Tinbergen's Legacy

Nobel laureate Niko Tinbergen laid the foundations for the scientific study of animal behavior with his work on causation, development, function and evolution. In this book, an international cast of leading animal biologists reflect on the enduring significance of Tinbergen's groundbreaking proposals for modern behavioral biology. It includes a reprint of Tinbergen's original article on the famous 'four whys' and a contemporary introduction, after which each of the four questions are discussed in the light of contemporary evidence. There is also a discussion of the wider significance of recent trends in evolutionary psychology and neuroecology to integrate the 'four whys'. With a foreword by one of Tinbergen's most prominent pupils, Aubrey Manning, this wide-ranging book demonstrates that Tinbergen's views on animal behavior are crucial for modern behavioral biology. It will appeal to graduate students and researchers in animal behavior, behavioral ecology and evolutionary biology.

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Function and Mechanism in Behavioral Biology

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSIGTY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
São Paulo, Delhi

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by
Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521874786

First published 2009

Printed in the United Kingdom at the University Press, Cambridge

This book is based on and expanded from a journal issue publication, originally published by Koninklijke Brill NV, Leiden, the Netherlands (http://www.brill.nl). This issue is entitled: *Animal Biology* (ISSN 1570-7555) volume 55, no. 4 (2005) "Evolution, Function, Development and Causation: Tinbergen's Four Questions and Contemporary Behavioural Biology", and was guest-edited by Johan J. Bolhuis and Simon Verhulst. Brill owns the copyright in all parts of the above special issue, with the exception of Niko Tinbergen's paper included therein. Brill has provided Cambridge University Press with a non-exclusive licence to reproduce the content of this issue of *Animal Biology*. Where applicable in this book, proper reference to the original articles in *Animal Biology* has been made.

A catalog record for this publication is available from the British Library

Library of Congress Cataloging in Publication data
Tinbergen's legacy : function and mechanism in behavioral biology / edited
by Johan J. Bolhuis, Simon Verhulst.
p. ; cm.
Includes bibliographical references and index.
ISBN 978-0-521-87478-6
1. Animal behavior – Research. 2. Tinbergen, Niko, 1907–1988.
I. Bolhuis, Johan J. II. Verhulst, Simon.
[DNLM: 1. Tinbergen, Niko, 1907–1988. 2. Ethology – history. 3. Behavior,
Animal. 4. Psychology, Comparative – history. QL 750.5 T587 2008]
QL751.T552 2008
591.5–dc22
2008021974

ISBN 978-0-521-87478-6 hardback
ISBN 978-0-521-69755-2 paperback

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Foreword: Four decades on from the "four questions"

As a former student of Niko Tinbergen, it is a pleasure to introduce this collection of papers written to commemorate the 40th anniversary of his classic paper on the "four questions" (Tinbergen, 1963, this volume). First a little history, because we need to remember the context in which Tinbergen came to write this memorable paper. It was designated as a salute to Konrad Lorenz, old friend and colleague, for his 60th Birthday, but its timing and content signified much more than this. During the late 1950s and early 1960s ethology was evolving rapidly and going through some turmoil. I suppose the original framework of "classical ethology" as it appeared to most of us at the time was encapsulated in Lorenz's 1950 Society for Experimental Biology Symposium paper and Niko's *The Study of Instinct* (1951). The number of people calling themselves ethologists was increasing rapidly especially in Germany, the Netherlands and Britain and many of them had close connections with Lorenz's and Tinbergen's groups. We were aware that this "new" approach to the study of animal behavior had plenty of antecedents both in Europe and in the USA. Tinbergen himself lists Whitman, Heinroth, and Verwey; nevertheless, I don't think we can be blamed for regarding it as new. After the Second World War, animal behavior was emerging from decades when American experimental psychology held sway – everyone should dip into Munn's (1950) heroic text to get some flavor of that influence – and Lorenz and Tinbergen seemed to signal a new era. They certainly came as a breath of fresh air to all zoologists and particularly to field workers. I joined Tinbergen's group at Oxford just 2 years after he arrived in Britain and so was privileged to be part of this wave of new work. We were definitely proud of our position; we called him the "Maestro" (in this

we followed Medawar as Desmond Morris (1979) has pointed out) and we called ourselves the "Hard Core!"

International ethology conferences were held every couple of years and, being quite small, they certainly had something of a family feeling. We seemed to manage quite well within a fairly proscribed theoretical framework with species-specific behavior very much at its heart. Each species exhibited a repertoire of behavior patterns which were "innate," i.e., whose development was largely under genetic control, and whose performance was under the control of particular motivational states and sets of external stimuli. These latter were matched by "innate releasing mechanisms" in animals, which responded preferentially only to certain aspects (sign stimuli) in the external world – often sign stimuli were specially evolved structures or displays from conspecifics ("releasers"). Both Lorenz and Tinbergen had provided models for the organization of instinctive behavior. Lorenz's famous "psychohydraulic" model was much discussed – it modeled field observations during the breeding season rather well. Tinbergen developed a hierarchical model which, although it used terms like "impulses" with a more physiological sound than Lorenz's reservoirs and spring loaded valves, was really just a set of "black boxes" endowed with certain properties and connections.

The publication of Lehrman's (1953) critique of Lorenz's behavior theory produced major ripples in this rather small pond. To change the metaphor, it began to open up a rift between two major groupings of ethologists. The German group – *sensu lato* – reacted most strongly, regarding Lehrman's criticisms as an almost total rejection of the reality of innate behavior and exhibiting an obsession with learning processes. There can be no doubt that Lehrman did go rather over the top in proposing that some behavior which appeared fully formed, as it were, at the first performance, could be the result of hitherto unconsidered earlier experience. For example, Lorenz was particularly infuriated by Lehrman's citing work suggesting that the rhythmic movements of the head of chicken embryos in the egg induced by the beating of its heart were the origin of the pecking movements that young chicks exhibited upon hatching. Lorenz, reasonably enough, pointed out that, whilst all embryo birds were subjected to the same passive head movements in the egg, most did not exhibit pecking movements upon hatching, but gaped upwards in order to solicit feeding from their parents! By contrast the "English-speaking ethologists" (this was Lorenz's term and, I think, must include the Dutch!) although not failing to make some strong challenges to Lehrman, were more

positive. They latched on to his key message; that a catch-all phrase like "innate" was in danger of making us ignore, or at least de-emphasize, the way behavior *develops*.

This will seem a modest conclusion and it is hard to believe it became such a contentious issue. Lorenz always asserted that his group actively studied development, e.g., the work on sexual imprinting in ducks, but in his writings and at meetings he always seemed to emphasize the contrast between innate and acquired components of behavior. Further, "acquired" seemed to equal "learnt." Great emphasis was put on so-called "Kaspar Hauser" experiments in which animals were reared in isolation of various degrees and later observed in their normal environment. Very often they performed remarkably well and so one could deduce that conventional learning and other types of experience were *not* required for normal development of this particular behavior – it is "innate." All too often this label was as far as it went. In fact, of course, such a result can best serve as a starting point for a study of development, i.e., to discover what type of experience *is* required and by what developmental processes does it make its mark?

Looking back on it, I find Lorenz's attitude unfathomable. The importance of his contributions to the new ethology were never in doubt. Perhaps he was just not interested in development as we, the English-speakers saw it. He certainly continued to believe that innate and acquired behavior came in distinct "packages" and it was almost as if he felt we devalued the beauty and power of innate behavior by pursuing its origins in the individual.

This was the background into which Tinbergen launched his four questions paper. He put it into the *Zeitschrift* because this was the main journal of the German-speaking ethologists at that time. It is now possible to understand his feelings in some detail. We have Kruuk's (2003) perceptive and certainly not uncritical biography and also Burkhardt's (2005) admirable history of ethology. Burkhardt has analyzed the correspondence between Tinbergen and Lorenz around this time which reveals that Tinbergen was seriously concerned by the rift and misunderstandings which were becoming so prominent. He was also well aware that Lorenz would not like some of the points he felt must be made. He says: "I have not hesitated to give personal views even at the risk of being considered rash or provocative." It was the attitude concerning development which was perhaps the most sensitive, but there were other issues from what we might call classical ethology which Tinbergen felt needed attention. I believe this remains the case today.

There has been quite a lot of navel-gazing by ethologists worrying about whether ethology has been overtaken by the emergence of other approaches or even perhaps, is now extinct! (See several essays in Bateson and Klopfer, 1989, for example.) Wilson's (1975) famous diagram in his *Sociobiology* text comes to mind where the giant amoebas of neurobiology and sociobiology are engulfing the last vestiges of ethology! I believe all this is a complete misinterpretation of what has happened. The great bulk of the classical ethological model outlined above is little considered now, similarly neither are Hull's behavior model or Skinner's. Ethology's enormous contribution was to reawaken the serious study of any animal's behavior, taking into account the selection pressures imposed by the environment in which it has evolved. In this sense it continues to dominate animal behavior studies; we are all ethologists now.

I have yet to meet anyone who does not accept that Tinbergen's four questions for the study of behavior – function, evolution, causation, and development – are the right ones. Of course, he discusses them with a very particular agenda in mind, which was to ensure progress on all four fronts with each paying close attention to the others. Further, he saw each question as applying to all levels of analysis, from physiology to population ecology. It is clear that, taking all this on board without any theoretical difficulty, progress in practice has been very uneven and a number of issues which Tinbergen discussed have effectively been left on the sidelines. Marian Dawkins (1989) referred to an ethological beast with four legs, one of whose legs is considerably longer than the others; this is "function."

Much of this is inevitable and simply relates to accessibility and the way science progresses. I have often reflected on Medawar's wise words in his *The Art of the Soluble* (1967).

> "Scientists study the most important problems they think they can solve. It is, after all, their professional business to solve problems, not merely to grapple with them. The spectacle of a scientist locked in combat with the forces of ignorance is not an inspiring one if, in the outcome, the scientist is routed. That is why some of the most important biological problems have not yet appeared on the agenda of practical research."

Having myself been pretty comprehensively routed in attempts to relate the organization and development of complex behavior to underlying genetic architecture, I feel I understand why functional approaches are so popular. After all, the growth of modern behavioral

ecology is a most natural extension of classical ethology. (I should declare here that I don't wish to distinguish between "behavioral ecology," "sociobiology," and "evolutionary psychology." We may note that there are now at least *three* specialist journals and that many of the papers in *Animal Behavior* concern behavioral ecology.) It often involves field work, it is always concerned with the way an animal's behavior has become adapted to maximize its fitness. There is much sophisticated modeling by new generations of mathematically more apt ethologists, many of them derived from Maynard Smith's (1982) invaluable development of the concept of the Evolutionarily Stable Strategy. I believe Tinbergen would have loved this elegant and precise way of linking function and evolution in exactly the way he demanded.

Modern studies have brought the ethological approach into areas of social behavior and the evolution of social systems which were scarcely touched at the time Tinbergen was writing. His own book entitled *Social Behaviour in Animals* (1953) was almost totally confined to dyadic encounters between parents and offspring, sexual partners, or rivals. Even at the level of the individual, the idea of function is now extended far, far beyond the way we once imagined it. Thus, classical ethology would interpret the feeding behavior of a bird in terms of appetitive searching behavior interrupted at intervals by its performing rather stereotyped feeding movement in response to the external stimulus of a food item it has perceived. This remains largely true, but it is only a fraction of the picture. The development and modeling of optimal foraging theory reveals that a bird may constantly be making second-to-second decisions about its feeding. How long should it stay in one place searching and when should it give up and move to another place? The answers will depend amongst other things on how hungry it is, its past experience, the distribution of the food items and their quality. What is remarkable is to discover that, when such behavior is modeled and predictions made as to the best strategy given certain parameters, the details of the bird's behavior often match them extremely well.

This is but one example of the sophisticated approach to function which now concerns many ethologists. It relies on the old ethological skills of observation and careful description, often combining field work and laboratory experiments, but goes far beyond to the examination of long sequences of behavior, the allocation of priorities and the trade offs between them leading to different outcomes. None of this would, I feel, surprise Tinbergen who often took delight in showing

just how perfectly behavior was matched to function. Black-headed gulls spend approximately 5 minutes per year removing eggshells from their nest, but he showed in detail how this behavior and its exact timing after the chicks hatched was adaptive against predators (Tinbergen *et al.*, 1962).

The allocation of function on such a broad scale and to such subtleties of behavioral changes even from second to second has not been without its critics. Gould and Lewontin (1979), using an interesting architectural metaphor – the Spandrels of San Marco – suggested that, with the eye of faith, it was all too easy to suggest functions for behavior, which might just be inevitable results of situation and conditions. They attacked some of the wilder shores of sociobiology on this account. The association of some behavior pattern or some structure with a particular behavioral outcome must not lightly be assumed to be an evolved, functional link. This is particularly the case when there are several possible functions and it may be well nigh impossible to distinguish between them by observation or experiment and in any case more than one function may be involved. One thinks of the behavior of helpers at the nest, for example (see Jamieson and Craig, 1987). A necessary caution then, but this should not inhibit the construction of functional hypotheses. "Everything is likely to be adaptive," is not a bad slogan to start out with so long as you keep a cool head! After all, the history of biology is full of examples where function was initially dismissed only to be amply proven by proper observation and experiment. Thus it had been suggested that insects had no color vision but von Frisch could not believe that the colors of flowers were without function. An early description of the beak of a crossbill (*Loxia curvirostra*) referred to it as "an abomination of nature" and so on. Robinson (1991) gives a number of examples of puzzling structures whose function is unfathomable until one watches behavior and sees them in action, just the course that Tinbergen recommends.

Modern behavioral ecology has established an astonishing body of data on the function and evolution of behavior; as we have described there has been no shortage of progress on these two of Tinbergen's questions. Even from the earliest days, ethology's emphasis on instinctive behavior presented formidable problems for the other two, mechanism (to be roughly equated with the causation question here) and development. It is certainly the case that there are now many beautiful studies showing how complex patterns of behavior develop. The crucial timing of various experiences for the development of bird song (Catchpole and Slater, 1995), the nature of sensitive periods and

experience in sexual imprinting or the development of social behavior (see Bateson and Martin, 2002), and so on. At every stage we can see how the animal's genetic potential interacts with its physical and social environment to shape its behavior. Such studies exemplify some of the very best of modern ethology. One set of problems which remains concerns those elements of instinctive behavior which are typically highly species-specific and whose variations in form cannot be accounted for by the environment or experience during development. Lorenz was one of the first to emphasize that behavior, like morphology is a "property" of a species and evolves like it. Just as different duck species reared similarly will develop their characteristic plumage features, so will they develop the characteristic courtship behavior patterns. Like the plumage, these are clearly similar but they have striking and consistent species-specific features present from the outset when the birds are mature.

How can behavior appear in appropriate form and to the appropriate stimulus situation, fully fledged, as it were, at its first performance? Obviously, there must be a considerable genetic component to its development. How can genes coding for proteins, code for behavior? In the mid 1960s the distinguished geneticist I.M. Lerner entitled an address to the Behavior Genetics Association, "Two cheers for behavior genetics." I think this is still a just portion: as far as the direct question given above is concerned, the field has not had a very productive history. There is much sophisticated genetics which through selection and hybridization enables us to apportion a behavioral character's variance into genetic and environmental components and to explore the nature of its genetic architecture. The variation which is being analyzed is entirely quantitative and we can often identify "quantitative trait loci" of greater or lesser effect. For almost any behavior we find that numerous loci affect its level of expression. There have been many studies in which fast-breeding and easily maintained animals – Drosophila and mice especially – have been subjected to artificial selective breeding for behavioral traits. Most have succeeded, sometimes dramatically, in altering the frequency of performance of instinctive behavior, although the behavior itself stays obstinately intact. Genetic changes seem commonly to alter the threshold for the elicitation of behavior patterns but when they appear their form is unchanged. Bakker's (1986) heroic genetic analyses of stickleback aggressive behavior provide a good example. By selective breeding in different contexts he was able to show that the same genes sometimes overlap to affect aggression in more than one situation, sometimes

more uniquely. This is a valuable result because it indicates how behavior's evolution may be constrained but it remains impossible to say much about the inheritance of the aggressive behavior patterns themselves.

The direct question asks how an animal is programmed to produce a repertoire of very stereotyped motor patterns in specific situations and often to a very specific set of stimuli – the classical ethological picture. Now clearly all kinds of interactions with the environment will be involved in the development of such patterns. Studying these will help us to identify more precisely the points at which genetically based information comes into operation. The diverse studies on bird song development offer many splendid examples and there are others in this volume. However, at the end we are often left with a very inaccessible problem of developmental neurobiology. How do genes so control the development of the nervous system that all the ducks or gulls or cichlid fish share some common repertoire of courtship movements but each species has emphasized elements of them in particular ways? We should not lightly dismiss the possibility that young individuals can copy from others (there are such instances in the behavior of birds and mammals) but here this is very improbable. It is one type of situation in which the Kaspar Hauser experiment can eliminate some routes of development. Genes must somehow "hard wire" the nervous system to operate in a very particular way. Expressed in this way, we are reiterating the exact kind of point which was made by Lorenz and others 40 years ago and we are little nearer to any kind of answer. Sometimes it has been possible to hybridize species whose instinctive repertoire is distinct at least in part. The songs of some crickets and of some pigeons are examples. Sometimes we see fairly clear dominance of one parent's behavior, more often we observe that a mixture, perhaps one should say jumble of genes in the F1 leads to a similar breakdown of behavior. It is not very informative and rarely is it possible to move on to an F2 generation where independent segregation from the two parental genotypes might suggest behavioral "units" of some kind.

The spectacular rise of molecular genetics has lent a new impetus to studies of single gene mutations and their effects on behavior. Now it is often possible to describe the gene's products and something of its actions on the nervous system, even the site of its action on occasions. This modern stage of the field is well summarized by Sokolowski (2001). However, it remains the case that, as outlined above, for the most part the genes described modulate the expression of behavior only and tell us very little about how the nervous system is organized to

produce it. The exception would be mutant studies on learning, where some genetic studies are indeed giving insights into neural mechanisms, but learning is a more general process function of the nervous system than are the specifics of instinctive patterns. Nevertheless, it looks as if the genetic control of behavioral development might begin to reveal striking parallels with morphological development. Genes coding for the same polypeptides may be involved in the regulation of behavior across groups even across phyla, e.g., Drosophila, bees, fish and rodents; see Robinson and Ben-Shahar (2002). Perhaps we must consider the possibility that there are behavioral homeoboxes!

I suspect that the mechanisms by which genes "build" a nervous system that can mediate instinctive behavior will remain elusive for a long time to come. They represent an example of Medawar's class of intractable problems. However, I suppose we can at least *in principle* imagine how genetic programming could wire up a developing nervous center to produce a specific type of stereotyped motor pattern. For an examination of the possibilities it is certainly worth revisiting Hoyle's (1984) lively setting out of the neurophysiological background to stereotyped species-specific behavior patterns and the discussion it provoked. Such a developmental phenomenon might eventually become accessible to the techniques of developmental neurobiology. But some modern studies of behavioral ecology require us to demand far more of the genes. It is quite certain that animals sometimes make a subtle choice of their response depending not just on the immediate situation, but on the circumstances which led up to it. Davies's (1992) beautiful studies of dunnocks (*Prunella modularis*) have shown that many females have two males on their territory. The alpha male is shadowed by a beta male who usually fathers some of the offspring. The beta male matches the amount of help he gives when feeding young to the amount of contact – "mating access" – he had during her most fertile period during egg-laying! Functionally, this obviously makes sense, but surely it raises formidable developmental questions.

Dunnocks are short-lived in the wild; there is no possibility of a male trying out various feeding strategies and learning the best outcome. Somehow he must inherit the ability to match "mating access" to helping at the nest several days later. This is just one well-worked example but there are numerous instances of short-lived animals making such choices. The optimum feeding strategies mentioned above provide many examples. The observations lead to clear hypotheses about behavior which work out in practice and the function and evolution of the behavior are well established, but what of its development

and causation? In such cases we tend to think of the simplest way that such behavior could be organized. We do not invoke conscious choice but fall back upon "rules of thumb." For example, Richard Dawkins once suggested that what genes might code for in the parental behavior of passerine birds is, "feed conspicuous gapes inside the nest rim." It is less easy to come up with a rule for the dunnocks but Davies's own studies have begun to close in on what aspects of the situation beta males might be responding to. However daunting the developmental problems, good ethological observation and experiment will remain one important way forward.

In conclusion, I turn to the other neglected aspect of Tinbergen's causation question – motivation, by which I mean to include "drives" in the old ethological sense. The rather simple exposition of instinctive drives set out by Lorenz and Tinbergen quickly proved to have severe limitations. Hinde's (1959, 1960) key papers criticizing the concepts were very influential and indeed some regarded them as having administered the *coup de grâce*. Slowly at first, but then more rapidly in the early 1970s neglect set in. Hogan (2005, this volume) describes this well. However inadequate were the original formulations, the phenomena they attempted to deal with remain as vivid as ever. In the first edition of her book which covered the modern approach to ethology, Marian Dawkins (1986) discussed them in a chapter she entitled "Some obstinate remnants." That rather makes the point; there is something to explain which won't go away! Thus, the old conflict hypothesis for the origins and causation of threat and courtship displays which postulates the simultaneous arousal and conflict between systems controlling aggressive and fearful responses retains considerable explanatory power for some situations. See, for example, Baerends (1985) on vertebrates and Maynard Smith and Reichart's (1984) study of spiders. Lorenz's concept of "action specific energy" building up over time and thresholds of response falling accordingly was attractive to behavior workers in the early days of ethology precisely because it seemed to model what they observed in nature. Deprived of suitable nest material a caged finch or ring dove will attempt to carry scraps of food, even its own feces to the empty nest site and perform the movements of building there. Now sometimes analysis of such situations has shown that what "switches off" the behavior is not its performance (as Lorenz's model suggested) but the animal's detection that a result has been achieved, i.e., in the example given here, it might be the presence of a nest at the site. Nevertheless, in the absence of such "consummatory stimuli" some central process must result in the compulsion – it is hard to

regard it otherwise – to nest build. Workers in what is now called "applied ethology" and concerned with the welfare of domestic animals have to face up to such issues all the time. Intensively reared chickens present many examples. Are hens distressed if they are unable to lay their eggs in a nest box, or dustbathe, or scratch for food? Certainly answers to questions of this type are not going to come from much of modern ethology. Domestic animals, removed from almost any trace of the environment in which their ancestors evolved, retain elements of what was adaptive behavior, and the associated motivational states. Applied ethologists try to put animals into situations where they can reveal their motivation by their choices, thus finding ways which enable them to express themselves and thereby improve their welfare.

The trouble is that the concept of an animal's "welfare" almost inevitably leads us to contemplate that, apart from its physical health and well-being, it may share with us those feelings which go with frustration and confinement. For us, powerful motivation is associated with emotion, emotion which has easily observable physiological consequences. Similar consequences are easily observed in animals too which raises all kinds of questions about their subjective experiences. By far from logical links I find myself thinking over a whole new body of modern research which concerns itself with complex cognitive capacities of animals and all the mental processes which might go with them. There is now much speculation and experiment directed towards the possibility that some animals have a mind with consciousness of their own existence and that of others outside themselves.

For ethologists the modern approach to these issues began with Don Griffin's (1976) book *The Question of Animal Awareness* (which may have been a deliberately provocative title) and a subsequent review (Griffin, 1978). These caused a considerable and rather uneasy stir amongst ethologists at the time. Of course Griffin was addressing issues which go much further back; the higher cognitive powers of animals and their subjective feelings were commonly assumed during the 19th century. However there was an almost complete rejection for most of the 20th especially amongst experimental psychologists for whom any trace of subjective thinking in regard to animals was anathema. Nevertheless Griffin's bold return to face issues which never go away struck a chord with some ethologists. It certainly emboldened them to undertake research which attempts to explore whether some animals have higher mental capacities. They see this approach as a direct extension of ethology itself, hence the title of Griffin's (1978)

review and the Festschrift Ristau (1991) edited for him which is called *Cognitive Ethology: The Minds of Other Animals*. This now comprises a very large literature and the best of it does strive to retain objectivity. Its proponents approach their research with Tinbergen's four questions firmly in mind. Unsurprisingly, the cluster of topics that comprise cognitive ethology attract much attention from those researching the welfare of domestic animals. Marian Dawkins (2006) provides a most valuable review which goes beyond just the welfare issues. The most difficult and the most contentious question remains that of animal consciousness. and, almost needless to say, the present position includes very extreme views on both sides.

I include cognitive ethology here because I cannot help wondering what Tinbergen himself would make of it, especially the debates around animal consciousness. Kruuk (2003) believes he would certainly *not* have approved and I agree with him absolutely. At the outset of *The Study of Instinct* (1951) Tinbergen dismisses any approach to subjective phenomena in animals, suggesting that, as it is impossible to observe them objectively, "it is idle either to claim or to deny their existence." Twelve years later in the Four Questions paper he sticks rigorously to his original definition of ethology as the objective study of the biology of behavior.

So perhaps there is one area of ethology which is going on into pastures new. No matter, the original four remain unchallenged. Although Medawar's rule applies and not all of them are equally easily accessible, they are nonetheless all equally important. This conclusion is developed and abundantly illustrated in the essays which make up this volume. The Maestro certainly *would* have approved for they show that his injunction retains its relevance and a fully rounded ethological approach remains as valuable as ever.

Aubrey Manning

Preface

This volume brings together a collection of papers written by contributors to a symposium entitled "Evolution, function, development, causation: Tinbergen's four questions and contemporary animal biology," held at the Institute of Biology, Leiden University, the Netherlands on 5 September, 2003. The symposium was organized by The Royal Dutch Zoological Society (KNDV) with the Dutch Society for Behavioural Biology (NVG), to commemorate the 40th anniversary of the publication of Niko Tinbergen's seminal paper "*On aims and methods of ethology*." Leiden was a fitting venue for the symposium, because Tinbergen held a chair there before he left in 1949 to become a demonstrator in the Department of Zoology at Oxford. Moreover, the symposium was held at the "van der Klaauw laboratory," and it was Professor Cornelis van der Klaauw who invited Konrad Lorenz to a symposium on "instinct" held in Leiden in November, 1936. That was the first time that Tinbergen and Lorenz met, a meeting that culminated in a life-long friendship. Indeed, Tinbergen's "aims and methods" paper was dedicated to Lorenz on the occasion of his 60th birthday.

In his paper, Tinbergen discussed the field of ethology, now usually known as behavioral biology, and defined it as "the biological study of behaviour." The "aims and methods" paper is best known for the identification of four major problems in the study of behavior: causation, development (ontogeny), function (survival value), and evolution. The main body of the paper comprises his views on each of these problems and, 40 years hence, is still a joy to read and has lost none of its brilliance. Tinbergen tackles difficult and sometimes controversial issues with wit and humor. In doing so, he set the agenda for animal behavior research that is still very much relevant in the 21st century. In fact, we would maintain that every student of animal behavior should attempt to grasp the message of this ground-breaking paper before

embarking on a research project. Tinbergen's aim with this paper was to "attempt an evaluation of the present scope of our science." He considered such an attempt worthwhile because "ethologists differ widely in their opinion of what their science is about." Indeed, in a different sense this still holds true today, in that many scientists studying topics closely related to the four major problems of behavioral biology probably do not consider themselves ethologists, but instead see themselves as, e.g., neurobiologists or ecologists. Indeed, Tinbergen himself already recognized the overlap between research fields, stating that "I have used the word 'Ethology' for a vast complex of sciences (…), such as certain branches of Psychology and Physiology." Perhaps one of the greatest challenges behavioral biology faces today is the integration of such widely diverging fields while maintaining the identity of "Behavioral Biology" as a research field.

Appropriately, the book opens with a facsimile of the classic paper by the "Maestro" – as Tinbergen was fondly known by his Oxford students; see Hans Kruuk's excellent biography *Niko's Nature* (2003). After a general introductory chapter by Hogan and Bolhuis, the following five chapters are concerned with Tinbergen's four questions. Hogan, Crews and Groothuis, Hogan and Bolhuis, Cuthill, and Ryan address Causation, Development, Function, and Evolution, respectively. These chapters clearly show how Tinbergen's ideas have inspired these authors and influenced their own thinking and research. Tinbergen readily acknowledged his debt to Julian Huxley for proposing causation, evolution, and survival value as the three main problems in biology, with Tinbergen adding development. The addition of development to Huxley's list of three suggests that Tinbergen thought it was an important problem in animal behavior. We agree – hence there are two chapters concerned with behavioral development, with the article by Crews and Groothuis addressing the topic of sexual and individual differentiation and the one by Hogan and Bolhuis providing a more general overview of developmental research since Tinbergen's paper. The chapter by Sherry concerns work involving an integration of Tinbergen's four questions. Finally, Bolhuis discusses some key issues in the debate that ensued after his critique of the integrative approach, and he evaluates recent relevant evidence bearing on this debate.

The symposium – and hence this volume – would not have been possible without the help of many different people. We are grateful to the board of Leiden University, to Frans Saris, then Dean of the Faculty of Natural Sciences, to the Scientific Director of the Institute of Biology,

Eddy van der Meijden, and to the current leader of the behavioral biology group at Leiden, Carel ten Cate, for their support and for hosting this meeting in their Institute. Thanks are due to the Netherlands Organization for Scientific Research (NWO) and to the Royal Netherlands Academy of Sciences for their generous support for the meeting. Also, we would like to thank our co-organizers, the Dutch Society for Behavioural Biology, and its former President, Dr. Menno Kruk. In addition, we would like to thank our fellow members of the Board of the Royal Dutch Zoological Society for their hard work in organizing the symposium: Johan van Leeuwen, Joris Koene, Thijs Zandbergen and particularly Evert Meelis; without his hard work and organizational skills, the symposium would not have been possible.

We are most grateful to the authors for their contributions. In addition, we thank Aubrey Manning – a leading figure in behavioral biology and a student of Niko Tinbergen – for writing a wonderful Foreword. We are extremely pleased that we could reprint the original Tinbergen paper, for which we are very grateful to Blackwell Publishing.

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