

The descent of Edward Wilson

A new book on evolution by a great biologist makes a slew of mistakes



The Social Conquest of Earth

By Edward O Wilson
(WW Norton, £18.99, May)

When he received the manuscript of *The Origin of Species*, John Murray, the publisher, sent it to a referee who suggested that Darwin should jettison all that evolution stuff and concentrate on pigeons. It's funny in the same way as the spoof review of *Lady Chatterley's Lover*, which praised its interesting "passages on pheasant raising, the apprehending of poachers, ways of controlling vermin, and other chores and duties of the professional gamekeeper" but added:

"Unfortunately one is obliged to wade through many pages of extraneous material in order to discover and savour these sidelights on the management of a Midland shooting estate, and in this reviewer's opinion this book can not take the place of JR Miller's *Practical Gamekeeping*."

I am not being funny when I say of Edward Wilson's latest book that there are interesting and informative chapters on human evolution, and on the ways of social insects (which he knows better than any man alive), and it was a good idea to write a book comparing these two pinnacles of social evolution, but unfortunately one is obliged to wade through many pages of erroneous and downright

perverse misunderstandings of evolutionary theory. In particular, Wilson now rejects “kin selection” (I shall explain this below) and replaces it with a revival of “group selection”—the poorly defined and incoherent view that evolution is driven by the differential survival of whole groups of organisms.

Nobody doubts that some groups survive better than others. What is controversial is the idea that differential group survival drives evolution, as differential individual survival does. The American grey squirrel is driving our native red squirrel to extinction, no doubt because it happens to have certain advantages. That’s differential group survival. But you’d never say of any part of a squirrel that it evolved to promote the welfare of the grey squirrel over the red. Wilson wouldn’t say anything so silly about squirrels. He doesn’t realise that what he does say, if you examine it carefully, is as implausible and as unsupported by evidence.

I would not venture such strong criticism of a great scientist were I not in good company. The Wilson thesis is based on a 2010 paper that he published jointly with two mathematicians, Martin Nowak and Corina Tarnita. When this paper appeared in *Nature* it provoked very strong criticism from more than 140 evolutionary biologists, including a majority of the most distinguished workers in the field. They include Alan Grafen, David Queller, Jerry Coyne, Richard Michod, Eric Charnov, Nick Barton, Alex Kacelnik, Leda Cosmides, John Tooby, Geoffrey Parker, Steven Pinker, Paul Sherman, Tim Clutton-Brock, Paul Harvey, Mary Jane West-Eberhard, Stephen Emlen, Malte Andersson, Stuart West, Richard Wrangham, Bernard Crespi, Robert Trivers and many others. These may not all be household names but let me assure you they know what they are talking about in the relevant fields.

I’m reminded of the old *Punch* cartoon where a mother beams down on a military parade and proudly exclaims, “There’s my boy, he’s the only one in step.” Is Wilson the only evolutionary biologist in step? Scientists dislike arguing from authority, so perhaps I shouldn’t have mentioned the 140 dissenting authorities. But one can make a good case that the 2010 paper would never have been published in *Nature* had it been submitted anonymously and subjected to ordinary peer-review, bereft of the massively authoritative name of Edward O Wilson. If it was authority that got the paper published, there is poetic justice in deploying authority in reply.

Then there’s the patrician hauteur with which Wilson ignores the very serious drubbing his *Nature* paper received. He doesn’t even mention those many critics: not a single, solitary sentence. Does he think his authority justifies going over the heads of experts and appealing directly to a popular audience, as if the professional controversy didn’t exist—as if acceptance of his (tiny) minority view were a done deal? “The beautiful theory [kin selection, see below] never worked well anyway, and now it has collapsed.” Yes it did and does work, and no it hasn’t collapsed. For Wilson not to acknowledge that he speaks for himself against the great majority of his professional colleagues is—it pains me to say this of a lifelong hero—an act of wanton arrogance.

The argument from authority, then, cuts both ways, so let me now set it aside and talk about evolution itself. At stake is the level at which Darwinian selection acts: “survival of the fittest” but, to quote Wilson’s fellow entomologist-turned-anthropologist RD Alexander, the fittest what? The fittest gene, individual, group, species, ecosystem? Just as a child may enjoy addressing an envelope: Oxford, England, Europe, Earth, Solar System, Milky Way Galaxy, Local Group, Universe, so biologists with non-analytical minds warm to multi-level selection: a bland, unfocussed ecumenicalism of the sort promoted by (the association may not delight Wilson) the late Stephen Jay Gould. Let a thousand flowers bloom and let Darwinian selection choose among all levels in the hierarchy of life. But it doesn’t stand up to serious scrutiny. Darwinian selection is a very particular process, which demands rigorous understanding.

The essential point to grasp is that the gene doesn’t belong in the hierarchy I listed. It is on its own as a “replicator,” with its own unique status as a unit of Darwinian selection. Genes, but no other units in life’s hierarchy, make exact copies of themselves in a pool of such copies. It therefore makes a long-term

difference which genes are good at surviving and which ones bad. You cannot say the same of individual organisms (they die after passing on their genes and never make copies of themselves). Nor does it apply to groups or species or ecosystems. None make copies of themselves. None are replicators. Genes have that unique status.

Evolution, then, results from the differential survival of genes in gene pools. "Good" genes become numerous at the expense of "bad." But what is a gene "good" at? Here's where the organism enters the stage. Genes flourish or fail in gene pools, but they don't float freely in the pool like molecules of water. They are locked up in the bodies of individual organisms. The pool is stirred by the process of sexual reproduction, which changes a gene's partners in every generation. A gene's success depends on the survival and reproduction of the bodies in which it sits, and which it influences via "phenotypic" effects. This is why I have called the organism a "survival machine" or "vehicle" for the genes that ride inside it. Genes that happen to cause slight improvements in squirrel eyes or tails or behaviour patterns are passed on because individual squirrels bearing those improving genes survive at the expense of individuals lacking them. To say that genes improve the survival of groups of squirrels is a mighty stretch.

With the exception of one anomalous passage in *The Descent of Man*, Darwin consistently saw natural selection as choosing between individual organisms. When he adopted Herbert Spencer's phrase "survival of the fittest" at the urging of AR Wallace, "fittest" meant something close to its everyday meaning, and Darwin applied it strictly to organisms: the strongest, swiftest, sharpest of tooth and claw, keenest of ear and eye. Darwin well understood that survival was only a means to the end of reproduction, so the "fittest" should include the most sexually attractive, and the most diligent and devoted parents.

Later, when 20th-century leaders of what Julian Huxley called the "Modern Synthesis" deployed mathematics to unite Darwinism with Mendelian genetics, they co-opted "fitness" to serve as a variable in their equations. "Fitness" became "that which is maximised in natural selection." "Survival of the fittest" thus became a tautology, but it didn't matter for the equations. The "fitness" of an individual lion, say, or cassowary, became a mathematical expression of its capacity to leave surviving children, or grandchildren, or descendants into the indefinite future. Parental care and grandparental care contribute to individual fitness because an individual's descendants are vehicles in which ride copies of the genes that engineer the caring.

But lineal descendants are not the only such vehicles. In the early 1960s, WD Hamilton, arguably the most distinguished Darwinian since RA Fisher, formalised an idea that had been knocking around since Fisher and Haldane. If a gene happens to arise which works for the benefit of a sibling, say, or a niece, that gene can survive in the same kind of way as a gene that works for the benefit of offspring or grandchildren. A gene for sibling care, under the right conditions, has the same chance of surviving in the gene pool as a gene for parental care. A copy is a copy is a copy, whether it sits in a lineal or a collateral relative.

But the conditions have to be right, and in practice they often aren't. Full siblings are usually harder to identify than offspring, and usually less obviously dependent. For practical reasons, therefore, sibling care is rarer in nature than parental care. But as far as Darwinian principle is concerned, sibling care and parental care are favoured for the same reason: the cared-for individual contains copies of the genes that programme the caring behaviour.

Half siblings, nephews, nieces and grandchildren are half as likely as full siblings or offspring to share a caring gene. First cousins are half as likely again, and are harder to identify. Hamilton summarised all this in the form of a simple equation, which has become known as Hamilton's Rule. A gene for altruism towards kin will be favoured if the cost to the altruist C is outweighed by the benefit to the recipient B

devalued by r , which is a subtle but computable index of probability of sharing genes. For example, r for full siblings and parents and offspring is $1/2$; r for grandchildren, half-siblings, nephews and nieces is $1/4$; r for first cousins is $1/8$, and so on. A gene for altruistic care will spread through the population if $rB > C$. It is extremely important not to forget B and C and conclude that only r matters in evaluating the success of the theory in particular cases. I am sorry to say that Wilson, in his allegation that Hamilton's ideas don't apply to particular cases, comes perilously close to doing just that. It is as though r is so interesting and novel that B and C are overshadowed.

Hamilton replaced "classical fitness" (which took account only of lineal descendants) by "inclusive fitness," which is a carefully weighted sum embracing collateral as well as lineal kin. I have informally (and a touch facetiously but with Hamilton's blessing) defined inclusive fitness as "that quantity which an individual will appear to maximise, when what is really being maximised is gene survival." In his previous books, Wilson was a supporter of Hamilton's ideas, but he has now turned against them in a way that suggests to me that he never really understood them in the first place.

"Inclusive fitness" was coined as a mathematical device to allow us to keep treating the individual organism ("vehicle") as the level of agency, when we could equivalently have switched to the gene ("replicator"). You can say that natural selection maximises individual inclusive fitness, or that it maximises gene survival. The two are equivalent, by definition. On the face of it, gene survival is simpler to deal with, so why bother with individual inclusive fitness? Because the organism has the appearance of a purpose-driven agent in a way that the gene does not. Genes lack legs to pursue goals, sense organs to perceive the world, hands to manipulate it. Gene survival is what ultimately counts in natural selection, and the world becomes full of genes that are good at surviving. But they do it vicariously, by embryologically programming "phenotypes": programming the development of individual bodies, their brains, limbs and sense organs, in such a way as to maximise their own survival. Genes programme the embryonic development of their vehicles, then ride inside them to share their fate and, if successful, get passed on to future generations.

So, "replicators" and "vehicles" constitute two meanings of "unit of natural selection." Replicators are the units that survive (or fail to survive) through the generations. Vehicles are the agents that replicators programme as devices to help them survive. Genes are the primary replicators, organisms the obvious vehicles. But what about groups? As with organisms, they are certainly not replicators, but are they vehicles? If so, might we make a plausible case for "group selection"?

It is important not to confuse this question—as Wilson regrettably does—with the question of whether individuals benefit from living in groups. Of course they do. Penguins huddle for warmth. That's not group selection: every individual benefits. Lionesses hunting in groups catch more and larger prey than a lone hunter could: enough to make it worthwhile for everyone. Again, every individual benefits: group welfare is strictly incidental. Birds in flocks and fish in schools achieve safety in numbers, and may also conserve energy by riding each other's slipstreams—the same effect as racing cyclists sometimes exploit.

Such individual advantages in group living are important but they have nothing to do with group selection. Group selection would imply that a group does something equivalent to surviving or dying, something equivalent to reproducing itself, and that it has something you could call a group phenotype, such that genes might influence its development, and hence their own survival.

Do groups have phenotypes, which might qualify them to count as gene vehicles? Convincing examples are vanishingly hard to find. The classic promoter of group selection, the Scottish ecologist VC Wynne-Edwards, suggested that territoriality and dominance hierarchies ("peck orders") might be group phenotypes. Territorial species are more spaced out, and species with peck orders show less overt aggression. But both phenomena are more parsimoniously treated as emergent manifestations

of individual phenotypes, and it is individual phenotypes that are directly influenced by genes. You may choose to treat a dominance hierarchy as a group phenotype if you insist, but it is better seen as emerging from each hen, say, being genetically programmed to learn which other hens she can beat in a fight and which normally beat her.

But what about the social insects, Wilson's area of expertise? Hamilton's, too, and indeed the social insects were an early, stunningly successful showcase for his theory.

Female bees, ants and wasps are genetically capable of developing into fertile queens or sterile workers. Each individual is switched into either the queen pathway or the worker pathway (one of several worker pathways in ants) by an environmental switch, and the point is utterly crucial. No gene for outright sterility could survive. But a gene for sterility under some environmental conditions but not others could easily be favoured, and it was. A female bee larva fed on royal jelly and housed in a large queen cell will develop into a fertile queen. Otherwise she will develop into a sterile worker. Genes that find themselves in sterile bodies programme them to work for copies of the same genes in fertile bodies—either the old queen (their mother), or young queens (their sisters) or young males. The result is that queens evolve to become more efficient, full-time specialist egg-layers, with all their needs taken care of by their sterile daughters or sisters.

Because of how the B , C and r values in Hamilton's Rule turn out for bees, genes for sterility are favoured under some conditions, hyper-fertility under others. The same is true for ants and wasps; and termites but with differences of detail (for example termites have male as well as female workers—alas I have no space to expound Hamilton's elegant explanation of this difference and many other intriguing facts). With more differences of detail, the same is true for some non-insect species such as naked mole rats and a few crustaceans.

It truly is a beautiful theory. Everything fits, exactly as it should. Darwin himself, with characteristic prescience but using the pre-genetic language of his time, got the point. As so often, he drew inspiration from domestication:

“Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety; breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family. I have such faith in the powers of selection, that I do not doubt that a breed of cattle, always yielding [sterile] oxen with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind.”

In modern, Hamiltonian terms we would interpret Darwin's “seeds of the same stock” as sharing genes with the vegetable that has been cooked. The sterile ox with the long horns shares genes with the same stock from which we breed. Darwin, lacking the concept of the discrete, Mendelian gene, spoke of going with confidence to the “same family” rather than the same genes. Wilson now interprets this as a form of “group selection,” the “group” in this case being the family. But what a staggeringly unpenetrating—even perverse—use of language. Kin share genes, that is the point, and Darwin would have loved it. The fact that a family can also be seen as a “group” is entirely beside the point and an unhelpful distraction from it.

When Hamilton's twin papers on inclusive fitness were first published in 1964, John Maynard Smith, who was the referee chiefly responsible for recommending them, published a short paper in *Nature* in which he called attention to Hamilton's brilliant innovation. Maynard Smith coined the phrase “kin selection” specifically in order to distinguish it from group selection, then in the process of being discredited by him and others such as the ecologist David Lack. Soon after this, Wilson, in *The Insect Societies* (1971), enthusiastically adopted Hamilton's ideas. He continued to press them in *Sociobiology* (1975), but in an oddly misleading way which indicates that he was already flirting with a

watered down version of his current folly. He treated kin selection as a special case of group selection, an error which I was later to highlight in my paper on “Twelve Misunderstandings of Kin Selection” as Misunderstanding Number Two. Kin may or may not cling together in a group. Kin selection works whether they do or not.

Misunderstanding Number One, which is also perpetrated by Wilson, is the fallacy that “Kin selection is a special, complex kind of natural selection, to be invoked only when the allegedly more parsimonious ‘standard Darwinian theory’ proves inadequate.” I hope I have made it clear that kin selection is logically entailed by standard Darwinian theory, even if the B and C terms work out in such a way that collateral kin are not cared for in practice. Natural selection without kin selection would be like Euclid without Pythagoras. Wilson is, in effect, striding around with a ruler, measuring triangles to see whether Pythagoras got it right. Kin selection was always logically implied by the neo-Darwinian synthesis. It just needed somebody to point it out—Hamilton did it.

Edward Wilson has made important discoveries of his own. His place in history is assured, and so is Hamilton’s. Please do read Wilson’s earlier books, including the monumental *The Ants*, written jointly with Bert Hölldobler (yet another world expert who will have no truck with group selection). As for the book under review, the theoretical errors I have explained are important, pervasive, and integral to its thesis in a way that renders it impossible to recommend. To borrow from Dorothy Parker, this is not a book to be tossed lightly aside. It should be thrown with great force. And sincere regret.

Edward Wilson replies:

Richard Dawkins’s review of *The Social Conquest of Earth* (*Prospect*, Issue 195, 24th May 2012) makes little connection to the part he criticizes. The central issue in the book, which he urges others not to read, is the replacement of inclusive fitness theory (kin selection theory) by multilevel selection theory (ie, individual and group selection combined), with a new and major role assigned to group selection in the origin of advanced social behavior. The original formulation was made by Martin Nowak, Corina Tarnita, and myself in 2010 (*Nature* 466: 1057–1062). We demonstrated that while inclusive fitness theory sometimes works, its mathematical basis is unsound, and inclusive fitness itself is an unattainable phantom measure. Multilevel selection in contrast is mathematically sound, analytically clear, and works well for real cases—including human social behavior.

The science in our argument has, after 18 months, never been refuted or even seriously challenged—and certainly not by the archaic version of inclusive fitness from the 1970s recited in *Prospect* by Professor Dawkins. While many have protested (incidentally, not including Steven Pinker and Robert Trivers, as Professor Dawkins claims), many others of equal competence are in favor of the replacement proposed. In any case, making such lists is futile. It should be born in mind that if science depended on rhetoric and polls, we would still be burning objects with phlogiston and navigating with geocentric maps.

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