THE BIG READ

Eusocial climbers

No one knows more about ants than EO Wilson. Which is why his U-turn on long-held beliefs about their biological altruism has met with outrage from academia. The unrepentant Pulitzer prizewinner and naturalist talks to **STEVE CONNOR**

There is a terrifying beauty in the bustling activity of an ants' nest. The selfless sacrifice of the sterile workers to the fertility of queen and colony appears to be an act of supreme altruism. It is both commendable and disturbing. If only ants could grow to the size of rats then theirs would probably be the superior social order, based not on individual free will but on blind obedience to their genetic code.

In some respects, the social organisation of ants is reminiscent of human society. Their organised workforce is a caste-based community

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Building bridges: ants are model organisms for the study of co-operation and communication in complex societies **ANDREW MOUNTER/GETTY IMAGES**

Ask me what ants have to say about how we should behave and what they tell us about our own morality. The answer is nothing

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of specialists serving the needs of the queen. Soldier ants behave as if they have been trained on a military parade ground, and some species regularly wage war, fight to the death and even take ant-child slaves from conquered colonies.

Other ants cut and gather leaves to act as fodder for fungus farms, or "milk" domesticated aphids for their sugary juices. Colonies are a mix of specialist female workers, fighting soldiers, fearsome guards and fertile breeders. But each ant is programmed to know its place in society, with a selfless dedication to the task of protecting and rearing the queen's offspring in well-tended nurseries.

The allegiance to a queen is central to ant society, even to the extent of sacrificing the reproductive potential of each sterile female worker. Indeed, this enforced infertility of worker ants has fascinated scientists trying to understand the evolution of true eusocial behaviour – a hyper-socialist version of community living.

The phrase covers the highest form of social organisation in the animal kingdom. It defines species where there is co-operative care of the brood, a mixture of overlapping generations living in the same nest or colony, and a division of labour into reproductive and non-reproductive groups who jointly defend the home nest where the young are reared.

Eusocial behaviour is a relatively new evolutionary invention and appears to be quite rare. Of the millions of species of animals that have lived during the 3.7 billion-year history of life on Earth, we only know of 20 ancestral lines that are true "eusocalists". Fourteen of them are insects (ants, bees, wasps and termites), three are species of marine shrimp, and three are mammals – two species of naked mole rats and, arguably, humans.

The reproductive division of eusocial animals into breeding and non-breeding individuals has mystified biologists as far back as Charles Darwin. Why would some individuals give up their ability to procreate for the sake of others? In simple Darwinian terms, it doesn't appear to make sense because a non-breeder would, by definition, not leave any offspring behind to pass on the non-breeding trait.

There was a time when this selfless act of biological altruism was explained away by the "benefit of the species" argument. Sterile female workers laid down their lives and ovaries for the benefit of the wider group because their colonies would out-compete rival colonies populated by more selfish individuals.

But then along came a concept known as "inclusive fitness", first formalised in mathematical terms by the late evolutionary theorist Bill Hamilton in the 1960s. Hamilton's insight was to show that relationships are important when it comes to evolution. There was no need to invoke so-called "group selection" to explain the evolution of eusocial behaviour because by helping your near kin, you also helped your own genes to be passed on.

His argument was encapsulated in a mathematical formula known as "Hamilton's rule", which stated that a gene for altruism towards your kin could spread if the benefit to the recipient of the altruistic act outweighed the cost to the altruist. And, the greater the relatedness of individuals, the easier it would be for altruism to spread by Darwinian evolution.

It explained why female worker ants are ready to lay down their sterile lives for their queen and sister. This was especially true given that each female shares 75 per cent of the genes of their sisters (and queen) – rather than the typical 50:50 share of siblings – because of their genetic makeup.

In these insects, females are more related to one another than they are to their mother. Genes carried in the bodies of sterile females are programmed to work for copies of the same gene in the fertile body of the queen. Female

worker ants appear unselfish but in fact they carry genes that are effectively working for their own selfish survival. It meant that something called "kin selection", which incorporates the concept of inclusive fitness, could explain the evolution of eusocial behaviour.

But this neat explanation, which has held sway for more than half a century, no longer cuts any ice with the world's most distinguished myrmecologist, and no one knows more about ants than the Harvard entomologist Edward Osborne Wilson, better known as the double Pulitzer-prizewinning author and naturalist EO Wilson.

He has thought about ant societies for longer and deeper than anyone alive. In a career spanning nearly 65 years, he has personally described more than 450 new species of ant. It is perhaps not surprising that ants have figured largely in his thinking and writing, and they take a leading role in his latest book *The Meaning of Human Existence*.

"Ants are wonderful model organisms for the study of certain phenomena of great interest to humans, namely the basics of the evolution and nature of co-operation, communication and altruism in the formation of complex societies," Wilson explains.

"But ask me what ants have to say about how we should behave and what they tell us about our own morality. The answer is nothing. Their societies are almost completely female. They eat their injured and they are in almost constant, obliterating war with colonies of the same species. And whereas we send our young men to war, they send their old ladies. There's not much there to be learnt," he says.

Despite a lifetime with his nose stuck in the forest undergrowth, Wilson, 85, has a remarkable track record in provoking controversy. When his seminal textbook *Sociobiology: The New Synthesis*, was published in 1975, he singlehandedly defined a new scientific discipline, but it led to a fierce reaction from academic leftists, including a few in his own university department at Harvard who were furious with him for comparing human society to that of insects.

Such was the outrage that Wilson even had a jug of water poured over him at one scientific conference by Marxist activists who denounced him as a quasi-fascist genetic determinist – which was odd given his liberal, Democrat leanings. Four decades later, his ideas on sociobiology and human social origins have been quietly absorbed into the scientific mainstream, forming, for instance, a theoretical basis for evolutionary psychology – the idea that human evolution over many tens of thousands of years may have shaped the way we think and behave today.

After such a stormy career, you might expect Wilson to be taking things a little easier in the late autumn of life. Not so. He has once again poked a stick into the wasps' nest of academia by publicly denouncing Hamilton's inclusive fitness and the concept of kin selection.

"It was a mistake and I went along with it to begin with. But it's finished. It's over," Wilson tells me, with a flick of his hand.

To add petrol to the fire, he has embraced "group selection", a concept thought to have been comprehensively debunked in popular style by the Oxford zoologist Richard Dawkins in his 1976 bestseller *The Selfish Gene*.

When Wilson co-authored a 2010 scientific paper in *Nature* magazine with two young Harvard mathematicians rejecting inclusive fitness in favour of group selection, he unleashed a torrent of criticism. About 140 evolutionary biologists wrote to *Nature* denouncing Wilson's revisionist thinking and re-affirming the central role played by the selection of genes and individuals rather than the "multilevel" group selection proposed by Wilson.

"What happened was confusion and unhappiness because a lot of people had based their life's work on this idea of inclusive fitness," Wilson says. He now believes that the protest was orchestrated by one person, whom he declined to name, rather than being the spontaneous outpouring it first appeared to be.

"We just corrected a mistake made originally by Hamilton and then repeated by a number of people, myself included," he says.

Wilson argues that multilevel selection – both at the level of individuals and groups – has led to the creation of eusociality in ants and humans. In the simplest terms, individuals who co-operate together in groups achieve more and enhance the survival of their group, while selfish individualism does not, even in terms of Hamilton's inclusive fitness and kin selection.

"Within groups, selfish individuals beat altruistic individuals but in the selection of other traits of individuals that are interactive with other individuals – social traits – then groups of altruists defeat groups of selfish individuals," Wilson explains. "In a nutshell, individual selection favours what we call sin and

group selection favours virtue." But for many evolutionary biologists, this is demonstrably untrue, at least in animals. For the past 40 years or more, biology students have been taught that natural selection works on the level of genes. Richard Dawkins was the first to articulate this approach to a mass audience, arguing that individuals and their bodies are mere vehicles or "gene machines" for carrying genes through one generation to the next.

Two years after the 2010 *Nature* paper, Dawkins wrote a scathing review in *Prospect* magazine of Wilson's support for group selection which Dawkins dismissively labelled "a bland, unfocused ecumenicalism".

Natural selection without kin selection is like Euclid without Pythagoras, wrote Dawkins. "Wilson is, in effect, striding around with a ruler, measuring triangles to see whether Pythagoras got it right," he said. "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."

Although Wilson has much to be arrogant about, few who have met him would accuse him of it. But the criticism must have hurt, and Wilson was evidently still feeling stung by it when writing his latest book, in which he rather waspishly describes Dawkins, a distinguished Fellow of the Royal Society and retired Oxford professor, as an "eloquent science journalist".

"What else is he? I mean journalism is a high and influential profession. But he's not a scientist, he's never done scientific research. My definition of a scientist is that you can complete the following sentence: 'he or she has shown that…'," Wilson says.

"I don't want to go on about this because he and I were friends. There is no debate between us because he's not in the arena. I'm sorry he's so upset. He could have distinguished himself by looking at the evidence, that's what most science journalists do. When a journalist named Dawkins wrote a review in *Prospect* urging people not to read my book, I thought the last time I heard something like that I think it came from an 18th-century bishop."

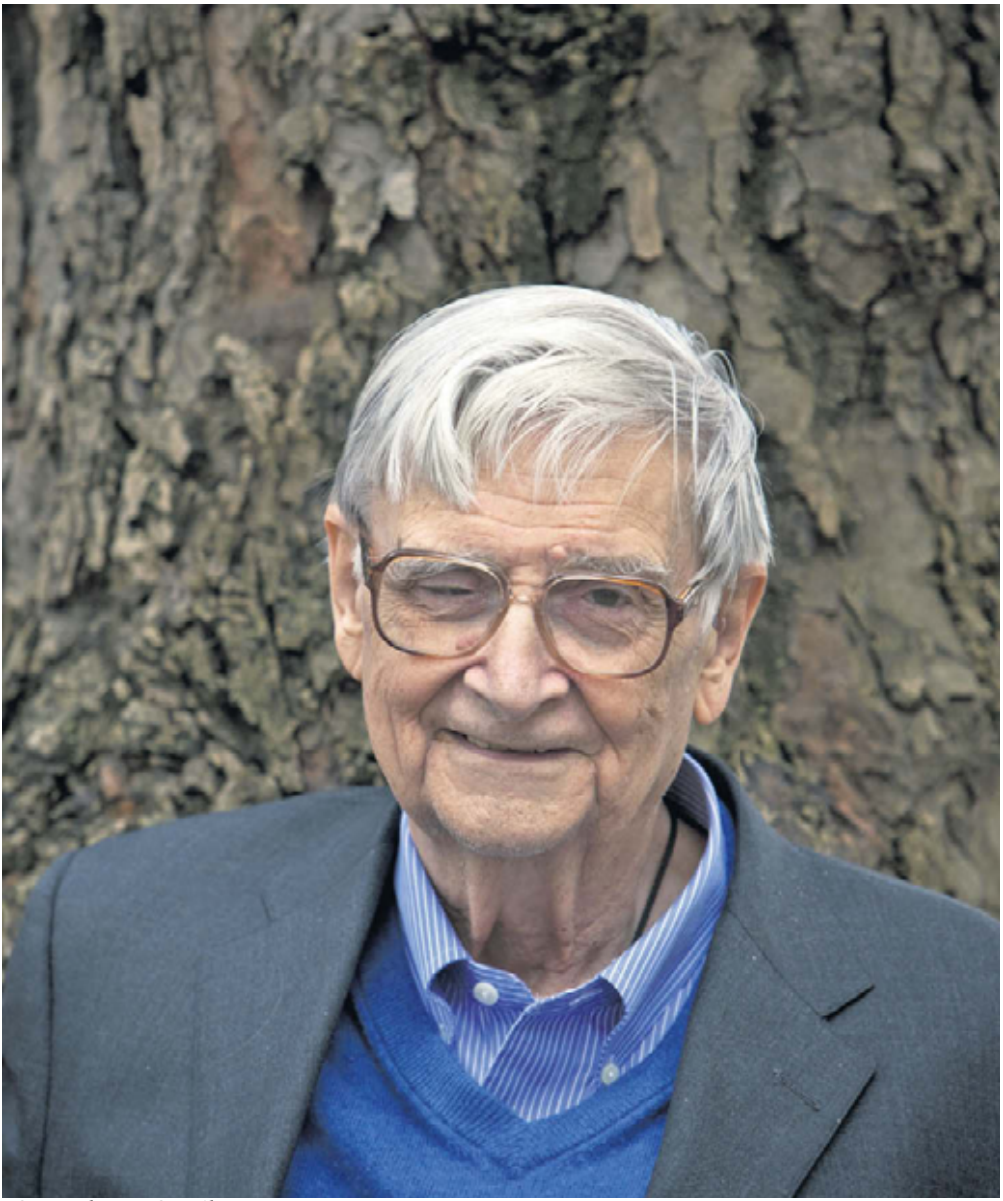
Despite his critics, Wilson is convinced that it was group selection over thousands of years of early evolution, combined with a deep fascination with one another, that led to human altruism. "While similarity of genomes by kinship was an inevitable consequence of group formation, kin selection was not the cause," he writes in *The Meaning of Human Existence*.

"The origin of the human condition is best explained by the natural selection for social interaction – the inherited propensities to communicate, recognise, evaluate, bond, cooperate, compete, and from all these the deep warm pleasure of belonging to your own special group," he says. "Social intelligence enhanced by group selection made *Homo sapiens* the first fully dominant species in Earth's history."

But if ants could grow bigger, it might have been so different.

'The Meaning of Human Existence', by Edward O Wilson (Liveright, £14.99) is published this week

We send our young men to war, they send their old ladies



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DAVID SANDISON