PublisherInfo				
PublisherName		BioMed Central		
PublisherLocation		London		
PublisherImprintName		BioMed Central		

## John Maynard Smith dies

ArticleInfo		
ArticleID		4942
ArticleDOI		10.1186/gb-spotlight-20040427-01
ArticleCitationID		spotlight-20040427-01
ArticleSequenceNumber		294
ArticleCategory		Research news
ArticleFirstPage		1
ArticleLastPage	$\begin{bmatrix} \vdots \end{bmatrix}$	4
ArticleHistory	:	RegistrationDate : 2004–4–27 OnlineDate : 2004–4–27
ArticleCopyright		BioMed Central Ltd2004
ArticleGrants	$\Box$	
ArticleContext		130594411

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One of the most renowned and influential evolutionary biologists of his generation, John Maynard Smith, died of lung cancer on April 19, at the age of 84.

Maynard Smith was probably most widely known for applying game theory to evolutionary biology. Originally developed in 1944 by John von Neumann and Oskar Morgentern, game theory is a mathematical model used by economists to study the outcomes of interactions between 'collaborators' and 'enemies' in situations in which neither can entirely predict the actions of the other, but can adapt their behavior according to what they see the other doing.

Maynard Smith applied game theory to interactions between competing individuals of the same species that use different stratagems for survival.

Imagine combat in which each individual must decide whether or not to escalate the fight without knowing his opponent's decision. Maynard Smith showed, with George Price, that the interests of both combatants are best served if both decide not to escalate the fight.

In 1982, he published *Evolution and the Theory of Games*. In it, he described an evolutionarily stable strategy (ESS). An ESS is a stable collaborative situation that, if adopted by the majority of individuals in a population, will resist invasion by individuals with a new survival strategy.

He was also known for his work on the adaptive value of sexual reproduction and for having demonstrated the 'twofold cost of sex'. Also known as the 'cost of males', this theory suggests that if an asexual individual were introduced into a sexually reproducing population, asexual reproduction would soon take over.

In a population of sexual individuals, it takes two individuals to produce one. Alone, a female capable of reproducing parthenogenetically can produce as many individuals as any pair of sexually reproducing individuals. Since males contribute nothing to the offspring, the asexual subpopulation will grow twice as fast as its sexual counterpart.

John Maynard Smith was born in Somerset, England. He was educated at prestigious Eton College, which he disliked. There, he discovered the work of geneticist H.B.S. Haldane, who was to become a lifelong influence.

"I found that he was the person my schoolmasters most hated," he wrote in his introduction to *On Being the Right Size*, a collection of Haldane's writings. "Feeling that anyone they hated could not be all bad, I went to seek his books in the school library."

He went on to study engineering at Cambridge and worked on military aircraft design during the war. Declaring "that aeroplanes were noisy and old-fashioned," he decided to study zoology instead and enrolled at University College London.

In 1965, Maynard Smith founded the School of Biological Sciences at the University of Sussex. He served as its dean until 1972 and was reelected in 1980.

"I think that it is his grandest epitaph that significant numbers of students who knew him over 20 years ago--who haven't even all gone on to be scientists - are emailing us to say 'I'm sad he's gone, he really influenced me.' They just felt that, if you like, he rocked them a bit," colleague David Harper told us.

"The real trick was that he would talk to anybody at all and he would talk to them in the same style. It didn't matter who you were, he was happy to talk science with you."

Maynard Smith retired from teaching in 1985, but never ceased his research. His most recent work was on the evolution of pathogenic bacteria, including tuberculosis. Even at this advanced stage in his career, he still pondered some of the most basic questions of biology. In an interview with *New Scientist* last year, he said: "The two major evolutionary questions that my current research bears on are: Why recombination, or in other words, why genetic exchange? And what are species?"

"John was giving real science guidance until the morning he died. I guess we're really grateful for that," Harper said, recalling that he went in to the department on the morning of the 19th expecting to meet Maynard Smith for a meeting.

"He was certainly working until the day he died. He fell asleep in his chair surrounded by his books. He showed us you could do that. We're all hurting like mad, but the one thing we can do is a bit more work."

Neurobiologist Steven Rose wrote in the Guardian Unlimited that "no biologist could avoid falling under the spell of John Maynard Smith. He appeared the classical absent-minded professor, with his untidy shock of white hair and owlish glasses masking a razor-sharp mind. The doyen of orthodox neo-Darwinians, he defended his corner vigorously against revisionists like Steve Gould and the heresy of group selection."

Smith was also well known for his eloquent science books, another activity he never gave up. His last book, *Animal Signals*, which he wrote with David Harper, was published last year. It attempts to make sense of the vast array of current theories about animal communication and signaling.

John Maynard Smith was awarded the Crafoord Prize in 1999 by the Swedish Academy of Sciences and the Kyoto Prize for lifetime achievement in 2001.

He is survived by his wife Sheila, and by their daughter and two sons.

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