found plentiful evidence for selection maintaining the adaptedness of populations. The most recent study claims that there is also evidence for "disruptive selection" in the data—that is, a greater variability of traits around the mean after selection. The implication within this study is that this might actually signal an early stage of directional selection. But this is not the only interpretation possible. Other kinds of selection could be responsible for increasing the variability of a population—forms of *balancing selection*, such as frequency- and density-dependent selection supplied with new mutants or recombinants, which would not be associated with evolutionary change.

Summarizing the argument up to this point, I think we need to acknowledge that with regard to any sort of complexity, natural selection is a very simple idea. Organisms have many functions, each of which involves many traits, and these traits are involved in more than one function. In this realistic setting perhaps some version of soft selection would be the most promising model of the maintenance of adaptation.

4 Selection and Temporally Generated Complexity

Finally, I raise an issue concerning developmental constraints on natural selection (for a general review of this area see [2, 58]), which to my knowledge has not been raised previously. Consider quantitative traits of organisms from Darwin's point of view of their getting "improved" by natural selection (so elimination of the manifestly unfit is not under consideration). Considering the possibility of such improvement in embryos, we note that they pass through several different developmental stages, each with its own, quite different morphology and way of life based on different traits and functions. It has often been suggested that there are embryonic adaptations (e.g., [61]), but there remains the question of to what extent early ontogeny can actually be scanned by natural selection (as proposed, e.g., by Buss [7]).

Consider first the process of genetic drift. In embryos, drift would be a consequence, not of small population size, but of prolonged delay between selective sorting and reproduction, during which time the embryos engage in an irreversible sequence of very different ways of being, none of which is repeated. So the viability component of fitness is quite peculiar in embryos. For example, consider three stages of development in a frog: blastula, tailbud, and larva. Selection distinguishing among blastulae would necessarily have to be based upon some of their characteristics, and will sort them accordingly. Those that pass on to being tailbuds will now be subjected to a whole other group of selection pressures, while pressures that had impinged upon them as blastulae have effectively become subliminal for good. Individuals will again be sorted—this time on criteria related to being tailbuds—completely irrespective of the criteria that affected them as blastulae. Moving on to the larval stage, we have the same phenomenon, this time with selection acting irrespective of criteria relating to both earlier developmental stages. Traits reflecting selection by the earlier selective pressures must as a consequence drift, with those of the earliest stages being deselected to a greater extent than those scanned in later stages.

In more detail, begin with fertilized eggs. Looking at some quantitative trait (it could be a molecular concentration, some relation between landmarks, or granule size differences), we find that it is initially broadly distributed in the population of ova—that is, there is lots of variability in the unselected offspring, and most possible measurements are well represented except at the very extremes. Now we get selection up to the blastula stage, shaping, say, a unimodal curve around a selected mean for one of the above traits. Moving on to selection in the tailbud stage, different traits are now selected in what is effectively a different kind of organism. As a result, our selected curve from the blastula stage (having now become virtual), measuring a trait no longer under selection, or even in manifest existence, changes. We can suppose, just arbitrarily, that its distribution as a result gets to be platykurtic around the original mean. This would be the effect of a kind of genetic drift. Moving on to selection among larvae, on yet further different traits again, the result on our curve selected in the blastula stage has changed again—this time, say, the virtual distribution got skewed to the left, even perhaps shifting its mean somewhat.

Moving on to selection in small froglets, on yet further different traits, the curve selected in the blastula stage gets virtually modified again—this time we might suppose the mode gets hollowed out, producing a bimodal curve. And so on, through subsequent stages up to that where the organism is definitive for its kind—here, a young adult frog. This sequential disruption of the effects of selection on the earliest stages produces virtual distributions of early-stage traits that would not have been as favorable for further developmental changes as the original curves would be if the distorted curves were to actually be projected back to the early-stage population. Note in addition that, as development continues, the cohort size decreases, gradually bringing in more traditional genetic drift effects (of small population size) on the original trait shaped in the blastula stage.

A key point in this example is that organisms in the different developmental stages are very different kinds of beings. This is a different situation from implicit comparisons between different ages of the definitive imago, as in the usual studies of natural selection, which do not raise this problem because selection pressures are not irreversible. A somewhat similar situation in a population of adults would be if a drastic environmental disaster struck a population so that one or two traits became especially important for survival. This will reorganize the gene pool in a way specializing it for this kind of perturbation. Now, if one or two generations later another, completely different kind of disaster struck the population, the effects of selection from the previous disaster would become significantly altered.

So the punch line here is that the results of selection in an early stage, functional at the time, become, as a result of further unrelated selection, effectively attenuated to different degrees by very different subsequent selection pressures. That is, the results of selection in early stages cannot be inherited, as such, by embryos in subsequent generations, because they can't be preserved in a cohort's population during development. So here we would have a type of *developmental constraint*, being a limitation on the degree to which selection can hone embryonic traits, especially in the earliest stages of development, where the effects of subsequent distortion via drift would be more pronounced. Perhaps development can continue to operate in subsequent generations because those early stages don't need to be other than relatively simple in form—and I think "vaguely embodied" might be a better description of their organization.

A possible quantitative objection to this idea is that, if the populations here are very large (as in the eggs of some fishes and frogs), since we are looking at effectively random events from one stage to another, then because of that randomness itself, no substantial change in the distribution of an early selected trait should accumulate—just back-and-forth fluctuations over time, averaging out to roughly the original distribution. My counters to this are: (a) this nullifying effect would be more powerful the more different stages are traversed cumulatively, but there just aren't that many different stages during embryonic development. As well, (b) as development continues, cohort size diminishes rapidly in many species, such as many kinds of fishes and frogs, instituting traditional genetic drift in some cases at least.

Furthermore, (c) I would bring in for support my original insight here—Fisher's reproductive value concept [12]: the age-specific expectation of future offspring for any individual, or the average likelihood, at each age, that it will contribute genes to the future gene pool (Figure 2). This decreases as an individual ages after the age of first reproduction, because it is then less likely to contribute to the selective responses of the population, mostly because its probability of dying increases with age. On this argument, properties of individuals at the age of first reproduction are the most intensively scanned by selection, because many individuals do not survive to later breeding seasons, and so the population sizes of those reproducing for the first time are the largest of all, making up the greater proportion of the effective population size in any breeding season. This situation has given rise to a Darwinian theory of aging, reviewed recently by Williams et al. [57].

My conjecture here is that the effect of distance from the reproductively most important stages in early maturity should work in the other direction, going forward into embryonic stages, as well. The reproductive value of a blastula is minuscule, and improves as development proceeds and the individual's likelihood of breeding improves, but it is low during all embryonic stages (Figure 2), so that any selection they have been subjected to would have little effect on the next generation compared to the selective pressures bearing upon reproductive imagos. Only in really huge populations could there be enough individuals to be sacrificed for improvement of earlier life history stages in addition to improvement of the definitive, reproductive stage—and living systems with huge populations (say, bacteria) do not have life history stages. Fisher himself worried, in one sentence, about the implications of this for prereproductive evolution, but backed off and dismissed the idea out of hand. Hamilton [19] considered this idea briefly again, but said nothing definite, as if shying away from the problem.

So, it seems that the evolution of development might need something more than natural selection to deal with it. Then, how is development kept orderly? Here we must note that, since development is epigenetic, with one trait being built upon another materially, the earlier forms are used as templates upon which to build later ones and so would leave a footprint in the future. Again, this could

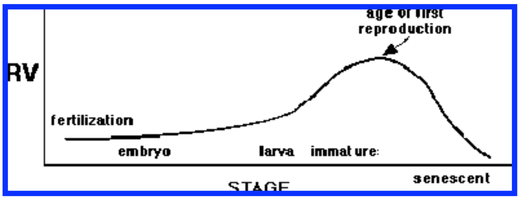

Figure 2. An idealized curve showing changes in reproductive value over a lifetime.

obviously be important for properties of definitive stages (juveniles) that are close to the age of reproduction, but the effects of selection in the earlier, embryonic stages on traits and functions present and relevant only in those stages must still be defaced to some extent. Selection in early stages could at best be "ballpark" only, with no refinements being possible. And, of course, larvae (in complex life histories) come into this story as well. For example, how could selection scan the elaborate properties of frog tadpole lips? Nothing in the adult (as far as we know) is templated upon these, which completely disappear at metamorphosis, and yet these complicated species-specific characteristics continue to be preserved in the populations of each species. It has been noted several times that larval evolution often does not follow imago evolution, the two seeming to run on parallel tracks. Wray [63] noted that this suggested that natural selection must be operating on larval forms directly. But, since they don't reproduce, how?

Finally, a thought worth considering in this context is that the absence of a possibility for selective refinement of traits in early embryos may be an important factor contributing to those stages retaining the generativity necessary for mediating larger evolutionary innovations. If selection could refine them, it would make the earliest developmental stages less vaguely embodied, and so less amenable to modification during ontogeny. I should mention here the idea that for evolutionary modification to occur, forms of stabilizing selection need to be lifted [57]. This aligns with the idea that selection is mostly a conservative force [3], and so it seems likely that the feebleness of its effects in early embryos must work to maintain the generativity of those early embryonic stages.

5 Discussion

Viewed as being composed of parts, an organism would in every particular be a structurally complex system, while our descriptive categories are explicit, and therefore simple, classifications. If we did not need, as mechanist, to seek the devil in the details, we would not be faced with the perplexity of complexity at all! In a situation where traits and even functions are defined only with difficulty, soft selection seems to be the only reasonable selection model. Soft selection is simplicity itself, but it carries no implications for particular differentiated functions or traits, both of which nevertheless do demonstrate in nature the effects of selection having culled them. Classical hard, or artificial, selection supposedly scans details individually, but is defeated by its limitations in the face of the actual properties of natural populations and organisms. I take the view that specific details, and concepts like artificial selection, are the products of philosophical mechanicism. As biologists and (significantly) physicians we scan an organism in exactly the same way as mechanics scan machines (see [17]). In order to heal we must find the problem and cure it. This single bias, or fact, explains the general approach used in scientific analyses, creating, in light of science's social role, its traditional philosophical mechanicism.

My view here should not pass without challenge by the fact that there are some remarkably machinelike organs in living systems, such as the flagellar motor of some microorganisms [36]. Examples like this seem to me, however, to sharpen even further the above conundrums about natural selection.

6 Conclusion

I conclude that complexity, in addition to anything else it might be held to be, is (whether structural or effective complexity) in the first place an illusion generated by the philosophical mechanicism used as a guide to scientific practice, and that natural selection can neither enhance it nor defeat its perplexity, since this characterizes all material systems given the way we view them. As a simple (i.e., plainly logical) theory, natural selection will continue to be betrayed by the vagueness of the world, so that, as it is represented in theory, it can hardly be held to be the agent of the evolution of any specific thing at all in nature. Curiously, if the perplexity of complexity is a kind of implication of mechanicism's structural complexity concept, then natural selection can be supposed, in the form of soft selection, to mediate—but not to create—it. As well, if selection could act strongly upon early-stage embryos, there is reason to believe that it would convert their vague embodiment to a more structurally complex condition, which, given their germinal role, would likely be functionally disabling.

Well, then, are the principles of natural selection as they are currently understood sufficient to explain the evolution of complexity in living systems? As soft selection, it can be construed to somehow work to maintain adaptedness within complex systems, but there is no evidence that it can create structural complexity in selected organisms. In selection theory, as Fisher's [12] Malthusian parameter, or as the Wright-Dobzhansky selection coefficient, selection is represented only as a negative force—less than the fastest reproductive rate in the first case, and a deficit from the current best fitness in the second. It does not have a generative role in neo-Darwinian theory, so selection must be insufficient to explain complexity increase.

In regard to selection in the context of artificial life, an immediate message from this viewpoint would be that, in stochastic search and adaptive computation approaches like genetic algorithms, the focus should be shifted upscale from optimizing individual functions to promoting higher level success depending upon several functions, making the system more extensionally complex as in real life. A further technical suggestion would be that, given an interest in greater verisimilitude to natural selection, some attention should be shifted from fully explicit techniques toward fuzzier ones, moving even through second-order fuzziness in the direction of vagueness (e.g., [24, 25]). More generally, while it is true that in simulations simple rules can generate complicated behavior and forms, we might note that the simulations themselves are the complex frameworks that allow this to happen [26, 39], just as the world itself is the complex framework within which natural selection will have to be working.

7 Summary

Many views of complexity have been suggested, applicable to the abiotic world as well as the biotic. Because interactions between phenotypes and their environments generate complexity, models of natural selection involving specific traits or functions do not well represent natural populations under selection. As mechanists, we do not have adequate ideas about how to represent phenotypic traits in models of biological systems. Given this, only models of selection like soft selection have any verisimilitude to a natural process in a complex setting. With respect to temporal complexity, there may be reason to suspect that the effects of selection in early stages of ontogeny may not be preserved, thus retaining the generative capacity of early embryos. Finally, natural selection cannot be held responsible for the complexity of living systems.

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