Mathematical ecologist **Dr Sasha Dall** discusses the theories that surround his work towards understanding the evolutionary imperatives governing animal behaviour, and outlines some of his recent achievements in the field.

How did the study of animal behaviour through an economics-based approach first emerge?

The first papers to develop mathematical models of animal behaviour based on theoretical approaches borrowed from economics appeared in 1966, one by legendary ecologist Professor Robert MacArthur and co-author Professor Eric Pianka, and the other by Professor John Emlen. These were published in the ecological literature – back-to-back in the same journal issue – and their focus was on trying to predict how broad animal diets are likely to be. They applied what is called utility theory in economics to predict what the optimal composition of the diets of economically efficient foragers should be, assuming that different food types can be ranked according to their energetic profitability. It wasn’t until 1973 that Professor John Maynard Smith and Dr George Price introduced game theory to evolutionary biology by applying it to the problem of how aggressively animals should fight over resources. They did so by presenting the now-famous Hawk-Dove game.

Are any other methods used for studying the evolution of animal behaviour through mathematics?

As well as the approaches borrowed from economics that I use, theoretical biologists interested in animal behaviour also make use of the mathematics of how features of organisms (including behaviour) are inherited. By doing this they can predict what type of animal behaviour is likely to have evolved in the long term and therefore be expressed by animals today, as well as how behavioural traits are likely to change over the next few generations in response to known environmental (social and/or ecological) pressures.

In terms of your research as a whole, could you recap your most significant findings to date?

I think it’s fair to say that my scientific career so far has not really been about coming up with specific findings that have been particularly influential. Rather, I have been lucky to have been involved with publishing ideas papers that have somehow coincided with the emergence of new ‘hot topics’ in evolutionary biology and ecology. In my PhD work, I focused on how information use plays a role in ecological specialisation. Afterwards I stuck with both themes: information use and specialisation, particularly at the level of individual behaviour. Since the turn of the century, it has suddenly become popular to study animal information use (particularly in social contexts), on the one hand, and individual behavioural differentiation (what’s being called ‘animal personality differences’) on the other. In 2004, I published one of the earliest ideas papers on how animal personalities might evolve, and in 2005, I published a synthesis paper on a systematic way to think about animal information use. These are probably the pieces of work that I’m best known for.

Have you come across any major challenges in the course of your research? How have these been overcome?

The biggest challenges I have faced in my research have involved funding as, generally speaking, the UK research committees that decide the fate of animal behaviour grant proposals do not see much value in modelling approaches. I’m not sure why this is, as projects involving modelling work are regularly funded in closely related fields, such as population ecology, which have similarly strong traditions of formal modelling. I hear similar concerns being raised by colleagues around the UK. Now, at one level, this shouldn’t really matter as modelling doesn’t cost that much – all you need is a computer and software if you’ve got the modeller. Most of my modelling work has not been directly funded since becoming a PI, and my modelling collaborations have involved colleagues whose salaries are independently funded. However, it does matter when academic career progression depends on the ability to win Full Economic Costing (FEC) grants. A number of my senior theoretically-focused colleagues, including one Fellow of the Royal Society, have remarked how they would have really struggled to stay employed in the modern UK university environment.

Do you have any work on the horizon that you would like to highlight?

We have just had a proposal accepted to write an ideas paper for *Science* about our new, non-behavioural project on genetic and epigenetic information integration during development. The manuscript is due in May, so look out for it in print later in 2014!
The game of life

Researchers at the University of Exeter, UK, have been conducting research into the methods animals use to overcome risk, and their reactions to uncertain social and ecological environments.

AT FIRST GLANCE, it may appear that the crossover between zoology and economics is minimal – with the possible exception of managing a zoo, or trading in pork futures. In fact, zoology makes frequent use of economic theories in one particular area: animal behaviour. Perhaps this is not so surprising; after all, animals must be programmed by evolution to act in the most resource-efficient way possible, otherwise they would quickly be replaced by other animals better able to make use of the same resources. To an extent, this is also true of the physical characteristics an animal has evolved, but these develop over a longer period of time, and do not have the same capacity as behavioural traits to quickly modulate the strategies implemented by an organism in its day-to-day life.

One of the economic theories that has proven most useful to behavioural biologists is game theory – a branch of mathematics that focuses on strategic decision making, most often in multiplayer ‘games’, and which was famously resolved by American mathematician John Nash in his Nobel Prize-winning theory: the ‘Nash Equilibrium’. In animal behaviour, it is often useful to think of the evolution of behavioural strategies as the result of games being played between the animal in question and other animals it competes with. An individual might gain an advantage over others and ensure the future of its progeny by implementing a new behavioural strategy to better make use of the resources around it.

A PROPHETIC PAPER

This kind of strategy is referred to as ‘evolutionarily stable’, it makes better use of the resources at hand, is more successful, and will therefore become more widely adopted. Crucially, once such a strategy has been implemented by a population, it cannot be invaded by another alternative strategy arising through mutation. Understanding the adoption and adaptation of these strategies is integral to modern animal behaviour research, as is the ability to reason backwards from existing strategies, in order to gain a deeper understanding of the physiology of an organism and its evolutionary background. Game theory enables researchers to understand the properties of evolutionarily stable strategies, as well as helping them to explain strategies that seem to run counter to the objective of self-preservation – such as altruistic behaviour or cooperation with strangers. However, although it is a powerful framework for analysis, this theory has only once been successfully used to predict behaviour de novo.

This landmark prediction was made by Dr Sasha Dall, Senior Lecturer in Mathematical Ecology at the University of Exeter. Along with a team of collaborators, Dall has been responsible for investigating a range of behaviours in a diverse array of animals, from zebra finches to whales, but his early work focused on the scavenging behaviour of the common raven (Corvus corax), a member of the highly intelligent family of birds known as the corvids. A common theme throughout Dall’s career has been the role of uncertainty in game theory models of animal behaviour, and its ability to help explain real animal behaviour. Over time, the Exeter group’s work has resulted in a number of fascinating discoveries that bring us ever closer to an understanding of the complex behaviours exhibited by so many animals.

RAVENOUS RESEARCH

Game theory is an interesting analytical framework when it comes to animal behaviour, because it relies on certain conditions being met, and generally makes a number of simplifying assumptions about a series of interactions that might otherwise be too complex to approach mathematically. As such, its investigative value usually comes more from highlighting pertinent questions such as ‘what factor prevents this model from being accurate?’ – than providing definitive answers. This was not the case with Dall’s work on ravens, however. As a postdoctoral fellow at Florida State University, USA, he was challenged to build a game theory model to explain a previously unsolved example of animal behaviour; he chose the perplexing scavenging behaviour of sub-adult ravens in Vermont.

After discovering a large carcass, a single young raven will return to the roost to recruit more juvenile birds before feeding. If these roosts were permanent communities then this behaviour could be explained away by the chance of future reciprocation, or possibly helping those with similar genes, like relatives; but these roosts are transient, and turnover...
GOVERNED BY MATHEMATICS

Dall’s mathematical model also made another prediction about raven behaviour under different conditions to those found in Vermont, where the arboreal landscape surrounding the roosts makes it relatively difficult to find carcasses. The model anticipated that in conditions where this is not the case and the surrounding area can be surveyd easily from afar, the scavenging itself would more likely be undertaken in gangs – because the loss of social prestige to birds finding carcasses alone would be more damaging than losing multiple sources of intelligence about where carcasses are. In 2003, researchers in Anglesey documented exactly this behaviour; the deforested sheep pastures of the Welsh countryside offered the exact conditions required by these scavenging gangs.

This remains the sole time that a mathematical model has not only helped to decode animal behaviour, but has actually predicted it under certain conditions.

UNCOVERING UNCERTAINTY

This is therefore the approach that the Exeter group takes in the pursuit of its various current projects. Dall is engaged in PhD research projects into topics which include the effects of urbanisation on grey squirrel risk-taking behaviour; zebra finch lifestyles in the Australian outback; and the influence of social organisation in dolphins and whales on their ability to persist in modern environments.

Ultimately, risk and uncertainty are prime drivers of natural selection, and in a current project involving collaborators from Bristol, UK, Berlin, Germany, and Stockholm, Sweden, Dall is investigating how young organisms cope with an uncertain environment. Developing organisms are tasked with the incredible job of integrating information from their genes, the environment they grow up in, and especially from their parents to maximise their fitness in a changeable, unfamiliar and uncertain socioecological environment. Answering the question of how they do this may provide one further piece in the seemingly endless jigsaw of animal life.