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Tribute to Tinbergen: The Four Problems of Biology. A Critical Appraisal

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(Invited Review)

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Abstract

Tinbergen's (1963, Z. Tierpsychol. **20**, 410–433) *four questions* have guided the conceptual thinking of behavioural biologists over five decades. This is partly based on a misunderstanding of the aims and virtue of this article. Tinbergen called attention to the fact that his classification of problems is somehow illogical. Here, an attempt is made to remove some of the inconsistency by reformulating the levels of analysis of biological (including behavioural) traits. Furthermore, important merits of Tinbergen's milestone paper that have remained largely unnoticed are put in perspective. Perhaps the most lasting of several functions of that article has been its pivotal role in establishing a new research discipline, *behavioural ecology*.

Fifty years ago Niko Tinbergen proposed a research programme for the scientific study of behaviour. His discussion 'On aims and methods of Ethology' has since guided our endeavour to understand how animals behave, and why. The 'four Tinbergen questions' are typically taught in the first lesson of behaviour classes worldwide, and the original paper has developed into THE citation classic of the field (1966 citations by 29 November 2013; source: Google scholar).

In this article, Niko Tinbergen extended Julian Huxley's alleged 'three major problems of Biology' – *causation, survival value* and *evolution* – by a fourth one: *ontogeny*. Tinbergen proposed that for a proper understanding of behaviour, these four levels need to be scrutinized: 'it is useful both to distinguish between them and to insist that a comprehensive, coherent science of Ethology has to give equal attention to each of them and to their integration' (p. 411). This was a keen statement, because at the time, ethologists mainly focused on causation and, to an extent ontogeny. But survival value was not regarded as something that could be scientifically studied, at least not by way of serious experiments; and comparative studies to unravel evolution were in their methodological infancy.

Multiple Purposes

It seems that this pivotal paper was destined to serve five major functions.

1 An appreciation of the scientific accomplishments of Konrad Lorenz on occasion of his 60th birthday. Apparently, the celebration of this anniversary was the immediate reason for this article.
2 The proposal of a separation of the four mentioned levels of analysis from each other to study biological traits. Tinbergen hailed the incessant intention of Lorenz to apply 'biological thinking' to the study of behaviour, so 'behaviour' was the focus of this article. But his claim to consider these four levels of analysis extended to all of biology.
3 An outline of appropriate scientific approaches to the four required levels of analysis.

4 The plea for the objective, scientific study of the survival value of behavioural (and other biological) traits.
5 The promotion of an integration of the different disciplines studying behaviour at the four mentioned levels of analysis into one, coherent science.

The second of these points is the one this paper is mainly renowned for (Dawkins 1989, 2014; Dewsbury 1992). This unbalanced focus is a pity, because in contrast to the other functions of this article, this particular point is somewhat problematic.

A logical flaw

The proposition to separate the four levels of analysis *causation, survival value, evolution* and *ontogeny* reflects a logic error. For instance, to understand *ontogeny*, the 'change of behaviour machinery during development' (Tinbergen 1963, p. 424) caused by a dynamic interplay between the developing organism and its environment, both *survival value* and *causation* should be considered. Furthermore, *survival value* is one aspect driving the *evolution* of traits, not an alternative question. This illustrates that the proposed levels are not separate, they cannot be regarded detached from each other in a meaningful way, and they do not provide the logic or methodical framework for which they have deemed fit. Tinbergen himself was well aware of this problem, in fact he has NOT suggested to use his proposal as a general classificatory scheme; 'in speaking of "the four problems of Biology" we apply a classification of problems which is pragmatic rather than logical.' (Tinbergen 1963, p. 426).

Tinbergen's four questions might be best understood as a depiction of a set of influences on a biological trait in an adult organism, such as a behaviour (Table 1). However, we have learnt that these levels are heavily intertwined; therefore, the value of viewing them individually may be limited.

Table 1: Critical influences on the expression of a biological trait (e.g. a behaviour), based on Tinbergen's four questions

	Influence on trait	Reflecting	Tinbergen's level
1	Genetic architecture	evolutionary history of a trait	evolution
2	Development	interplay of genes and environment	ontogeny
3	Regulatory mechanism	morphological/ physiological causes	causation
4	Fitness effects	feedback on trait evolution	survival value

A modified Concept

To move towards a consistent conceptual framework, it seems worth considering alternatives to this classification. An important thought to keep up from Tinbergen's scheme is the separation into *ultimate* and *proximate* causes of biological traits. This separation was proposed by Tinbergen already in his seminal book on 'The study of instinct' (Tinbergen 1951), which was in fact the first textbook in ethology. The separation of ultimate from proximate levels dates back to Baker (1938) and was prominently promoted by Mayr (1961; cf. Burkhardt 2014). It somehow guides the scientific approach in biology ever since, particularly in the study of behaviour (Alcock & Sherman 1994), even if feedback between these levels needs to be considered (Laland et al. 2011; MacDougall-Shackleton 2011). Another classificatory separation inherent in Tinbergen's ideas is the distinction between the levels of *genotype* and *phenotype*, where the former reflects the evolutionary history of a trait and the latter incorporates all genetic, epigenetic and environmental influences on the expression of traits in an individual. Combining these classificatory levels, we may think of an alternative scheme that is rooted in Tinbergen's 'four problems', but which may have less logical friction (Table 2).

If we consider this alternative scheme, the four categories do contain Tinbergen's levels. *Fitness effects* include 'survival value', the *underlying machinery* reflects 'causation', and *evolution* accounts for the evolutionary history of traits and their dynamics. We might ponder where 'ontogeny' comes into play. As Tinbergen has mused already, this is not a separate category, because ontogeny has fitness effects and an underlying machinery, it depends strongly on interactions between genes and the environment, and it evolves. Therefore, it is rather a different dimension to look at than part of this classification of analysis levels. This means that traits of individuals in adult-

Table 2: Classificatory scheme of the levels of analysis inspired by Tinbergen's 'four problems of biology'. *Fitness effects* refers to survival value and reproduction, *underlying machinery* incorporates all morphological and physiological structures and processes responsible for the expression of a trait (i.e. Tinbergen's 'causation'), *evolution* includes both the course of evolution and the dynamics, as outlined by Tinbergen (1963; p. 427–429), and *gene/environment interplay* concerns the processes involved in the translation of genetic information, including epigenetic effects

	Ultimate	Proximate
Phenotype	fitness effects	underlying machinery
Genotype	evolution	gene/environment interplay

hood and in their ontogeny can be analysed using the same categories as outlined in Table 2.

Is such scheme useful? Can it ever be? Yes and no. Yes, because it helps to organize one's thoughts about different methodological approaches. Researchers studying behaviour can typically associate their *major* focus with one of these categories. The risk of such pigeonholing, however, is that it can fool us into believing that these partitions reflect a fundamental separation between the involved mechanisms (cf. Laland et al. 2011), which seems ambiguous for instance when epigenetic inheritance is concerned (Danchin et al. 2011).

Requisite Tools

Apart from classifying questions and analysis levels, Tinbergen (1963) provided a number of important guidelines for the study of behaviour. We should be aware that ethology as a fundamental research discipline was still young and that the ways how scientists approached the study of behaviour sometimes appeared arbitrary and unsystematic. For instance, one of the themes at these times was whether and to which extent unprejudiced, purely descriptive observation should be part of the study of animal behaviour, as proposed by Konrad Lorenz and his disciples. Tinbergen clearly supports this approach: 'the starting point of our work has been and remains inductive … we would deceive ourselves if we assumed that there is no longer need for descriptive work … naive, unsophisticated, or intuitively guided observation may open our eyes to new problems. Contempt for simple observation is a lethal trait in any science' (p. 411–412). However, he does not deem impartial observation sufficient: 'our science will always need naturalists and observers as well as experimenters' (p. 413). For the latter purpose, Tinbergen proposes, for instance, the use of animated dummies, and he stresses over and over again that it is important to study animals in their natural context to make sense of behavioural responses. In addition, Tinbergen suggests using comparative methods to unravel whether 'similarity can be due to … common descent or … convergent evolution' (p. 421).

Foundations of Behavioural Ecology

Quite likely the most important purpose of this paper, however, was its pioneering role for the scientific study of the evolutionary function of behaviour. Here, the founding father of behavioural ecology has delivered its inaugural address. Even if the name of this new research discipline had not yet seen the light of day, Tinbergen proposed nothing less than the philosophy, methodology and purpose of behavioural ecology. 'We have to keep emphasising that the survival value of the attributes of present-day species is just as much open to experimental inquiry as is the causation of behaviour or any other life process' (p. 418), which he illustrates by referring to his own, elegant eggshell removal experiments in gulls (Tinbergen et al. 1962). Tinbergen does clearly not stop there but explains 'the experimental demonstration of survival value involves quite a number of steps. Much of the experimental evidence is not complete, because it has (often of necessity) been done in a situation which differs essentially from the natural context' (p. 422). He describes how the right eggshell removal experiments would need to be done for a 'strict test' of survival value, before concluding 'the ultimate test of survival value is survival itself, survival in the natural environment' (p. 423).

In his chapter on 'survival value', Tinbergen disclosed his own deep bias towards the subject that was to become the core of behavioural ecology: 'Being myself both a naturalist and an experimenter at heart, one of my primary interests has always been to find out, if possible by experimentation, how animal behaviour contributes to survival' (p. 417), and he predicts the future impact of this field of research: 'the study of survival value … is an aspect of Ethology which may well fertilize other fields of Biology' (417). He further makes a passionate plea for the integration of the study of survival value and causation: 'If we would agree to take survival as the starting point of our enquiry, our problem would just be that of causation; we would ask: "How does the animal – an unstable, 'improbable' system – manage to survive?" Both fields would fuse into one: the study of the causation of survival. Indeed, logically, survival should be the starting point of our studies' (p. 418). Ironically, for the first 30 years or so of its history, behavioural ecology has ignored this prudent suggestion. Most studies at that time remained stuck with what Tinbergen wisely defined as 'the starting point'. The pendulum swayed from one extreme to the other, from the focus on mechanisms ('causation') to one on function ('survival value'; cf. Dawkins 1989). Fortunately, recent aim in behavioural science seeks for a better balance between the study of 'proximate' and 'ultimate' levels. Ethologists have realized that an exclusive focus on 'how' or 'why' questions falls short of understanding behaviour, not to mention the fact that this dichotomy reflects a flawed argument; asking *why* a biological trait exists necessarily encompasses the question of *how* it effects fitness and *how* it was

selected. To understand *how* a mechanism works naturally involves the question of *why* its components cause the overall function.

Visions and Terms

Tinbergen (1963) aimed to sketch 'what … modern Ethology [is] about', without meaning 'to be balanced or comprehensive' (p. 430). This paper is a milestone in behavioural science, because it attempted to clarify levels of analysis, appropriate approach and methodology, prudent research focus, integration of diverse fields of investigation and, last but not least, adequate terms for different study disciplines. For instance, he termed the study of causation of behaviour as 'Physiology of behaviour', which should 'include the study of causation of animal movement with respect to all levels of integration' (p. 416). Based on his perception that 'Ethology is "*the biological study of behaviour*"' (p. 411), he also proposed a new name for the integrative and coherent science he envisaged, 'the fusing of many sciences, all concerned with one or another aspect of behaviour, … for which the only correct name is "Biology of behaviour" (p. 430; or in German 'Verhaltensbiologie', p. 431). Interestingly, he did *not* coin a term for the subdiscipline he has promoted most emphatically – the study of function or '*survival value*'. This is perhaps the reason why many behavioural ecologists, unfortunately, have missed that their science is rooted in this very article.

Not considering one's roots is a common mistake in the development of scientific disciplines, hence what happened in behavioural ecology is nothing special (Taborsky 2010). However, due to the disregard of Tinbergen's seminal treatment of ethology's 'aims and methods', behavioural ecologists have long believed that the study of function or *ultimate causes* of traits is sufficient for their comprehension. Candid consideration of Tinbergen's programme will help to regain balance in the science that – following Tinbergen's intention – should be most aptly called '*behavioural biology*'.

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