



CURRENT ISSUES - PERSPECTIVES AND REVIEWS

Tribute to Tinbergen: Questions and How to Answer Them

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(Invited Review)

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Abstract

Despite the major advances that have occurred in the study of animal behaviour in the 50 years since the publication of Tinbergen's (*Zeitschrift für Tierpsychologie*, 20, 1963, 410) 'Aims and Methods' paper, the framework he outlined still remains the best way we have of guiding and organizing behavioural research. His distinction between four different types of question – adaptation, phylogeny, immediate causal mechanism and development – and his insistence on being clear on what would count as answers to each of them are still as good an introduction to the subject today as they ever were.

It is October 2013 and the beginning of a new academic year in Oxford. Students are assembling for their first lecture in animal behaviour and top of the reading list for this lecture is a 50-year-old paper describing what the subject is about. Is this a sign of a backwards-looking course in animal behaviour or a tribute to a paper that is still the best way we have of guiding, directing and organizing our thoughts about the hugely diverse subject of the behaviour of animals?

As one of Tinbergen's last graduate students, my abiding memory of him was his emphasis on asking the right question and having a very clear idea of what would count as an answer ('aims and methods', I suppose, would be another way of putting this: Tinbergen 1963). His quiet but devastating intervention in seminars, 'But what question are you asking?' could puncture the confidence of even the most eminent speaker, from which no appeal to the complexity of their mathematical modelling or quantities of the data they had collected could rescue them. And for him, no question was worth asking unless at the same time it was clear how an answer could be obtained. Right from the start, we were taught that we could study any behaviour but only if we could define what we meant and observe what we had defined. We could test hypotheses about the internal causation of the behaviour even though we could not see what

was happening inside the animal, provided that we could make predictions that would come out differently depending on what causes we were postulating. But the one thing we could not do, Tinbergen insisted, was to ask what the animal was feeling because there was no answer that would be different depending on whether it did or did not have subjective feelings to accompany its behaviour. Tinbergen was thus a behaviorist not because he thought animals did not have feelings but because he could see no methods for discovering whether they did or not. Clarity of question was important, but it had to be accompanied by equal clarity about the kind of empirical evidence that would count as an answer.

This made for rigorous and somewhat intimidating discussion of every single suggestion we students might make to him, subsequently more than compensated for by the encouragement he gave us if we could finally convince him that we had clearly thought through what we wanted to do. When I said I wanted to study 'search images' in birds – that is, whether birds could learn by experience to see cryptic prey they initially overlooked, he was interested but insisted that I should be more specific about what I was going to do. However, I managed to convince him that 'learning to see' could be empirically separated from other processes such as learning where to look and developing a preference for a new prey type. His support and

interest then became extraordinary. On the other hand, he remained highly sceptical of my later attempts to study 'suffering' in animals for the entirely laudable and consistent reason that the question 'do animals suffer?' might be clear, but the methods by which it could be answered were definitely not.

Tinbergen's genius was that he used his insistence on asking the right question to positive creative ends and not just to criticize other people's less rigorous thinking. He showed us that it was possible to ask questions about the adaptive significance of behaviour and to get answers with the simplest of equipment. It is the clarity of his questions that still remains instructive for us today. His classic paper on eggshell removal (Tinbergen et al. 1962) is not simply a demonstration that natural selection favours parent gulls that remove empty eggshells from the vicinity of their nests over parents that leave them there. That could have been inferred from an armchair far away from any sand dune. His contribution was to ask exactly why natural selection favours parent gulls that remove shells over those that do not and then to systematically go through the various possible answers: that it reduces chances of infection for the chicks, that it stops chicks being injured by the shell edges, that it stops the parent brooding the chicks properly or that it reduces the chances of predation. The question he ended up with was the quite specific one of whether eggshell removal protected the nest against predation by herring gulls *Larus argentatus* and crows, as opposed to any of the other possible explanations. Once he had the question clear in his mind, he could see what would answer it one way or the other. So he first showed experimentally that empty eggshells do attract predators to eggs. Then, he and others demonstrated that removing eggshells occurs in black-headed gulls *Chroicocephalus (Larus) ridibundus* that nest on the ground and are in danger of having their nests raided, but does not occur in closely related black-legged kittiwakes *Rissa tridactyla* that nest on cliff ledges where predators cannot land (Cullen 1957). Eggshell removal was thus specifically associated with the risk of predation, which ruled out the alternative hypotheses, because kittiwake chicks could also potentially be infected from microbes growing on the empty shell, be cut by the broken shells' sharp edges, and their parents could also find it difficult to brood chicks or eggs with empty shells in the way. Yet, empty eggshells remain littered around kittiwake nests, implying that they are not sufficiently hazardous to favour removal. It was the herring gulls and crows that accounted for the difference between the different behaviours in the two species of gull

because the predators cannot land on the narrow ledges where the kittiwakes nest. By asking the right question, Tinbergen had gone beyond simply showing that natural selection happens. He had uncovered the cause of death and loss of fitness and been able to test a specific adaptive hypothesis.

Much of course has changed in 50 years. Every single one of Tinbergen's 'four questions' has undergone a massive explosion of data and understanding of processes that were unknown to him when he set out the aims and methods of a very young science. The study of adaptation is, despite it is not always knowledgeable critics (Gould & Lewontin 1979) now well established, building on the foundations that Tinbergen laid. His comparisons between ground-nesting and cliff-nesting gulls have developed into a sophisticated 'Comparative Method' (Harvey & Pagel 1991) which looks at hundreds of species at a time. His simple experimental methods have become refined quantitative and much more controlled. The study of mechanism has been transformed almost beyond recognition from the days of Tinbergen's simplistic motivational models. We now understand in much more detail how nerves and muscles control behaviour and how sense organs respond to the world. We have computational neuroscience, intracellular recordings and real-time imaging to tell us how the brain works, but even here, his distinction between 'adaptive' and 'causal' explanations is as valid as ever. People studying the human brain ask evolutionary as well as mechanism questions (Rolls 2012) in a way that the psychologists of Tinbergen's day simply did not. The study of development of behaviour now has an understanding of genes and how they are switched on and off during development, as well as a knowledge of what changes in the brain when learning occurs, that were unimaginable 50 years ago. And the study of phylogeny has undergone a revolution with the advent of molecular techniques for inferring evolutionary relationships. All Tinbergen could do then was to study living species and try to put them in some sort of order to indicate the way behaviour might have changed over evolutionary time. Now we can use molecular evidence to decide whether or not a particular behaviour was likely to have been present in an ancestral species and even whether a signal or the response to that signal was the first to appear in evolutionary time.

With all these revolutionary changes, it might be thought that the questions and answers that suited the young science of ethology 50 years ago would no longer be up to the job of coping with the science of animal behaviour as it is today. But there are good reasons for thinking that Tinbergen's 'four questions',

and his insistence on asking the right one are, as good a guide to progress now as they were then. First, although it may seem obvious to those of us reared on 'Aims and Methods' that questions about adaptation and questions about mechanism are different and require different sorts of answers, I am constantly amazed that this distinction is not obvious to everyone. For example, many people seem puzzled that animals might choose to do things that are bad for their fitness – for example eating too much food, or choosing something that is bad for health or fighting themselves endlessly in a mirror. But understanding both the connectedness and at the same time the separateness of the four questions removes the mystery. A behaviour can be adaptive in the wild, but the causal route by which it achieves that balance could be one of many different mechanisms. Depending on what that mechanism is, animals may end up showing maladaptive behaviour or highly adaptive behaviour in the unnatural conditions of a farm or zoo.

Secondly, the four questions are far more informative and helpful than just two. Many biologists (including some very prominent authors of behaviour textbooks) make the distinction between 'proximate' and 'ultimate', roughly coinciding with 'causal' and 'adaptive' or evolutionary. This is of course a major step forward if it stops people confusing the two types of question. But the study of behaviour needs more than this. Just as there is a big difference between understanding how a car works and understanding how it is made, so there is a big difference between how a behaviour is controlled from moment to moment (its causal mechanism) and how an animal's body arrived at its current state from a developing zygote (its development). Causal questions are worth distinguishing clearly from developmental questions because they need completely different sorts of evidence to answer them. Similarly, adaptive questions (particularly ones about what current selection pressures are operating on a behaviour) are distinct and quite need different sorts of empirical evidence to answer them from questions about phylogeny and what happened in the past. I am probably biased, but four questions seem to me to fit the range of questions we need to ask about behaviour a great deal better than just two. They make us more specific in what we ask and therefore clearer in what we would count as answers, which was precisely Tinbergen's purpose in writing his paper.

The four questions have served the subject well over the last 50 years. They have helped to defy Wilson's (1975) prediction of the irrevocable splitting

of animal behaviour into neurobiology on the one hand and sociobiology on the other by stressing the common ground between diverse subject areas and the value of keeping them together. They have helped ethology's offspring, Behavioural Ecology, to return from an overemphasis on just one question (adaptation) to a more balanced view that understanding mechanism might just be important, too (Dawkins 1989). They have helped psychologists to understand the importance of our evolutionary heritage and to untangle the evolution of the brain (Rolls 2012). They have every prospect of providing a way of bringing together our new understanding of genetics, the extraordinary advances being made in understanding brain function and the adaptive significance of how brains and bodies are constructed. The new information we now have has filled in many of the knowledge gaps of 50 years ago, but it has fitted in to a framework that is still an extraordinarily helpful way of making sense of the study of behaviour. Paradoxically, the more we learn and the more different kinds of data we collect, the more we need the distinction between Tinbergen's four questions and his clarity of thinking about what constitutes answers to them.

Literature Cited

- Cullen, E. 1957: Adaptations in the kittiwake to cliff-nesting. *Ibis* **99**, 275–302.
- Dawkins, M. S. 1989: The future of ethology: how many legs are we standing on? In: *Perspectives in Ethology*. Vol. 8. 'Whither Ethology' (Bateson, P. P. G. & Klopfer, P. H., eds). Plenum Press, London and New York, pp. 47–54.
- Gould, S. J. & Lewontin, R. C. 1979: The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B Biol. Sci.* **205**, 581–598.
- Harvey, P. H. & Pagel, M. D. 1991: *The Comparative Method in Evolutionary Biology*. Oxford Univ. Press, Oxford.
- Rolls, E. T. (2012) *Neuroculture: On the Implications of Neuroscience*. Oxford Univ. Press, Oxford.
- Tinbergen, N. 1963: On aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.
- Tinbergen, N., Broekhuysen, G. J., Feekes, F., Houghton, J. C., Kruuk, H. & Szuk, E. 1962: Egg-shell removal by the black-headed gull, *Larus ridibundus* L.: a behaviour component of camouflage. *Behaviour* **3**, 1–38.
- Wilson, E. O. 1975: *Sociobiology*. Belknap Press of Harvard Univ. Press, Cambridge, MA.