J. theor. Biol. (1991) **152**, 469-484

Feedback Theory and Darwinian Evolution

DOUGLAS S. ROBERTSON

15 *Pavilion Drive, Gaithersburg, MD* 20878, *U.S.A.*

(*Received on* 9 *September* 1990, *Accepted in revised form on* 6 *June* 1991)

Feedback loops can have a significant impact on biological systems that are evolving under Darwinian natural selection. Many of the striking and sometimes bizarre patterns that characterize the evolution of such systems have simple, natural explanations that involve the effects of feedback loops. The two fundamental types of feedback loops, positive and negative, have effects that are radically different: negative feedback tends to produce stability and resistance to change; positive feedback produces instability and even catastrophe. Both types of feedback loops are important in biological systems, and both can produce chaos, whose mathematical complexity often produces strange, beautiful and totally unexpected patterns that have only begun to be explored using the computational capabilities of modern electronic computers. An understanding of the patterns that can result from the effects of feedback loops can produce important new insights into the patterns that mark the evolutionary development of biological systems.

Darwin's theory of evolution is one of the great triumphs in the history of science. Yet, like all scientific theories, Darwin's work is imperfect, or at least imperfectly understood. This paper explores some of the problems that are posed by the presence of feedback loops in biological systems that are evolving under Darwinian natural selection.

Feedback loops provide a simple and natural explanation for a variety of patterns that are found in the historical development of life forms. One example is the phenomenon of neoteny, the retention of juvenile characteristics in adults (see Gould, 1977: 63-9). Another is "Cope's rule of phyletic size increase", the observation that all species tend to evolve toward larger size. Gould describes two exceptions to Cope's rule, one a graptolite and the other a protozoan, and says that such exceptions are "surpassingly rare". He notes that the reasons for the rule are "[as] yet poorly specified" (Gould, 1983: 313). Although there may be many possible explanations for these phenomena, we shall see below that a natural extension of the assumptions underlying Darwin's theory provides an interesting alternative explanation for these and other puzzling patterns found in the fossil record. The explanation, which involves feedback loops, is attractive for its simplicity, its lack of *ad hoc* assumptions, and for the fact that it may be subject to important tests, tests that could falsify the ideas as Popper suggested (Popper, 1959).

None of these ideas is completely novel. The existence and function of feedback loops is widely recognized in biological systems. Yet some of their implications described here appear to warrant further investigation and development.

0022-5193/91/200469+16 $03.00/0

The conventional picture of Darwinian evolution was summarized by Gould as based on two undeniable facts and an inescapable conclusion (Gould, 1977: 11):

(1) Organisms vary, and these [random] variations are inherited (at least in part) by their offspring.

(2) Organisms produce more offspring than can possibly survive.

(3) On average, offspring that vary most strongly in directions favored by the environment will survive and propagate. Favorable variation will therefore accumulate in populations by natural selection.

Using these axioms Darwin's theory is able to explain how species change by adapting themselves better to their environment, maximizing their "fitness". If this were the whole story, life might be a lot less interesting than it is. But to complete the picture, we need to add one more undeniable fact:

(4) The organisms which are being altered by evolution to adapt to their environment are themselves a significant component of that environment.

This is seen, for example, in competition for mates, in which the obvious critical element of an individual's environment is the extant population of other individuals of the species. It is equally clear in predator-prey relationships. As Van Valen put it: "There is evidence that most environmental pressure is biotic rather than physical" (Van Valen, 1985).

This single fact, so obvious that it hardly needs stating, (and well-understood by Darwin) has the most startling and profound implications for evolutionary theory. It introduces the possibility, even the necessity, of feedback loops, which in turn imply that ordinary Darwinian evolution may display highly non-linear behavior, chaos instead of order, periodic extinctions, neoteny, Cope's rule, the patterns that spawned the discredited ideas of orthogenesis and racial senescence, and many other puzzling phenomena. These could all be examples of the instabilities introduced into systems evolving under Darwinian natural selection by the presence of feedback loops; if so, then the proper interpretation of these phenomena cannot be attained without an understanding of these loops. Feedback loops introduce a fundamental instability into the basic fabric of Darwinian evolution, an instability that is independent of external catastrophes, falling asteroids, periodic glaciation, changing climate and sea level, and other ambient environmental changes. Paradoxically, at the same time feedback loops can also create a hyper-stability in counterpoise to this instability.

To understand why feedback loops engender this curious combination of stability and instability we need to explore a little of the theory of such loops. This theory was developed first by electrical engineers, but it is now finding wide application in other fields. For example, a recent article by Arthur (1990: 92-9) describes the effects of positive feedback loops in the economy.

The body of theory developed to handle feedback loops in electrical engineering provides important insights into the behavior of any system where feedback effects are found. In engineering parlance, a "system" is defined as any set of circuits that has an output signal that is a function of an input signal. A feedback loop occurs whenever the system's output signal is "fed back", or used to modify the input signal.

The most important fact about feedback loops is that they come in two varieties, positive and negative. Positive feedback occurs when the feedback signal has the same sign as the input signal. Negative feedback occurs when the feedback signal has the opposite sign to the input signal. A third case, zero or no feedback, can be considered to be intermediate between positive and negative or it can be considered to be a separate case altogether.

The effects of positive and negative feedback loops are diametrically opposite. Negative feedback tends to produce stability by damping the effects of any changes in the input signal. Negative feedback loops tend to resist change. Positive feedback tends to reinforce the effects of changes in the input signal, producing instability, oscillation, and even catastrophic destruction of the system. In ordinary electronic circuitry both types of feedback are employed in a variety of common applications. The stabilizing aspects of negative feedback are employed to improve the stability of amplifiers and other circuits. The destabilizing aspects of positive feedback are used to produce oscillators. And feedback is essential to the functioning of control-system circuits (see e.g. Cannon, 1967: 627–710.)

In biological systems it is easy to find examples of all three cases, positive feedback, negative feedback, and no feedback. The systems with no feedback are easiest to understand. They occur whenever a species is adapting to an environmental effect that is not affected by changes in that species. For example, polar bears may adapt to colder climates by growing thicker fur, but the climate is not affected by the increased fur, and so no feedback loop is set up.

Negative feedback is also not difficult to find in biological systems. Negative feedback loops are the basis of nearly all of the so-called "balances" of nature. In the balance of a predator–prey relationship, for example, an excess of prey animals allows an increase in the number of predators, which tends to decrease the original signal (an excess of prey). Other parameters, such as sex ratios, are also controlled by powerful negative feedback loops. Notice that, in these cases, the organisms that are adapting under natural selection are themselves the critical or controlling elements of the environment to which they are adapting. This is the key requirement for the existence of feedback loops.

Positive feedback loops are perhaps more subtle and less well-understood and appreciated in biological systems, but their effects can be quite spectacular. To illustrate the functioning of positive feedback loops in biological systems it may help to construct a simple model. The model will focus on a single parameter that is commonly affected by evolution, the size of the organism. (This, of course, is the parameter that underlies Cope's rule.) It does not matter much how size is defined—body weight, distance between the eyes, length of neck, etc. And for this argument it doesn't matter much precisely how "fitness" is defined either. Fitness could be the simple ability to win a fight, or the probability of passing an individual's genes to the next generation.

Whatever the definition of the fitness curve, some of its properties are fairly easy to understand intuitively. First, the curve will probably not be perfectly flat. (A flat curve would be exceedingly uninteresting.) Second, extreme high and low values of body size will probably have relatively low values of fitness. From these facts an elementary theorem of calculus tells us that the curve must have at least one maximum value between these extremes, and may have more than one such maximum. The simplest case can be treated schematically as a simple Gaussian curve $f(x) =$

$A\,e^{-k(x-x_0)^2}$, (where x represents the size of the organism) as shown by the top curve in Fig. 1. In the real world the shape of this curve is determined largely by the basic physics of body engineering, bone and muscle strength as a function of size, lung and intestine surface area, etc, as well as by the behavior of the organism, what he does, and how, and where. The actual curve may have a quite complicated shape, but the simple model of a gaussian curve shown will allow us to illustrate the effects of feedback loops that can control the evolution of species. The arguments are not strongly affected by the details of the shape of the curve except for the important case of a curve with multiple extrema, which will warrant separate treatment.

The second curve in Fig. 1 displays schematically the expected distribution of body size of the species that is responding to the evolutionary pressure represented by the first curve (responding according to classical Darwinian theory without feedback effects). We would expect the distribution to have a peak at the same place as the fitness curve above. And the random variations required by evolution theory prevent this distribution from clustering too close to the maximum value.

Now let us invoke fact no. 4, that organisms themselves are critical components of the environment to which they are adapting. This is easiest to understand in cases that involve competition for food or mates within a species, or in predator–prey relationships between species. Often the critical factor in such competition is that small increases in body size can produce a disproportionate competitive advantage. An individual only slightly larger than its fellows will often have a substantial advantage in gathering food, in capturing and subduing prey, and in competing for

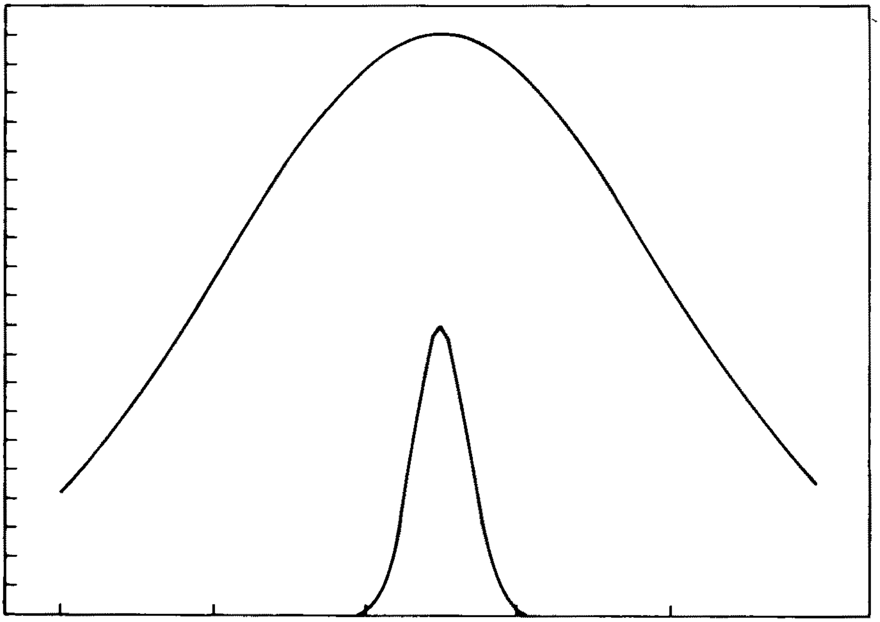

FIG. 1. Fitness curve (top) and distribution of individual size (bottom).

mates. This is illustrated schematically in Fig. 2. The new curve at the bottom of the figure depicts the "fitness" advantage conferred by an increase in body size. The important feature of this curve is that its peak always lies to the right of the peak of the curve showing the distribution of individual sizes, no matter where that curve peaks.

The upper curve in Fig. 2 represents the sum of the "fitness" curve as displayed in Fig. 1 plus the additional term resulting from the competition within the species†. As seen in Fig. 2, the peak distribution of body size is (almost by definition) to the left of the maximum of the combined fitness curve. The combined fitness curve will therefore drive the species toward larger body size, producing the curve shown in Fig. 3. But the local maximum in the fitness curve is still to the right of the peak of the size distribution curve, because it is controlled by the (changing) distribution of body size. We thus have a classic positive feedback loop. The drift toward larger size (no matter how slight) constantly moves the peak of the fitness curve to the right, thereby driving still further increases in size.

Notice that the fitness curve is now bi-modal, having two maxima. If the distribution of body size is broad enough to encompass both maxima (which it generally will be at some point in the evolutionary history) then a small population could

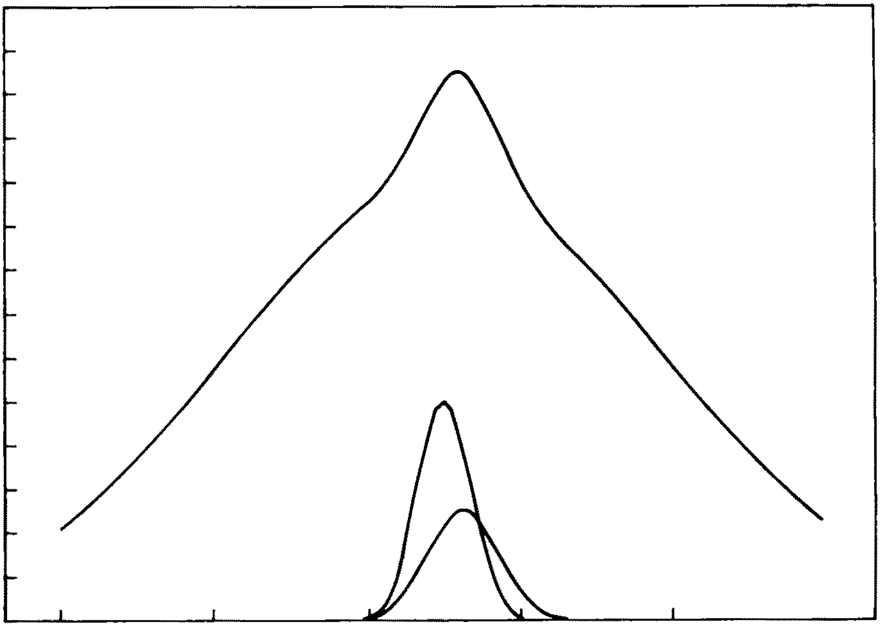

FIG. 2. The new curve to the right of the size distribution curve represents the fitness advantage conferred by slightly larger body size.

---

† Assuming that fitness has the property that mathematicians call "linearity", (see discussion in the Appendix) which means simply that superposed fitness curves would add. Exact linearity is not necessary for this discussion of feedback (and indeed exact linearity would be fairly unlikely) but linearity is a useful approximation to whatever functional form the combination of the curves would take.

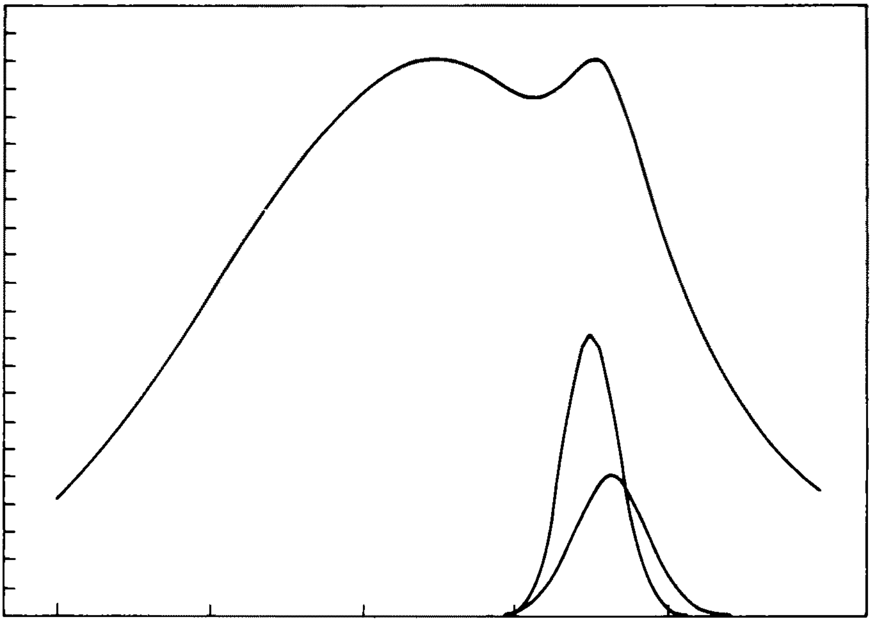

FIG. 3. Time evolution of the curves shown in Fig. 2.

remain near the original maximum. This leads to the picture shown in Fig. 4, showing the two different populations. (At some point they are different enough to constitute two different species.) But if the population density of the left-hand species becomes great enough for competition to again cause significant feedback effects, the process will start again. This suggests the interesting idea that the evolution of the species will behave something like the stripes on a barber pole, continually and repetitively regenerating from the same base. A better analogy would be a dripping faucet (itself a classic theme in the study of non-linear mechanics and chaos theory).

Notice that the "dripping faucet" model not only produces Cope's rule, but also other patterns commonly seen in the fossil record. For example, the evolution of horned dinosaurs produced one suite of species in the Judith river age, another similar but different set in the Horseshoe Canyon age a few million years later, and a third set in the Lancian age yet a few more million years later. A similar pattern is seen much earlier, in the successive waves of mammal-like reptiles of the Permian and early Triassic (see Bakker, 1986: 246-7, 406-24). Of course these examples do not prove that these species developments result from a "dripping faucet" pattern of evolution†, but the pattern is suggestive, nevertheless. Other examples could probably be found without much difficulty.

What happens when the distribution peak moves too far to the right? Several possibilities exist. If the underlying fitness curve becomes too steep, the local peak

---

† Other suggestions that lead to similar patterns of evolution can be found, for example, in Van Valen (1975).

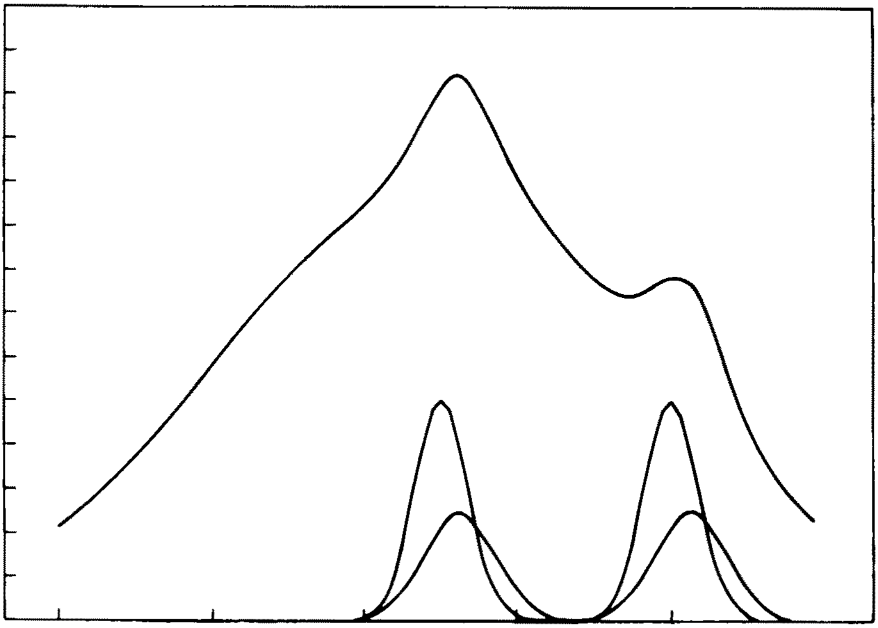

FIG. 4. As the two maxima separate, a population may remain under the orginal maximum.

could flatten out, and the feedback effects would stop. Alternatively, the distribution could move to the point where the peak is so low that extinction becomes highly probable. We thus have the seeming paradox of ordinary natural selection driving a species toward extinction. This is possible only with systematic time variations of the fitness curve; such time variations can be produced by positive feeback loops†. The species always moves toward the nearest local maximum of the fitness curve, but that very maximum can move in such a fashion as to approach very low probabilities of survival.

This is one of the insights offered by the theory of feedback loops, that pure Darwinian natural selection is able to drive a species toward extinction. It offers a natural explanation for the observed fact of quasi-regular extinction of species. Bakker observed that "on average, a species of dinosaur endured two or three million years before becoming extinct and being replaced by a new species. That's a brisk rate of evolutionary turnover, as fast as the mammals' (Bakker, 1986: 184)‡. Feedback loops provide a natural mechanism for regularly driving species toward

---

† There are cyclical effects such as periodic climate variations that could also cause periodic changes in the fitness functions and thus cause periodic extinctions. The resulting pattern of extinction might be difficult to distinguish from the patterns resulting from the effects of feedback loops. Yet there are important differences that might be exploited to separate the two phenomena. It is hard to see how periodic climate variations could produce Cope's rule, or a dripping faucet pattern of species changes, for example.

‡ This is not to be confused with the suggestion of periodic simultaneous or mass extinctions, such as the one at the Cretaceous-Tertiary boundary. These appear to be a different phenomenon, perhaps related more to falling asteriods than to feedback loops.

extinction. Indeed, the average time elapsed between such periodic extinctions may be a measure of the intensity of the feedback loop.

Many of the conventional insights derived from an evolutionary theory that lacks feedback can be carried over into a theory that includes feedback loops, but in a carefully restricted sense. Species still adapt toward the maximum of the "fitness" curve, but only locally. Organisms in the right-hand distribution in Fig. 4, for example, will move toward the local maximum in the fitness curve, and be relatively unaffected by the higher maximum farther to the left. Statements such as "Darwinian evolution decrees that no animal shall develop a harmful structure" (Gould, 1977: 90) need to be interpreted in this restrictive sense. Thus organisms in the right-hand distribution in Fig. 4 cannot develop structures that move them away from the local maximum in the fitness curve. But nothing prevents that maximum itself from moving far from the global maximum, so that the species adapting to it ends up with a very low probability of survival.

The "dripping faucet" model also provides a natural explanation for the sometimes puzzling presence of ancestral types co-existing with their more highly adapted descendants. Classical Darwinian theorists explained such juxtaposition by invoking geographical separation of different populations. Such geographical effects may well be important, but at the same time may not be needed to explain all the instances of such juxtapositions.

Competition within a species for food and mates is not the only mechanism that will produce the positive feedback effects described here. Competition between species will often produce very similar effects. A predator species will develop larger fangs and claws, and the prey species responds with thicker skin and armor. Thus, a binary (two-species) feedback loop will govern the further evolutionary changes†. Of course these feedback mechanisms are not independent, but rather are deeply interrelated: longer claws and thicker skin may well be accompanied by larger body size.

Feedback loops may be responsible for other odd patterns of evolutionary development. Neoteny, for example, the tendency of species to retain juvenile characteristics into adulthood, could result from a sexual-selection feedback loop related to the duration of care for infants. Long-term care of juveniles, which has obvious benefits for the survival of a species, is effected in *Homo sapiens* and presumably in other species by the formation of a strong emotional bond between parents and their offspring. This bond could easily produce, as an incidental side-effect, a tendency among adults to prefer other adults whose appearance is similar to the juveniles to which they are so strongly bonded. The preference of adult humans for child-like characteristics is fairly well-documented (e.g. Gould, 1982: 95–107). But a preference for adults with child-like features could well produce a strong sexual selection for precisely those features, which would, in turn, set up a powerful feedback loop driving the species toward neoteny. One irony of this scenario is that large brain size in humans is one of the most important of the neotenous features. It would be amusing to discover that humans evolved large brains not because brain size was

---

† This particular feedback loop is sometimes referred to as "escalation" or an "arms race" (see e.g. Vermeij, 1987).

favored but only because the long-term care of juveniles was favored. This feedback loop model provides a natural explanation, without *ad hoc* assumptions, for the vexing problem of why the human brain developed as far and as fast as it did. As Gould puts it,

> "... all 'savages,' from our actual ancestors to modern survivors, had brains fully capable of developing and appreciating all the finest subtleties of European art, morality, and philosophy; yet they used, in the state of nature, only the tiniest fraction of that capacity..." (Gould, 1982: 55).

Indeed, there may be some question as to whether modern man generally employs any more than a tiny fraction of the capacity of his brain. This sexual-selection feedback loop provides a natural explanation for the development of a brain whose capacity may be far in excess of anyone's actual use of it.

There is a simple test that would check the hypothesis of the existence of this particular feedback loop. If neoteny is driven by sexual selection resulting from a fondness or preference for juvenile features, then it will be most prevalent in species that provide long-term care for their offspring, and absent in species that do not. The correlation (or lack of correlation) between these two effects would be a strong piece of evidence for or against the hypothesis†.

The concept of the feedback loop as an essential component of evolutionary theory is a potentially interesting hypothesis, but its scientific usefulness is limited unless there is some way to test the idea, even to falsify it. It seems to me that the critical tests involve investigations of cases that do not exhibit feedback loops. The feedback loop described above that could produce Cope's rule, for example, should be commonly found in dominant species with large populations of individuals that compete for prey and mates. Conversely, species that do not compete in this fashion should be relatively immune to the effects of feedback. Filter feeders, for example, that burrow in the mud and spawn by releasing eggs and milt into the ocean, do not often interact directly with others of their species and should not show the dramatic size increases that characterize this particular feedback loop. One such example is the brachiopod *Lingula*, which is found virtually unchanged from Ordovician fossil beds right up to live specimens in the present era. And Bakker notes that "Most types of clams go on for many millions of years with hardly any adaptive shifts". (Bakker, 1986: 401). Other similar examples are probably not difficult to find.

There is some question as to how much proof this hypothesis really requires. No one would seriously doubt that feedback loops exist in biological systems. And given that they exist, their unstable, non-linear, chaotic behavior follows as a mathematical consequence. The only serious remaining question is their ubiquitousness; do they control the overall patterns of evolution, or are they rare, isolated, and unimportant phenomena? The scarcity of exceptions to Cope's rule strongly suggests that feedback-controlled effects are quite common, and may perhaps be

---

† The correlation need not be perfect, of course. Creatures such as the Axolotl have probably developed neotenous features (retention of gills) for environmental reasons unrelated to parental care.

the dominant controlling element in ordinary Darwinian evolution. It might not be too far-fetched to suggest that feedback loops are responsible for the evolution of everything *except* clams.

Feedback theory provides a radically different picture of Darwinian evolution from the no-feedback case, in which organisms quietly evolve toward better adaptation to a constant or slowly varying environment. Feedback theory predicts the existence of both extreme stability and wild instability, depending on the sign of the feedback effects. One is tempted to identify these opposite phenomena with the two components of the concept of punctuated equilibrium (in which species characteristics remain static for long periods of time, and then change rapidly, often too fast for the transitional forms to have any significant probability of being preserved). We shall see later that positive feedback alone may provide a better explanation for the observed punctuated equilibrium.

Feedback theory implies a different paradigm for the structures that characterize diagrams of species ancestry. Gould often contrasts the common "ladder" model with the more common "bush" model (Gould, 1977: 56–62). Figure 5 illustrates these two models. But the "dripping faucet" model described above leads to the "comb" picture† also illustrated in Fig. 5. Of course these three possibilities are not

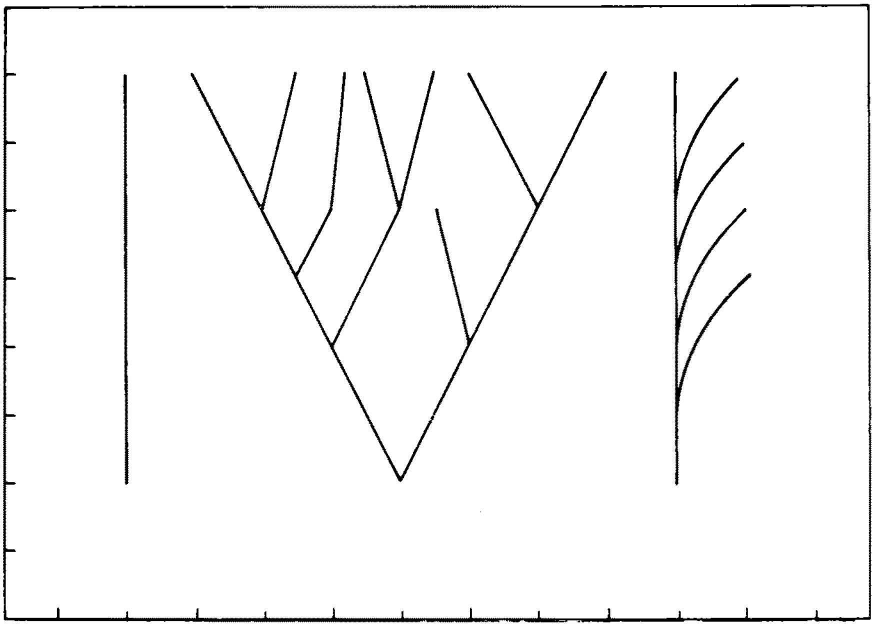

FIG. 5. Schematic pictures of various evolution models, the "ladder" at left, the "bush" in the center, and the "comb" at the right.

---

† Sometimes called "iterative parallelism" in the lierature.

mutually exclusive, and bushes can (and will) consist of both ladders and combs in different sections. Nevertheless the comb pattern is a striking one, and one that could pose particular problems for paleontologists if they try to assign ancestor-descendant relationships to successive "teeth" in the comb.

The major difference between evolution theory with and without feedback loops is surprisingly small, although the effects of the difference may be large. The key elements of the Darwinian theory, variation and natural selection, are identical in both cases. The only effect of the feedback loop is to change the fitness function. The systematic changes (time variations) of the fitness function that are generated by feedback loops can produce effects such as Cope's rule and periodic extinctions.

The picture of feedback loops as diagrammed in Figs 1–4 is, of course, a serious oversimplification. The "fitness" curves are unlikely to be as simple as is indicated in these diagrams, and the effects of multiple extrema in the curves will be examined later. But a more serious oversimplification arises from the fact that the curves are shown as one-dimensional, as though the complexity of species development could be reasonably characterized by a single parameter. The simple addition of a second parameter, converting the curves into two-dimensional surfaces, introduces serious mathematical complications. In one dimension we only need to worry about the maxima of the curves. But in two dimensions we can have maxima and "saddle points", where the surface has a maximum in one direction and a minimum in another. Also, in one dimension, a species can move in only two directions from any given point. But in two dimensions, there is an infinity of directions to move. Additional parameters (dimensions) complicate the mathematics immensely, and a complete description of the development of a species is likely to require a very large rather than a small number of parameters. Tracking the complicated effects of feedback loops in such a large multi-dimensional space will be a daunting problem, even if we avail ourselves of the number-crunching power of modern computers.

Much of this essay has been concerned with positive feedback loops, partly because their effects are so spectacular, and partly because their effects are so poorly understood. But I do not wish to imply that negative feedback is unimportant. Biological systems tend to consist of complex networks of negative feedback loops, maintaining such things as sex ratios. These negative feedback loops are probably more common than positive loops, not because they are any more likely to occur, but because they tend to persist for long periods of time. Positive loops on the other hand tend to destroy themselves, often in spectacular fashion, in a relatively short time.

We should not make the mistake of assuming that feedback loops are the only story, the only factor involved in evolution. Other effects, such as volcanic explosions, asteroid impacts, climate fluctuations, sea-level changes and the like really do occur, and do not induce feedback loops. But they produce changes that need to be understood in the context of an unstable evolutionary process, one in which chaotic instability is the norm even in the absence of these environmental changes. This is another fundamental new idea introduced into evolutionary theory by the concept of feedback loops.

The attempt to explain phenomena such as the giant antlers of Irish Elk and the tails of Peacocks without invoking feedback loops has led to a variety of improbable *ad hoc* hypotheses, including the ideas of orthogenesis and racial senescence or decadence. Orthogenesis proposes that evolution proceeds in "straight lines", and that certain trends, once started, cannot be stopped even though they lead to extinction (see Gould, 1977: 79-90). Racial senescence proposes that species have predestined life-spans, and that they will develop bizarre forms at the end of their appointed time (see Bakker, 1986: 325).

More recent and more plausible hypotheses involve what Julian Huxley termed "allometry", that the huge antlers of the Irish Elk were simply a by-product of larger body size. But there are a number of problems with this hypothesis. Not all large deer have large antlers. And allometry requires another mechanism to explain why Irish Elk became extinct (maybe the climate changed). Finally, allometry fails utterly to explain phenomena such as Peacock tails, unless we assume that grouse and turkeys and swans also possess magnificent tails. In sharp contrast, the concept of feedback loops produces a natural explanation for these phenomena without any *ad hoc* assumptions at all. These bizarre phenomena could reflect nothing more than the natural consequences of the inherent instability introduced into Darwinian selection by the presence of feedback loops.

Other patterns that sometimes puzzle biologists can be shown to be the result of the non-linear behavior of feedback loops. In his latest book describing the Burgess Shale, Gould identifies two major puzzles seen in this remarkable suite of fossils. First, they display a much larger variety of body types than is found at any later period. Second, the few body types that survive to later periods have no obvious advantage over the ones that simply disappear (Gould, 1989: 227-39). The first puzzle, the presence of so many varied body types, may be a simple consequence of the speed of the operation of the positive feedback loops that drive organisms rapidly into a large number of extrema in the multi-dimensional fitness curve. The second phenomenon, the subsequent dominance of a few types that have no obvious advantages over the others, is a well-documented feature of systems controlled by feedback loops. The effect of the loops is to powerfully amplify the effects of small advantages. Arthur documents a similar phenomenon in a rather different context, in which feedback loops permitted a poorer video recording technology (VHS) to dominate a superior technology (Beta). He writes:

> "Positive feedback magnifies the effects of small economic shifts; the economic models that describe such effects differ vastly from conventional ones... There is no guarantee that the particular economic outcome selected from among the many alternatives will be the 'best' one".

This phenomenon could be termed "lock-in", because the magnification of small advantages often allows a marginally different product to dominate a market out of all proportion to its advantages over the competition. In Arthur's words: "As one technology gains more adherents... further adoption [of the technology] is increasingly likely". This "lock-in" effect is a fundamental characteristic of systems that are controlled by positive feedback loops. Arthur comments on the obvious applicability of this concept to biological evolution and to punctuated equilibrium in particular (Arthur, 1990).

One important example of the "lock-in" effect of positive feedback loops is found in the fact that the organic molecules from which terrestrial organisms are constructed display a strong chiral asymmetry. Most ordinary sugars and amino acids (along with many other organic molecules) have two chirally symmetric forms, called L and D, that are mirror images of each other. In living organisms these molecules are found to consist almost exclusively of L-amino acids and D-sugars. Although there are reasons to expect that both types of molecules will not be combined in the same organism, there is no obvious reason why this particular combination should have been chosen over its symmetric counterpart. Yet as far back as 1953, F. C. Frank showed that if the presence of one symmetry in organisms increased the population growth rate of that type of organism, then a positive feedback loop would be set up that would quickly lead to the complete dominance of that type over the other. The dominant choice of symmetry would thus depend only on which type first gained a tiny predominance through random fluctuations. And it is easy to find reasons why the presence of one symmetry would indeed favor the growth of organisms that require that form: more food would be available to them, for example (see Hegstrom & Kondepudi, 1990).

Another example of the effects of this "lock-in" phenomenon is seen in the distribution of species within ecological niches. Such niches can be generally thought of as corresponding to local maxima in the fitness curve. One might naively think that if two species differ by some quantity, say 10%, in their fitness for a particular niche, they might then share the niche in a 55–45% ratio of population. But such sharing is almost never found. It is axiomatic in biology that only one species is found in each ecological niche. And this is exactly what would be expected if the competition between the species is controlled by positive feedback loops. The dominant species would "lock-in" to the niche and eliminate the competing species altogether.

Both the "lock-in" effect and the "Cope's rule" type of instability are critical to understanding the effects of feedback loops on complicated fitness curves that have multiple peaks. If we start with an ecosystem that is empty, then positive feedback loops provide a rapid and forced method of exploring the whole range of the fitness curve fairly quickly and efficiently, without getting "stuck" in one of the lower maxima. The positive feedback loops of the sort that may drive Cope's rule would thus guarantee that many of the peaks of the fitness curve will be quickly explored and populated. And the "dripping faucet" model would still apply at the extreme end of the fitness curve, where no further maxima exist to complicate the picture.

But what will then happen to the species on the lower peaks? Each of them will be driven by a feedback loop toward the next higher peak, but that peak will be filled by a species that has the advantage of already occupying that particular ecological niche. Because of the "lock-in" phenomenon even a species that had some advantage over the species already present might have difficulty dislodging that species. The result would be a metastable state, with feedback loops allowing extant species to successfully resist displacement even by species that may have some "fitness" advantages over them†. There is no reason that such a metastable state could not persist for long periods of time (even by geological standards) and thereby produce the "equilibrium" portion of "punctuated equilibrium" scenarios. But at some point a critical state could be reached, either by the emergence of a species having a great enough advantage to dominate even an extant species, or perhaps by the removal of a dominant species by some other mechanism. The ecological niche represented by the maximum in the fitness curve would then be filled very quickly‡ by another species operating under its own feedback loop, thereby producing the "punctuation" or rapid species development so regularly documented in the fossil record.

The "equilibrium" state is therefore not a situation of quiet stasis, in which no evolutionary forces are acting upon the system, but rather a state of dynamic equilibrium, with powerful and opposed forces delicately balanced in a state of considerable dynamic tension. The situation is perhaps analogous to a soap-bubble froth, in which a dynamic stasis is achieved when the surface tension of each bubble balances that of its neighbors. The equilibrium persists for an extended time, until one bubble bursts. The remaining bubbles then quickly adjust to a new dynamic equilibrium that again persists for an extended time.

Positive feedback loops are capable of producing the type of powerful and opposed forces that would lead to such a dynamic equilibrium. Indeed, "punctuated equilibrium" is the normal behavior of systems operating under the control of such feedback loops. The appearance of "punctuated equilibrium" scenarios in the fossil record is perhaps important evidence for the dominant role of feedback effects in biological systems.

These are only a few examples that show the effects of feedback loops in biological systems, but they serve to illustrate the incredible variety of phenomena that may owe their existence to the presence of feedback loops. If feedback is indeed responsible for some or all of these phenomena, then they obviously cannot be understood without understanding the underlying feedback loops. This simple concept, that a biological system can operate on itself to generate feedback loops, is likely to be essential to developing a complete understanding of the behavior of biological systems. A great deal of further work is needed just to identify the feedback loops that underlie the patterns seen in the fossil record, not to mention the loops that control living systems today. And considerable work will need to be done to explore and understand the behavior of these loops in any detail.

The implications of the non-linearities inherent in feedback loops lead directly into the mathematics of chaos theory, with all of the attendant difficulties and inherent unpredictabilities characteristic of that new branch of science. As Lesurf (1990) recently observed, in the context of electronic amplifiers with feedback circuits: "... adding feedback to a nonlinear circuit with gain is a recipe for chaos".

---

† The situation resembles that of a "relaxation oscillator" in electrical engineering, in which a circuit stays in a metastable state until some critical barrier is reached. The circuit then quickly re-sets itself into another stable state.

‡ The word "quickly" is meant in a geological sense. It could mean a time span that allows thousands of generations of individuals of the species, or even more.

Lesurf points out that negative as well as positive feedback can lead to chaos in spite of the fact that negative feedback is commonly used to reduce non-linearities and to thereby attempt to avoid chaotic behavior. The trick to producing chaos with negative feedback is through the use of errors, distortions, delays, and non-linearities in the feedback loop itself. This type of distortion is inevitable in any real physical system, and it can produce profoundly chaotic effects. A classic example of chaotic behavior in systems controlled by a negative feedback loop can be found in May's analysis of the behavior of predator-prey populations (May, 1972).

Thus, if chaos is a problem in electronic circuits for which an immense engineering effort has been expended to produce linear and non-chaotic behavior, we should expect it to occur in biological systems, where non-linear behavior is the norm, and even approximations to linear behavior are rare. Biological systems that are evolving under Darwinian evolution possess all three of the ingredients of Lesurf's "recipe" for chaos (feedback, non-linearity, and gain). The biological analog of electronic gain is growth, both individual and population growth. And growth commonly follows an exponential curve, which has more than mildly non-linear properties. Thus, we should expect that a full understanding of the mathematical properties of evolution will require a mastery of the mathematics of chaos. It seems likely that chaos theory will be found to be the natural mathematical milieu for evolution, just as the calculus is the natural milieu for Newtonian mechanics.

Of course there are many mechanisms that produce chaotic effects in biolgical systems. Almost any non-linear behavior is generally sufficient to generate chaos (see e.g. May, 1974, 1979). Feedback is only one non-linear mechanism among many. However, it is a mechanism whose effects appear to be particularly spectacular, abundantly evident in the fossil record, and ripe for further study.

A complete understanding of the implications of chaos theory for feedback loops in Darwinian processes will require a great deal of work. Yet the theory already provides a number of important insights. For example, Haldane (1932: 75–6) notes that the tendency of related species to evolve in parallel directions has been used as an argument for orthogenesis, as though there were some internal cause that drives the evolution of species in some particular direction. But the infinite replication of similar patterns is a characteristic of certain types of chaotic behavior, perhaps most familiarly in the patterns found at the boundary of the Mandelbrot set. No *ad hoc* assumptions such as orthogenesis are needed to explain a phenomenon that is now recognized as a familiar mathematical consequence of the behavior of chaotic systems. Other important implications of chaos theory involve the instability of chaotic phenomena and the unpredictable nature of the final state of chaotic systems, and the related tendency of chaotic systems to strongly select one alternative end-state from a near-infinity of almost equally probable alternatives.

The theory of even very simple chaotic systems is so complicated that only the incredible capabilities of newly developed computers has allowed us to make progress in this area. Only with the computer revolution are we beginning to develop tools that have sufficient calculating power to begin to approach the complexity that may be inherent even in a system evolving under pure Darwinian natural selection.

I am very grateful to L. M. Van Valen, whose insight and thoughtful comments led to many substantial improvements to this paper.

REFERENCES

Arthur, W. B. (1990). Positive feedbacks in the economy. *Sci. Am.* **262**(2), 92-99.

Bakker, R. T. (1986). *The Dinosaur Heresies.* New York: Kensington.

Cannon, R. H. (1967). *Dynamics of Physical Systems.* New York: McGraw-Hill.

Dewdney, A. K. (1985). Computer recreatuins: a computer microscope zooms in on the most complex object in mathematics. *Sci. Am.* **253**(2), 16-24.

Gould, S. J. (1977). *Ever Since Darwin.* New York: W. W. Norton.

Gould, S. J. (1982). *The Panda's Thumb.* New York: W. W. Norton.

Gould, S. J. (1983). *Hen's Teeth and Horses Toes.* New York: W. W. Norton.

Gould, S. J. (1989). *Wonderful Life.* New York: W. W. Norton.

Haldane, J. B. S. (1932). *The Causes of Evolution.* Longmans, Green & Co. (Reprinted by Princeton U. Press, 1990).

Hegstrom, R. A. & Kondepudi, D. K. (1990). The handedness of the universe. *Sci. Am.* **262**(1), 108-115.

LeSurf, J. (1990). Chaos on the circuit board. *New Sci.* **126**(1723), 63-66.

May, R. (1972). Limit cycles in predator-prey communities. *Science* **177**, 900-902.

May, R. (1974). *Stability and Complexity in Ecosystems* 2nd edn. Princeton: Princeton University Press.

May, R. (1979). Bifurcations and dynamic complexity in ecological systems. *Ann. N.Y. Acad. Sci.* **316**, 517-529.

Popper, K. (1959). *The Logic of Scientific Discovery.* New York: Basic Books.

Van Valen, L. M. (1975). Group selection, sex, and fossils. *Evolution* **29**, 87-94.

Van Valen, L. M. (1985). A theory of origination and extinction. *Evol. Theory* **7**, 133-142.

Vermeij, G. J. (1987). *Evolution and Escalation.* Princeton: Princeton University Press.

APPENDIX

Note on the mathematical significance of linearity: Mathematicians use the term "linear" in a variety of related contexts, linear algebraic equations, linear differential equations, etc. As used here, "linear" signifies one of two common properties of linear systems, proportionality and superposition. Proportionality simply means that changes in the input to a system will cause proportionate changes in the output. Thus if an input signal (parameter) "a" produces an output "x", then $2a$ will produce $2x$. The related idea of superposition simply means that if there are two inputs, a and b, that separately produce outputs x and y, then input $a+b$ will produce output $x+y$. Mathematicians have long known that systems of equations that are linear tend to be simple (if tedious) to solve, while systems of non-linear equations tend to be difficult to impossible, with emphasis on impossible. Recent research into the theory of chaos has produced new insights into exactly how difficult the solutions to even simple non-linear equations can be. Very simple non-linear equations have been shown to lead quickly to literally infinite complexity. The famous fractal curve called the Mandlebrot set, for example (see e.g. Dewdney, 1985) arises from a very simple iterated quadratic equation. (The iteration, of course, entails a feedback loop.)

For our purposes, we can take as a rough rule of thumb that systems without feedback will tend to exhibit linear responses, systems with negative feedback will tend to exhibit responses that are much smaller than those of linear systems, and systems with positive feedback will exhibit much larger (non-linear) responses, in this case responses that may include oscillation, chaos and catastrophic destruction.