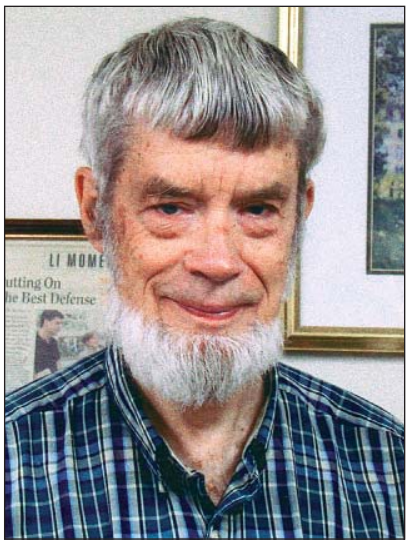
Stretching the Limits of Evolutionary Biology

In shaping current thinking about natural selection and adaptation, Williams's influence has spread beyond his field to encompass economics and medicine as well

STONY BROOK, NEW YORK—On a recent sunny Saturday, scientists from the United States, Canada, and Europe gathered at the State University of New York (SUNY), Stony Brook, to talk about their research. A geneticist from Harvard University spoke about preeclampsia, a potentially fatal condition during pregnancy. An ichthyologist described the loyalty—or lack thereof—that male fish show to the mothers of their offspring. Psychologists discussed economic decision-making. A psychiatrist reviewed some of the genes associated with clinical depression.

This lineup might seem like a random trawl through the sciences. But the researchers who assembled in the auditorium were there for a common purpose: to honor the lanky, white-bearded man who sat quietly in the fourth row, George C. Williams. He may not be as familiar as his peers Richard Dawkins or the late Stephen Jay Gould. But Williams, who spent 25 years at Stony Brook, is generally considered one of the major architects of the study of evolutionary biology, and the meeting's far-ranging talks reflected the scope of his influence.



Darwinian. George Williams's dogged focus on natural selection has won both converts and skeptics.

"George Williams was instrumental in making natural selection an intellectually rigorous theory," says Stephen Pinker of Harvard University, one admirer who wasn't at the meeting. "He forced people to think about how selection actually works and how we can see its fingerprints in the natural world."

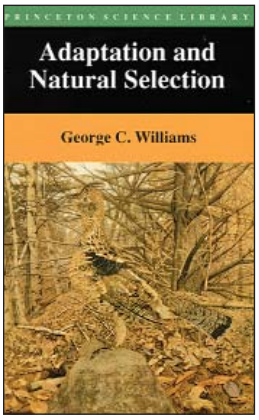
In the 1950s, when Williams was doing his graduate work at the University of California, Los Angeles, the science of evolutionary biology had just gone through two decades of spectacular advances. Ronald Fisher and Theodosius Dobzhansky, among others, had used the new science of genetics to work out some of the molecular underpinnings of evolution. Natural selection was now recognized as a change in the frequency of genes in a population. Yet one important part still hadn't been nailed down: the nature of adaptations. It was clear that adaptations evolved, but few biologists had given serious thought to the rules that govern the process.

Williams was struck by the ad hoc way that even prominent biologists would explain an adaptation. They'd claim that it had evolved because it provided some benefit; often, an entire population or species supposedly benefited. Williams recalls a lecture he heard by Alfred Emerson, a zoologist at the University of Chicago, about why people age and die. "He said growing old and dying is a good thing," Williams says. "We've evolved to do it so we get out of the way, so the young people can go on maintaining the species."

"I thought it was absolute nonsense," says Williams. Whenever people like Emerson claimed that an adaptation was for the good of a species, they never offered an explanation of how, from one generation to another, that potential benefit produced real evolutionary change. Williams suspected that in most cases, no such explanation existed. For him, the primary engine of evolutionary change was the one Darwin had written about in the *Origin of Species*: competition among individuals of the same species. Most biologists in the 1950s simply failed to think seriously enough about how natural selection could produce adaptations, he says.

Williams wrote a series of papers critiquing the notion that adaptations were generally good for a group or a species, rather than an individual. Ultimately, his work led to his classic 1966 book *Adaptation and Natural Selection*. In it, Williams explained that almost every aspect of biology, no matter how puzzling, was the result of strict natural selection working on individuals.

Take a school of fish, for example. It seems as if every individual cooperates for the good of the group, working with others to avoid predators, even if it means that individual gets devoured in the process. Williams argued that the schooling behavior could instead be the product of individual fish trying to boost their personal chances of survival—by trying to get in the middle of the school and by watching other fish for signs of approaching predators.



Williams's book had an immediate, profound effect. "It fundamentally changed how biologists think about how natural selection works," says Randall Nesse, a psychiatrist at the University of Michigan, Ann Arbor, whose own studies of depression and other disorders are influenced by Williams.

One reason that the book was so effective was that Williams demonstrated how natural selection could influence the full course of a species' life history. It wasn't necessary to think of growing old as being for the good of the species, for example. Instead, Williams argued that the decline of old age could be caused by pleiotropy—in other words, the harmful side effects of genes selected for advantages they offered during youth. Just as long as the advantages of these genes outweighed the disadvantages, they would become widespread.

Ironically, cancer, declining stamina, deteriorating vision, and various diseases of old age could all be the result of natural selection, says Williams: "Pleiotropy is the ultimate reason for all these things."

Williams argued that an organism faces these sorts of evolutionary tradeoffs throughout its lifetime: how much energy to invest in maturing before starting to reproduce, for example, or how much to invest in raising offspring before searching for another mate. Natural selection should find a balance between an animal's current investment in itself and its offspring and in potential future benefits. Williams speculated that animals could also keep track of how these factors change and adjust their behavior accordingly—like an investor deciding which stocks to keep or sell.

Researchers have now amassed a wealth

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of evidence showing that animals do alter their strategies in the face of changing conditions, as Williams proposed, investing more or less care in raising their young. Williams also suggested that his argument could apply to humans as well as animals, helping lay the groundwork for a Darwinian approach to human behavior (frequently referred to as evolutionary psychology).

"George was a supportive figure from the get-go," said Martin Daly of McMaster University in Ontario, a leading evolutionary psychologist. At the meeting, Daly and his wife, psychologist Margo Wilson, illustrated Williams's influence by describing an experiment they published in the 7 May issue of *Biology Letters*.

The experiments grew out of a well-known economic phenomenon called "future discounting." People typically choose a small amount of money they can get today over a larger amount they will get in the distant future. Daly and Wilson proposed that the value people put on resources in the present and the future is influenced by natural selection: The better one's prospects for reproductive success look in the near term, the more one will discount the future.

"We wanted to see if we could do an experiment that would manipulate people's discount rate," said Wilson. First, they ran a simple discounting experiment on a group of male subjects who, as expected, tended to choose small money now over bigger sums far in the future. Then they ran the experiment again, but after showing the men a picture of an attractive woman. (They gave their subjects no explanation about the picture.) Daly and Wilson found that seeing that picture made the men even more likely to choose money in the short term. (Pictures of cars, by comparison, didn't affect future discounting.)

Although Williams has convinced many people of the value of his ideas, the notion that human behavior can be broken down into such finely tuned reproduction-boosting adaptations is, to say the least, controversial. The late Stephen Jay Gould liked to call this approach "Darwinian fundamentalism," and he credited Williams's *Adaptation and Natural Selection* as "the founding document for this ultimate version of Darwinian reductionism."

Likewise, Gould and others—such as Elliot Sober of the University of Wisconsin, Madison, and David Sloan Wilson of SUNY Stony Brook—have accused Williams's followers of focusing obsessively on individuals and reflexively dismissing the possibility of group selection or species selection. Sober and Wilson, for example, argue that cooperative behavior may have evolved in our own species because cooperative groups outcompeted uncooperative ones. It's a testament to Williams's stature that Sober is careful to distinguish between Williams and Williams's followers. "Williams is less hostile to group selection than his followers are. It's ironic that he's become the icon for the anti–group selectionists."

Although speakers at the meeting didn't directly address these controversies, they did confront a major disappointment: the failure of Williams's adaptationism to influence medicine. Since the early 1990s, Williams has argued that because medicine compensates for the shortcomings of our adaptations, doctors should get a sound grounding in evolutionary biology. Exploring the evolutionary forces that have shaped our bodies could produce new hypotheses about the causes of diseases, he maintains, and point the way to more effective treatments.

Tradeoffs. Like investors deciding which stocks to keep or sell, animals may weigh how much to invest in current and future offspring.

At the meeting, evolutionary biologist David Haig of Harvard University offered an example of the insights that the Williams approach can offer to pregnancy. Haig pointed out that during a pregnancy, the evolutionary interests of mother and child overlap in some ways but conflict in others. The investment a mother puts into the child can potentially reduce the amount of energy she could put into future children. The child, on the other hand, benefits if its mother focuses all her attention on it.

Haig showed how this perspective on pregnancy can shed light on preeclampsia, a mysterious condition that causes dangerously high blood pressure in pregnant women. Haig suggested that preeclampsia might be the result of a fetus trying to draw nutrients to the placenta. He proposed that, when in need, a fetus might release factors into the maternal bloodstream that damage the walls of the mother's blood vessels, thereby raising the resistance of her circulatory system. Because the resistance in the vessels feeding the placenta would be lower, more blood would flow to the fetus.

At the Stony Brook meeting, Haig reported on recent research by Ananth Karumanchi of Harvard Medical School in Boston and his colleagues, who studied a curious protein released by the fetal placenta that blocks the repair of damaged blood vessels. Karumanchi and his co-workers found that levels of this substance—known as placental soluble Fms-like tyrosine kinase 1 (sFlt1)—rose significantly in women with preeclampsia just before the symptoms emerged, a finding that Haig cites as "evidence of the antagonistic relationship of fetal and maternal factors."

"It's an outstanding hypothesis," Karumanchi says of Haig's research. "It makes a lot of sense in my mind." He points out that even in normal woman who do not experience preeclampsia, levels of sFlt1 rise toward the end of pregnancy. "As the fetus is growing, it needs to get more blood to itself, and so it secretes more of the protein," he speculates.

Yet at the meeting, Haig readily admitted that this evolutionary approach has not yet penetrated the medical community. "Darwinian ideas are not making a big impact" on the way doctors think, said Haig, pointing out that at his own Harvard Medical School, students still get no training in evolutionary biology.

Karumanchi admits that he learned about Darwinian medicine only when Haig approached him recently. "I'd never thought that evolutionary biology was important before now," he says. "There's a big barrier between people like me who are physicians and people who are in biology departments. Those barriers need to be broken."

Mart Gross, a biologist at the University of Toronto, agreed that Williams's ideas have yet to produce as much impact outside of evolutionary biology as he and other followers believe they deserve. He, for one, puts an optimistic stamp on the situation. "It's still very early on," says Gross. "After all, think how long it took for Darwin's ideas about natural selection to really take hold. I think Williams is at the same stage." It is clear that just as Darwin remained controversial long after his death, the legacy of George Williams's work will stimulate research for decades to come. **–CARL ZIMMER**

Carl Zimmer is the author of *Soul Made Flesh: The Discovery of the Brain—and How it Changed the World.*

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