Human Chauvinism

by Richard Dawkins: Review of Full House by Stephen Jay Gould (New York: Harmony Books, 1996; also published as Life's Grandeur by Jonathan Cape, London). In Evolution (Vol. 51 June 1997 No. 3)

This pleasantly written book has two related themes. The first is a statistical argument which Gould believes has great generality, uniting baseball, a moving personal response to the serious illness from which, thankfully, the author has now recovered, and his second theme: that of whether evolution is progressive. The argument about evolution and progress is interesting – though flawed as I shall show – and will occupy most of this review. The general statistical argument is correct and mildly interesting, but no more so than several other homilies of routine methodology about which one could sensibly get a bee in one's bonnet.

Gould's modest and uncontroversial statistical point is simply this. An apparent trend in some measurement may signify nothing more than a change in variance, often coupled with a ceiling or floor effect. Modern baseball players no longer hit a 0.400 (whatever that might be – evidently it is something pretty good). But this doesn't mean they are getting worse. Actually everything about the game is getting better and the variance is getting less. The extremes are being squeezed and 0.400 hitting, being an extreme, is a casualty. The apparent decrease in batting success is a statistical artefact, and similar artefacts dog generalisations in less frivolous fields.

That didn't take long to explain, but baseball occupies 55 jargon-ridden pages of this otherwise lucid book and I must enter a mild protest on behalf of those readers who live in that obscure and little known region called the rest of the world. I invite Americans to imagine that I spun out a whole chapter in the following vein:

"The home keeper was on a pair, vulnerable to anything from a yorker to a chinaman, when he fell to a googly given plenty of air. Silly mid on appealed for leg before, Dicky Bird's finger shot up and the tail collapsed. Not surprisingly, the skipper took the light. Next morning the night watchman, defiantly out of his popping crease, snicked a cover drive off a no ball straight through the gullies and on a fast outfield third man failed to stop the boundary . . ." etc. etc.

Readers in England, the West Indies, Australia, New Zealand, India, Pakistan, Sri Lanka and anglophone Africa would understand every word, but Americans, after enduring a page or two, would rightly protest.

Gould's obsession with baseball is harmless and, in the small doses to which we have hitherto been accustomed, slightly endearing. But this hubristic presumption to sustain readers' attention through six chapters of solid baseball chatter amounts to American chauvinism (and I suspect American male chauvinism at that). It is the sort of self-indulgence from which an author should have been saved by editor and friends before publication – and for all I know they tried. Gould is normally so civilised in his cosmopolitan urbanity, so genial in wit, so deft in style. This book has a delightfully cultivated yet unpretentious 'Epilog on Human Culture' which I gratefully recommend to anyone, of any nation. He is so good at explaining science without jargon yet without talking down, so courteous in his judgement of when to spell out, when to flatter the reader by leaving just a little unsaid. Why does his gracious instinct desert him when baseball is in the air?

Another minor plaint from over the water, this time something which is surely not Dr Gould's fault: may I deplore the growing publishers' habit of gratuitously renaming books when they cross the Atlantic (both ways)? Two of my colleagues are are at risk of having their (excellent, and already well-named) books retitled, respectively, "The Pelican's Breast" and "The Pony Fish's Glow" (now what, I wonder, can have inspired such flights of derivative imagination?) As one embattled author wrote to me, "Changing the title is something big and important they can do to justify their salaries, and it does not require reading the book, so that's why they like it so much." In the case of the book under review, if the author's own title, Full House, is good enough for the American market, why is

the British edition masquerading under the alias of Life's Grandeur? Are we supposed to need protection from the argot of the card table?

At the best of times such title changes are confusing and mess up our literature citations. This particular change is doubly unfortunate because Life's Grandeur (the title, not the book) is tailor-made for confusion with Wonderful Life, and nothing about the difference between the titles conveys the difference between the contents. The two books are not Tweedledum and Tweedledee, and it is unfair on their author to label them as if they were. More generally, may I suggest that authors of the world unite and assert their right to name their own books.

Enough of carping. To evolution: is it progressive? Gould's definition of progress is a human-chauvinistic one which makes it all too easy to deny progress in evolution. I shall show that if we use a less anthropocentric, more biologically sensible, more 'adaptationist' definition, evolution turns out to be clearly and importantly progressive in the short to medium term. In another sense it is probably progressive in the long term too.

Gould's definition of progress, calculated to deliver a negative answer to the question whether evolution is progressive, is "a tendency for life to increase in anatomical complexity, or neurological elaboration, or size and flexibility of behavioral repertoire, or any criterion obviously concocted (if we would only be honest and introspective enough about our motives) to place Homo sapiens atop a supposed heap." My alternative, 'adaptationist' definition of progress is "a tendency for lineages to improve cumulatively their adaptive fit to their particular way of life, by increasing the numbers of features which combine together in adaptive complexes." I'll defend this definition and my consequent, limited, progressivist conclusion, later.

Gould is certainly right that human chauvinism, as an unspoken motif, runs through a great deal of evolutionary writing. He'll find even better examples if he looks at the comparative psychology literature, which is awash with snobbish and downright silly phrases like 'subhuman primates', 'subprimate mammals' and 'submammalian vertebrates', implying an unquestioned ladder of life defined so as to perch us smugly on the top rung. Uncritical authors regularly move 'up' or 'down' the 'evolutionary scale' (bear in mind that they are in fact moving among modern animals, contemporary twigs dotted all around the tree of life). Students of comparative mentality unabashedly and ludicrously ask, 'How far down the animal kingdom does learning extend?' Volume 1 of Hyman's celebrated treatise on the invertebrates is entitled 'Protozoa through Ctenophora' (my emphasis) – as if the phyla exist along an ordinal scale such that everybody knows which groups sit 'between' Protozoa and Ctenophora. Unfortunately all zoology students do know – we've all been taught the same groundless myth.

This is bad stuff, and Gould could afford to attack it even more severely than he attacks his normal targets. Whereas I would do so on logical grounds (Dawkins, 1992), Gould prefers an empirical assault. He looks at the actual course of evolution and argues that such apparent progress as can in general be detected is artefactual (like the baseball statistic). Cope's rule of increased body size, for example, follows from a simple 'drunkard's walk' model. The distribution of possible sizes is confined by a left wall, a minimal size. A random walk from a beginning near the left wall has nowhere to go but up the size distribution. The mean size has pretty well got to increase, and it doesn't imply a driven evolutionary trend towards larger size.

As Gould convincingly argues, the effect is compounded by a human tendency to give undue weight to new arrivals on the geological scene. Textbook biological histories emphasise a progression of grades of organization. As each new grade arrives, there is temptation to forget that the previous grades haven't gone away. Illustrators abet the fallacy when they draw, as representative of each era, only the newcomers. Before a certain date there were no eucaryotes. The arrival of eucaryotes looks more progressive than it really was because of the failure to depict the persisting hordes of procaryotes. The same false impression is conveyed with each new arrival on the stage: vertebrates, large brained animals, and so on. An era may be described as the 'Age of Xs' – as though the denizens of the previous 'Age' had been replaced rather than merely

supplemented.

Gould drives his point home with an admirable section on bacteria. For most of history, he reminds us, our ancestors have been bacteria. Most organisms still are bacteria, and a serviceable case can be made that most contemporary biomass is bacterial. We eucaryotes, we large animals, we brainy animals, are a recent wart on the face of a biosphere which is still fundamentally, and predominantly, procaryotic. To the extent that average size / complexity / cell number / brain size has increased since the 'age of bacteria', this could be simply because the wall of possibilities constrains the drunkard from moving in any other direction. John Maynard Smith recognized this possibility but doubted it when he considered the matter in 1970:

> The obvious and uninteresting explanation of the evolution of increasing complexity is that the first organisms were necessarily simple . . . And if the first organisms were simple, evolutionary change could only be in the direction of complexity.

Maynard Smith suspected that there was more to be said than this 'obvious and uninteresting explanation', but he didn't go into detail. Perhaps he was thinking of what he later came to term The Major Transitions in Evolution (Maynard Smith and Szathm‡ry, 1995), or what I have called 'The Evolution of Evolvability' (Dawkins 1989).

Gould's empirical treatment follows McShea (1996), whose definition of complexity is reminiscent of J W S Pringle's (1951); also of Julian Huxley's (1912) definition of 'individuality' as 'heterogeneity of parts'. Pringle called complexity an epistemological concept, meaning a measure applied to our description of something rather than to that something itself. A crab is morphologically more complex than a millipede because, if you wrote a pair of books describing each animal down to the same level of detail, the crab book would have a higher word-count than the millipede book. The millipede book would describe a typical segment then simply add that, with listed exceptions, the other segments are the same. The crab book would require a separate chapter for each segment and would therefore have a higher information content. McShea applied a similar notion to the vertebral column, expressing complexity in terms of heterogeneity among vertebrae.

With his measure of complexity in place, McShea sought statistical evidence for any general tendency for it to increase in fossil lineages. He made a distinction between passive trends (Gould's statistical artefacts) and driven trends (a true bias towards increased complexity, presumably driven by natural selection). By Gould's enthusiastic account, he concluded that there is no general evidence that a statistical majority of evolutionary lineages show driven trends in the direction of increased complexity. Gould goes further, pointing out that since so many species are parasites and parasite lineages commonly favour decreased complexity, there may even be a statistical trend in the opposite direction to the one hypothesized.

Gould is sailing dangerously close to the windmill tilting that he has previously made his personal art form. Why should any thoughtful Darwinian have expected a majority of lineages to increase in anatomical complexity? Certainly it is not clear that anybody inspired by adaptationist philosophy would. Admittedly people inspired by human vanity might (and historically Gould is right that many have fallen for this vice). Our human line happens to have specialised in complexity, especially of the nervous system, so it is only human that we should define progress as an increase in complexity or in braininess. Other species will see it differently, as Julian Huxley (1926) pointed out in a piece of doggerel entitled Progress:-

> The Crab to Cancer junior gave advice:
> 'Know what you want, my son, and then proceed
> Directly sideways. God has thus decreed –
> Progress is lateral; let that suffice'.
>
> Darwinian Tapeworms on the other hand
> Agree that Progress is a loss of brain,

And all that makes it hard for worms to attain
The true Nirvana – peptic, pure and grand.

Man too enjoys to omphaloscopize.
Himself as Navel of the Universe . . .

The poetry is not great (I couldn't bear to copy out the ending), and there is a confusion of timescales between the crab verse (behavioral time) and the tapeworm verse (evolutionary time), but an important point lurks here. Gould uses a human-chauvinistic definition of progress, measuring it in terms of complexity. This was why he was able to use parasites as ammunition against progress. Huxley's tapeworms, using a parasite-centred definition of progress, see the point with opposite sign. A statistically minded swift would search in vain for evidence that a majority of evolutionary lineages show trends towards improved flying performance. Learned elephants, to borrow a pleasantry from Steven Pinker (1994), would ruefully fail to uphold the comforting notion that progress, defined as a driven elongation of the nose, is manifested by a statistical majority of animal lineages.

This may seem a facetious point but that is far from my intention. On the contrary, it goes to the heart of my adaptationist definition of progress. This, to repeat, takes progress to mean an increase, not in complexity, intelligence or some other anthropocentric value, but in the accumulating number of features contributing towards whatever adaptation the lineage in question exemplifies. By this definition, adaptive evolution is not just incidentally progressive, it is deeply, dyed-in-the wool, indispensably progressive. It is fundamentally necessary that it should be progressive if Darwinian natural selection is to perform the explanatory role in our world view that we require of it, and that it alone can perform. Here's why.

Creationists love Sir Fred Hoyle's vivid metaphor for his own misunderstanding of natural selection. It is as if a hurricane, blowing though a junkyard, had the good fortune to assemble a Boeing 747. Hoyle's point is about statistical improbability. Our answer, yours and mine and Stephen Gould's, is that natural selection is cumulative. There is a ratchet, such that small gains are saved. The hurricane doesn't spontaneously assemble the airliner in one go. Small improvements are added bit by bit. To change the metaphor, however daunting the sheer cliffs that the adaptive mountain first presents, graded ramps can be found the other side and the peak eventually scaled. Adaptive evolution must be gradual and cumulative, not because the evidence supports it (though it does) but because nothing except gradual accumulation could, in principle, do the job of solving the 747 riddle. Even divine creation wouldn't help. Quite the contrary since any entity complicated and intelligent enough to perform the creative rôle would itself be the ultimate 747. And for exactly the same reason the evolution of complex, many-parted adaptations must be progressive. Later descendants will have accumulated a larger number of components towards the adaptive combination than earlier ancestors.

The evolution of the vertebrate eye must have been progressive. Ancient ancestors had a very simple eye, containing only a few features good for seeing. We don't need evidence for this (although it is nice that it is there). It has to be true because the alternative – an initially complex eye, well-endowed with features good for seeing – pitches us right back to Hoyle country and the sheer cliff of improbability. There must be a ramp of step-by-step progress towards the modern, multifeatured descendant of that optical prototype. Of course, in this case, modern analogs of every step up the ramp can be found, working serviceably in dozens of eyes dotted independently around the animal kingdom. But even without these examples, we could be confident that there must have been a gradual, progressive increase in the number of features which an engineer would recognize as contributing towards optical quality. Without stirring from our armchair, we can see that it must be so.

Darwin himself understood this kind of argument clearly, which is why he was such a staunch gradualist. Incidentally, it is also why Gould is unjust when he implies, not in this book but in many other places, that Darwin was against the spirit of punctuationism. The theory of punctuated

equilibrium itself is gradualist (by Gad it had better be) in the sense in which Darwin was a gradualist – the sense in which all sane evolutionists must be gradualists, at least where complex adaptations are concerned. It is just that, if punctuationism is right, the progressive, gradualistic steps are compressed into a timeframe which the fossil record does not resolve. Gould admits this when pressed, but he isn't pressed often enough.

Mark Ridley quotes Darwin on orchids, in a letter to Asa Gray: "It is impossible to imagine so many co-adaptations being formed all by a chance blow". As Ridley (1982) goes on, "The evolution of complex organs had to be gradual because all the correct changes would not occur in a single large mutation." And gradual, in this context, needs to mean progressive in my 'adaptationist' sense. The evolution of anything as complex as an advanced orchid was progressive. So was the evolution of echolocation in bats and river dolphins – progressive over many many steps. So was the evolution of electrolocation in fish, and of skull dislocation in snakes for swallowing large prey. So was the evolution of the complex of adaptations that equips cheetahs to kill, and the corresponding complex that equips gazelles to escape.

Indeed, as Darwin again realised although he did not use the phrase, one of the main driving forces of progressive evolution is the coevolutionary arms race, such as that between predators and their prey. Adaptation to the weather, to the inanimate vicissitudes of ice ages and droughts, may well not be progressive: just an aimless tracking of unprogressively meandering climatic variables. But adaptation to the biotic environment is likely to be progressive because enemies, unlike the weather, themselves evolve (Vermeij, 1987). The resulting positive feedback loop is a good explanation for driven progressive evolution, and the drive may be sustained for many successive generations. The participants in the race do not necessarily survive more successfully as time goes by – their 'partners' in the coevolutionary spiral see to that (the familiar Red Queen Effect). But the equipment for survival, on both sides, is improving as judged by engineering criteria. In hard fought examples we may notice a progressive shift in resources from other parts of the animal's economy to service the arms race (Dawkins & Krebs, 1979). And in any case the improvement in equipment will normally be progressive. Another kind of positive feedback in evolution, if R A Fisher and his followers are right, results from the linkage disequilibrium generated by sexual selection (Arnold 1983). Once again, progressive evolution is the expected consequence.

Progressive increase in morphological complexity is to be expected only in taxa whose way of life benefits from morphological complexity. Progressive increase in brain size is to be expected only in animals where braininess is an advantage. This may, for all I know, constitute a minority of lineages. But what I do insist is that in a majority of evolutionary lineages there will be progressive evolution towards something. It won't, however, be the same thing in different lineages (this was the point about swifts and elephants). And there is no general reason to expect a majority of lineages to progress in the directions pioneered by our human line.

But have I now defined progress so generally as to make it a blandly useless word? I don't think so. To say that the evolution of the vertebrate eye was progressive is to say something quite strong and quite important. If you could lay out all the intermediate ancestors in chronological order you'd find that, first, for a majority of dimensions of measurement, the changes would be transitive over the whole sequence. That is, if A is ancestral to B which is ancestral to C, the direction of change from A to B is likely to be the same as the direction of change from B to C. Second, the number of successive steps over which progress is seen is likely to be large: the transitive series extends beyond A, B and C, far down the alphabet. Third, an engineer would judge the performance to have improved over the sequence. Fourth, the number of separate features combining and conspiring to improve performance would increase. Finally, this kind of progress really matters because it is the key to answering the Hoyle challenge. There will be exceptional reversals, for instance in the evolution of blind cave fish where eyes degenerate because they are not used and are costly to make. And there will doubtless be periods of stasis where there is no evolution at all, progressive or otherwise.

To conclude this point. Gould is wrong to say that the appearance of progress in evolution is a

statistical illusion. It does not result just from a change in variance as a baseball-style artefact. To be sure, complexity, braininess and other particular qualities dear to the human ego should not necessarily be expected to increase progressively in a majority of lineages – though it would be interesting if they did: the investigations of McShea, Jerison (1973) and others are not a waste of time. But if you define progress less chauvinistically – if you let the animals bring their own definition – you will find progress, in a genuinely interesting sense of the word, nearly everywhere.

Now it is important to stress that, on this adaptationist view (unlike the 'evolution of evolvability' view to be discussed shortly), progressive evolution is to be expected only on the short to medium term. Coevolutionary arms races may last for millions of years but probably not hundreds of millions. Over the very long timescale, asteroids and other catastrophes bring evolution to a dead stop, major taxa and entire radiations go extinct. Ecological vacuums are created, to be filled by new adaptive radiations driven by new ranges of arms races. The several arms races between carnivorous dinosaurs and their prey were later mirrored by a succession of analogous arms races between carnivorous mammals and their prey. Each of these successive and separate arms races powered sequences of evolution which were progressive in my sense. But there was no global progress over the hundreds of millions of years, only a sawtooth succession of small progresses terminated by extinctions. Nonetheless, the ramp phase of each sawtooth was properly and significantly progressive.

Ironically for such an eloquent foe of progress, Gould flirts with the idea that evolution itself changes over the long haul, but he puts it in a topsy turvy way which has undoubtedly been widely misleading. It is more fully expounded in Wonderful Life but reprised in the present book. For Gould, evolution in the Cambrian was a different kind of process from evolution today. The Cambrian was a period of evolutionary 'experiment', evolutionary 'trial and error', evolutionary 'false starts'. It was a period of 'explosive' invention, before evolution stabilised into the humdrum process we see today. It was the fertile time when all the great 'fundamental body plans' were invented. Nowadays, evolution just tinkers with old body plans. Back in the Cambrian, new phyla and new classes arose. Nowadays we only get new species!

This may be a slight caricature of Gould's own considered position, but there is no doubt that the many American nonspecialists who unfortunately, as Maynard Smith (1995) wickedly observes, get their evolutionary knowledge almost entirely from Gould, have been deeply misled. Admittedly what follows is an extreme example, but Daniel Dennett has recounted a conversation with a philosopher colleague who read Wonderful Life as arguing that the Cambrian phyla did not have a common ancestor – that they had sprung up as independently initiated life forms! When Dennett assured him that this was not Gould's claim, his colleague's response was "Well then, what is all the fuss about?"

Even some professional evolutionists have been inspired by Gould's rhetoric into committing some pretty remarkable solecisms. Leakey and Lewin's The Sixth Extinction (1996) is an excellent book except for its Chapter 3, 'The Mainspring of Evolution', which is avowedly heavily influenced by Gould. The following quotations from that chapter could hardly be more embarrassingly explicit:-

"Why haven't new animal body plans continued to crawl out of the evolutionary cauldron during the past hundreds of millions of years?"

"In early Cambrian times, innovations at the phylum level survived because they faced little competition."

"Below the level of the family, the Cambrian explosion produced relatively few species, whereas in the post-Permian a tremendous species diversity burgeoned. Above family level however, the post-Permian radiation faltered, with few new classes and no new phyla being generated. Evidently, the mainspring of evolution operated in both periods, but it propelled greater extreme experimentation in the Cambrian than in the post-Permian, and greater variations on existing themes in the post-Permian."

"Hence, evolution in Cambrian organisms could take bigger leaps, including phylum-level leaps, while later on it would be more constrained, making only modest jumps, up to the class level."

It is as though a gardener looked at an old oak tree and remarked, wonderingly: "Isn't it strange that no major new boughs have appeared on this tree for many years. These days, all the new growth appears to be at the twig level!"

As it happens, recent molecular clock evidence indicates that the 'Cambrian Explosion' may never have happened. Far from the major phyla diverging from a point at the beginning of the Cambrian, Wray, Levinton and Shapiro (1996) present evidence that the common ancestors of the major phyla are staggered through hundreds of millions of years back in the Precambrian. But never mind that. That is not the point I want to make. Even if there really was a Cambrian explosion such that all the major phyla diverged during a ten million year period, this is no reason to think that Cambrian evolution was a qualitatively special kind of super-jumpy process. Baupläne don't drop out of a clear Platonic sky, they evolve step by step from predecessors, and they do so (I bet, and so would Gould if explicitly challenged) under approximately the same Darwinian rules as we see today.

"Phylum-level leaps" and "modest jumps, up to the class level" are the sheerest nonsense. Jumps above the species level don't happen, and nobody who thinks about it for two minutes claims that they do. Even the great phyla, when they originally bifurcated one from another, were just pairs of new species, members of the same genus. Classes are species that diverged a very long time ago, and phyla are species that diverged an even longer time ago. Indeed it is a moot – and rather empty – question precisely when in the course of the step by step, gradual mutual divergence of, say, mollusc ancestors and annelid ancestors after the time when they were congeneric species, we should wish to say that the divergence had reached 'Bauplan' status. A good case could be made that The Bauplan is a myth, probably as pernicious as any of the myths that Stephen Gould has so ably combatted, but this one, in its modern form, is largely perpetuated by him.

I return, finally, to the 'evolution of evolvability' and a very real sense in which evolution itself may evolve, progressively, over a longer timescale than the individual ramps of the arms race sawtooth. Notwithstanding Gould's just scepticism over the tendency to label each era by its newest arrivals, there really is a good possibility that major innovations in embryological technique open up new vistas of evolutionary possibility and that these constitute genuinely progressive improvements (Dawkins 1989; Maynard Smith & Szathm‡ry 1995). The origin of the chromosome, of the bounded cell, of organized meiosis, diploidy and sex, of the eucaryotic cell, of multicellularity, of gastrulation, of molluscan torsion, of segmentation – each of these may have constituted a watershed event in the history of life. Not just in the normal Darwinian sense of assisting individuals to survive and reproduce, but watershed in the sense of boosting evolution itself in ways that seem entitled to the label progressive. It may well be that after, say, the invention of multicellularity, or the invention of metamerism, evolution was never the same again. In this sense there may be a one-way ratchet of progressive innovation in evolution.

For this reason over the long term, and because of the cumulative character of coevolutionary arms races over the shorter term, Gould's attempt to reduce all progress to a trivial, baseball-style artefact constitutes a surprising impoverishment, an uncharacteristic slight, an unwonted demeaning of the richness of evolutionary processes.

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