and others developed quantitative ways of coping, well before the photon had been conceived. Photon scattering can now accommodate all scattering phenomena, but as Johnsen points out, it is computationally messy.

Chapter six is a tough one for those of us who belong to the rays and waves tradition. It includes transparency, reflection and refraction but is titled simply 'Scattering with interference'. We are in quantal territory here. The first paragraph is wonderfully uncompromising, and I can't resist quoting it in full:

> "Light does not bend in a lens, it doesn't bounce off the surface of glass, and it doesn't spread out after passing through a small hole. It doesn't even travel in a straight line. The happiest day of my scientific life came when I read Feynman's QED and learned that refraction, reflection, and diffraction — things I had known since the fifth grade — were all lies. More accurately they are illusions. It appears that light bends, bounces and spreads out. The illusions are so good that you can base solid mathematical predictions on them, but careful thought and further experiments show that more is going on."

In classical optics, electromagnetic waves travel through space at the speed of light and interfere with each other when they meet to add their amplitudes or cancel each other, depending on their phase relationships. In quantum optics, all that can be observed is the emission or absorption of a photon. Between these events the wave in transit has phase and is capable of interference, but cannot be located. It can only be described in terms of the probability that it will encounter an atomic electron, and then release all its unitary energy. For someone with a basically Newtonian mindset, the bizarreness of this formulation comes from the idea that the energy of the photon somehow dissipates into a probability cloud, and then gets itself together again for an interaction with matter. It seems I am not alone in this failure of imagination. But, having admitted this failing, it has to be said that quantum optics provides an accurate and apparently complete account of all the well-known optical phenomena — reflection, refraction, diffraction and so on. The reader should consult Feynman [1] to be convinced of this. In his classic textbook [4], Rodney Loudon tells us: "It is never the photons themselves that interfere, one with another, but rather the probability amplitudes that describe their propagation from the input to the output." Fortunately, most of the formalisms that describe the interference phenomena that form the basis of classical optics also hold for the probability waves of quantum optics.

I will give a single example of the jolt I received from the new photon thinking. I have worked on multilayer reflectors (butterfly wings, fish scales) on and off since about 1970. In a thin film some light is reflected from the upper surface and some from the lower surface, and these two wavefronts interfere, constructively or destructively, to produce a high reflectance for some wavelengths and low for others. This, I now learn, is wrong. What really happens is that photons are scattered from molecules *throughout* the film, some continue forwards, delaying the phase of the continuing beam (refraction), and some backwards (reflection). The surfaces themselves are unimportant, as is explained by Feynman [1] on pages 103–109. It turns out that the many probability amplitude vectors from the backscattered photons add up to give a resultant that can be resolved into two vectors that *look as though* they have come from the upper and lower surfaces. And the mathematics is magically the same.

In his last chapter, Johnsen gets into what he describes earlier as the truly weird parts of quantum mechanics that are not relevant to biology. Quantum entanglement is a phenomenon in which two photons emitted simultaneously from the same crystal appear to communicate with each other over vast distances. As Johnsen says: "If nothing else about light bothers you, quantum entanglement really should". Enough. I am grateful to this book for forcing me to come to terms with a number of aspects of light that I had been delinquent enough to ignore, and in a way that was a pleasure — like a long walk in hilly country.

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## Q & A

# David Sumpter

*David Sumpter was educated at Woodmill High School, Dunfermline and the University of Edinburgh, before completing a PhD in applied mathematics at the University of Manchester. He has since worked at both mathematics and biology departments in Oxford and Umeå. He was appointed professor in Uppsala, Sweden in 2007. His research is on 'Collective Animal Behaviour', which is also the title of a book he published last year.*

***Were you interested in biology from an early age?*** No, not at all. When I was nine years old, my parents bought a home computer. I became fascinated with programming and would spend hours typing in programs from magazines and trying to write my own code. At that time, I think I saw computers and biology as opposites. At school, biology was about dredging in ponds and writing long lists of the names of all the messy stuff you found there. Computers were structured. You could control them and when you learnt something it was logical and made sense in other contexts. When I was 13 I dropped biology studies at school and concentrated on the other sciences and mathematics instead.

***So when did your interest in biology start?*** When I finished my undergraduate degree in computer science and statistics I wanted to apply these skills to making mathematical models and computer simulations of 'something'. I didn't mind too much what this something was.

With this in mind, in the first few weeks of my PhD studies, I read Tom Seeley's book '*Wisdom of the Hive: Social Physiology of Honey Bee Colonies*'. Seeley had set out to disentangle the inner workings of the honey bee colony. He didn't just want to describe the behavior of the bees, but to get to the bottom of a set of logical processes and interactions. For example, his study of how bees regulate and balance the in-flow of water, nectar and pollen in to the hive, led him to think in general about regulatory feedback. Similar feedbacks are equally important in developmental biology, neurobiology and even economics.

For me this book was a revelation. The study of animal behavior wasn't just about writing long lists of animals and categorizing what they did, but about studying a set of mechanisms and understanding how these mechanisms had evolved. I could see how mathematical modeling could help here and was eager to be involved.

***So how did you get involved?*** I started talking to biologists. I was very lucky because at that time there were lots of bright PhD students and postdocs in the UK interested in social insects and other animal groups. First I started talking to Madeleine Beekman and Stephen Pratt, who were interested in developing models of the organization of insect societies. Then, together with Iain Couzin, we started working on locusts with Steve Simpson and on fish with Ashley Ward and Jens Krause. I also became friends with Dora Biro, before I knew she studied homing pigeons, and we ended up working on group navigation together. Five years after the end of my PhD, I found I was working on species throughout the animal kingdom.

Working with all these people (and many more) gave me a broad perspective of how mathematical models could be applied. I became more and more interested in biological questions in themselves. It is these questions that drive my current research. Working on mathematical models of lots of different systems allows you to get a better feeling for the underlying mechanisms. Today, my research group is working on everything from acellular slime moulds up to humans.

***What is your favourite example of mathematical modeling in action?*** In 2001, I was a postdoc at the Newton Institute for Mathematical Sciences in Cambridge. One of the researchers I had looked forward to discussing research with there was Matt Keeling, who had recently written a series of nice papers on spatial modeling. This happened to be the summer of the foot and mouth outbreak in the UK, and Matt was on the team of scientists modeling how the disease would spread and what could be done to prevent it. He didn't have time to discuss the latest mathematical techniques because he was busy applying them to an urgent problem. It must have involved many late nights of calculations, fitting the new data to models and then the next day finding ways to present these results to ministers and officials, who had difficult decisions to make.

I can't claim that my research has achieved the same level of immediacy, but I do have a similar emphasis on interaction between modelling and observations/experiment. There is a real excitement when you can propose a model, make a testable prediction and then do an experiment to test that prediction. Often your predictions are wrong and you need to make new models and propose new mechanisms. The fun comes from working together to try and understand what is going on. My aim is to publish papers that include both a modeling and an experimental component.

***Any criticisms of the use of modeling in biology?*** Mathematics is such an open-ended and wonderful world that it is easy to get lost in it and forget the questions you were trying to answer in the first place. This can be a problem for young mathematicians who start working with a model and want to 'prove' things that have no relevance to the application. It even happens to experienced biologists who can get lost in a theoretical paradise. A lot of recent debate on evolutionary theory has become completely detached from experiment, with experimentally untestable arguments about the best framework for studying co-operation. This happens because researchers become more interested in their models than what they are modeling.

***What are the key properties of a good model?*** Mathematical models should be judged on three things. Firstly, whether they can predict the outcome of experiments on specific systems. Secondly, if they simplify our understanding of the systems they model. Then lastly, whether or not they help us make sensible comparisons between different systems. Most of all, models should be useful and interesting.

***What would you advise young researchers interested in using mathematical models?*** I would emphasise that modelling is for everyone. You often hear that it is more difficult to make the switch from biology to mathematics than it is from mathematics to biology. This isn't true. To become a successful mathematical biologist you are going to have to understand both areas, and it doesn't matter which order you do it in. Often when I teach mathematics courses for Masters and PhD students in biology I find that they can use their biological intuition to help formulate and solve mathematical models, in a way that those with only a mathematical training can't. So get started today!

***What do you think are the big questions to be answered by mathematical modelling?*** The big questions revolve around the principles of pattern formation. We study fish schools and ant trails because they are good examples of complex patterns formed by individuals interacting in a simple manner. Similar complex patterns are seen in everything from developmental biology, to neurobiology to human social systems. The aim of theory and models is to cut through this complexity and give a simple description of how these systems work. Despite some small successes, we are still a long way from achieving this goal in a general sense. We have a subset of patterns, such as branching networks and aggregation patterns, which we understand very well and others that we simply don't understand at all.

This is where I would sell collective animal behaviour as an important research area, not just because these groups are fascinating in their own right, but also because they provide a good test bed for theories about how complex patterns are created and how they have evolved. They are easy to observe and we can relate to them directly. Hopefully, the progress we make on modeling animal groups can be applied more widely in other areas of biology.

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