The Behavior of Animals

Mechanisms, Function, and Evolution

SECOND EDITION

Edited by
JOHAN J. BOLHUIS
LUC-ALAIN GIRALDEAU
JERRY A. HOGAN

WILEY Blackwell

the behavior of animals

MECHANISMS, FUNCTION, AND EVOLUTION

SECOND EDITION

EDITED BY JOHAN J. BOLHUIS, LUC-ALAIN GIRALDEAU AND JERRY A. HOGAN

WILEY Blackwell

This edition first published 2022

Edition History

John Wiley & Sons, Inc. (1e, 2004)

Registered Office(s)
John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA

Editorial Office
111 River Street, Hoboken, NJ 07030, USA

For details of our global editorial offices, customer services, and more information about Wiley products visit us at www.wiley.com.

Wiley also publishes its books in a variety of electronic formats and by print-on-demand. Some content that appears in standard print versions of this book may not be available in other formats.

A catalogue record for this book is available from the Library of Congress
Paperback ISBN: 9781119109501; ePub ISBN: 9781119109525; ePDF ISBN: 9781119109518.

Cover image: © Mike Truchon/Shutterstock
Cover design by Wiley

Set in 10/12.5pt Rotis Serif Std by Integra Software Services, Pondicherry, India

Contents

List of Illustrations

List of Tables

contributors

Professor Gregory F. Ball
Department of Psychology
University of Maryland
2141 Tydings Hall
7343 Preinkert Drive
College Park, MD 20742
USA
Professor Jacques Balthazart
University of Liege
GIGA Neurosciences
Quartier Hôpital
15 Avenue Hippocrate
Tour Pharmacie (Bat. B36, 1er étage)
B-4000 Liège
Belgium
Professor Johan J. Bolhuis
Cognitive Neurobiology
Department of Psychology
Utrecht University
PO Box 80.086
Yalelaan 2
3584 CM Utrecht

The Netherlands
Professor Gillian R. Brown
School of Psychology & Neuroscience
University of St. Andrews
South Street
St. Andrews, Fife, KY16 9JP
United Kingdom
Dr Harald Burghagen†
Universität Kassel
Fachbereich Naturwissenschaften
Abteilung Zoologie/Physiologie, Neurobiologie
Heinrich-Plett-Str. 40
D-34132 Kassel
Germany
Dr Catharine P. Cross
School of Psychology & Neuroscience
University of St. Andrews
South Street
St. Andrews, Fife, KY16 9JP
United Kingdom
Professor Dr Jörg-Peter Ewert
Universität Kassel
Fachbereich Naturwissenschaften
Abteilung Zoologie/Physiologie, Neurobiologie
Heinrich-Plett-Str. 40

D-34132 Kassel
Germany
Professor David Fraser
Animal Welfare Program
Faculty of Land and Food Systems
University of British Columbia
2357 Main Mall
Vancouver, British Columbia
Canada V6T 1Z4
Professor Luc-Alain Giraldeau
Institut national de la recherche scientifique
490, rue de la Couronne
Québec QC
Canada G1K 9A9
Professor Geoffrey Hall
Department of Psychology
University of York
York YO10 5DD
United Kingdom
Professor Robert A. Hinde, FRS†
St. John’s College
Cambridge CB2 1TP
United Kingdom
Professor Jerry A. Hogan
Department of Psychology

University of Toronto

Toronto, Ontario

Canada M5S 3G3

Professor Kimberly Kirkpatrick

Director, Cognitive and Neurobiological Approaches to Plasticity Center

Department of Psychological Sciences

Kansas State University

496 Bluemont Hall

Manhattan, KS 66506

USA

Professor Kevin N. Laland

Centre for Biological Diversity

School of Biology

University of St. Andrews

Sir Harold Mitchell Building

St. Andrews

Fife KY16 9TF

United Kingdom

Professor Ralph E. Mistlberger

Department of Psychology

Simon Fraser University

8888 University Drive

Burnaby, British Columbia

Canada V5A 1S6

Dr Anders Pape Møller

Directeur de Recherche

Ecologie Systématique Evolution

Université Paris-Saclay

CNRS, AgroParisTech

F-91405 Orsay Cedex

France

Professor Pierre-Olivier Montiglio

Groupe de Recherche en Ecologie Comportementale et Animale

Département des Sciences Biologiques

Université du Québec à Montréal

CP 8888, succursale centre-ville

Montréal, Québec,

Canada H3C 3P8

Professor Stephen Nowicki

Department of Biology

Duke University

130 Science Drive

Durham, NC 27708

USA

Professor Denis Réale

Groupe de Recherche en Ecologie Comportementale et Animale

Département des Sciences Biologiques

Université du Québec à Montréal

CP 8888, succursale centre-ville

Montréal, Québec,
Canada H3C 3P8
Professor Benjamin Rusak
Departments of Psychiatry and Psychology & Neuroscience
Dalhousie University
5909 Veterans Memorial Lane
Halifax, Nova Scotia
Canada B3H 2E2
Professor Michael J. Ryan
Department of Integrative Biology
University of Texas
Austin, TX 78712
USA
Professor William A. Searcy
Department of Biology
University of Miami
Coral Gables, FL 33124
USA
Professor David F. Sherry
Advanced Facility for Avian Research
Departments of Psychology and Biology
Western University
1393 Western Road
London, ON
Canada N6G 1G9

Professor Ian Tattersall
Division of Anthropology
American Museum of Natural History
New York, NY 10024
USA
Professor Daniel M. Weary
Animal Welfare Program
Faculty of Land and Food Systems
University of British Columbia
2357 Main Mall
Vancouver, British Columbia, Canada V6T 1Z4

foreword

ROBERT A. HINDE

Writing a foreword for such a stimulating series of chapters, which represent the state of animal behavior studies at this time, is a considerable responsibility. Perhaps I can do best by looking not forward, as might seem appropriate, but backward, and thus attempt to provide a context for the chapters that follow. Of course it cannot be a fully objective backward view, because I am looking from where I am now, and what I see is biased by my own experience. It is bound also to involve simplification. But I hope that it will provide a useful perspective.

In the early decades of the twentieth century, most studies of animal behavior fell into two groups. In one were the naturalists, mostly amateurs, without scientific pretensions but with a long tradition stretching back beyond the nineteenth century. In the other were the psychologists, producing an increasing body of data and theory mostly concerned with learning processes. Of course this dichotomy is already unjust and simplistic. Darwin himself could be called a naturalist; and an originator of learning theory (J.B. Watson) started from naturalistic observation. However, the work of the learning theorists, impressive in its own right, was not to have much impact on the traditions that led to the chapters in this book until much later.

Those traditions can be said to stem from the emergence of ethology in the 1930s. This was due to Lorenz, an Austrian MD with a PhD in comparative anatomy, and Tinbergen, a Dutch zoologist who moved to England a few years after the end of World War 2. Both men had a passionate interest

in animals, but this was expressed in very different ways. Lorenz kept a menagerie of diverse animals in his home, though also studying the local jackdaws and the semi-tame geese that he reared. Tinbergen, by contrast, was a dedicated field naturalist. Although he later worked with captive animals, it was always with problems that he had brought in from the field, and he liked best to be in the field himself. Tinbergen's first pupil, Baerends, suggested that the contrast lay in their attitudes to their subjects: Tinbergen saw himself as a nonparticipant hidden observer of animals, Lorenz as an adopted alien member and protector. Lorenz was a thinker who tried to relate or contrast his observations with current biological and philosophical views, while Tinbergen was much more empirical, an experimenter as well as an observer.

But both rejected the vitalist view that the phenomena of "instinct" were unanalysable and the misuse of the Gestalt concept to imply that analysis is unnecessary because the whole is always more than the sum of its parts. They also rejected the focus of most learning theorists on the input/output relations of the whole organism, with neglect of the "physiological machinery," and the sterility of the artificial environments used to study animals in many psychological laboratories.

The term "ethology" has been applied primarily to the work of students who, though differing widely in the problems they tackled, the methods they used, the level of analysis at which they worked, and the theoretical interpretations (if any) that they adopted, shared certain orienting attitudes. They insisted that the proper description of behavior is a necessary preliminary to its analysis; and that the behavior of an animal must be studied in relation to the environment to which it has become adapted in evolution. In addition they held that full understanding of behavior required knowledge not only of its development and causation but

also of its biological function and its evolution. The result was a vast amount of data on the behavior of animals and a certain amount of model-building to elucidate the mechanisms underlying behavior. In 1973 Lorenz and Tinbergen (together with von Frisch) were awarded the Nobel Prize in Physiology and Medicine.

Although ethology was primarily a European phenomenon in the early postwar years, two research workers in the USA were to have a considerable influence on its development, though in very different ways. Beach, a behavioral endocrinologist interested primarily in the hormonal control of sexual behavior, met Tinbergen in the USA and became a powerful supporter of ethology. Schneirla, a comparative psychologist working at the American Museum of Natural History, was intensely critical. One of his students, Lehrman, published a hard-hitting critique of ethology in 1953. There were three main issues. Lehrman and Schneirla took exception to Lorenz's distinction between "innate" and "acquired" behavior as neither empirically valid nor heuristically valuable. They objected to the energy model of motivation that Lorenz used, though this also came in for criticism from within ethology. And both were unhappy about the ethologists' tendency to apply concepts across a wide range of species differing in their levels of cognitive capacity. On their side, the ethologists felt that the adjective in "comparative psychology" was a sham, for contrasting distantly related species did not constitute comparison in a biological sense. They were also unhappy about the manner in which many comparative psychologists (though not so much those influenced by Schneirla) generalized on the basis of studies of a few mammalian species, predominantly the laboratory rat. For a while the differences between the two groups seemed irreconcilable. However, soon after his critique was published, Lehrman came to Europe and met a number of

European ethologists. Tinbergen, Lorenz, and Lehrman were all bird watchers, with a passionate enthusiasm for natural history. Lehrman had an infectious geniality, and friendships were soon made. This brought about a rapprochement between ethology and many of the members of Schneirla's group, a rapprochement that came not so much from academic discussion, but from the compatibility of personalities. On the issue of ontogeny, both sides changed their emphasis, the comparative psychologists withdrawing from their extreme emphasis on experience, and the differences in approach to the "comparative" issue were recognized.

It seems to happen not infrequently in the history of science that those regarded as originating a branch of science are subsequently seen to have been wrong in many of their generalizations. For instance, Freud (psychoanalysis) used a misleading model of motivation, Piaget (developmental psychology) based generalizations on a tiny sample of subjects, and Jeffreys (geophysics) refused to accept the evidence for continental drift. This was also the case with ethology. Many of the concepts that had been invaluable tools in the early days of ethology—the "innate releasing mechanism" and "fixed action pattern" for instance—were subsequently seen to involve oversimplification, and now seldom figure in the literature. But not surprisingly the change in outlook was not adopted simultaneously by all ethologists, and this led to some divisions within ethology. Lorenz, whose influence was particularly strong in Germany and the USA (through two research workers who had worked with him, Hess and Barlow), was slower to relinquish the innate/acquired dichotomy and energy model of motivation than Tinbergen and workers in the Netherlands and the UK.

An issue important for the nature/nurture debate became prominent in the 1960s. Both Tinbergen and Lorenz had

long argued on the basis of empirical evidence that species were specially equipped for particular learning tasks that were biologically important for them. Thorpe's book on birdsong, published in 1961, showed that the chaffinch was predisposed to learn the species-characteristic song pattern. A few years later, Rozin, Garcia, and others demonstrated a predisposition to avoid toxins in mammals. Such findings were directly contrary to the orientation of the learning theorists, who were searching for laws of learning valid for all species and all situations. It thus became apparent that, in many cases, what was "innate" was a predisposition to learn some things in particular contexts. This was to be of special importance for the study of human behavior.

Lorenz, originally a comparative anatomist, had used species differences and similarities as a taxonomic tool, and Tinbergen had always had an interest in the function of behavior. But, of the four problems of causation, development, function, and evolution, the main (though by no means the only) emphasis in ethology had been on the first two. In the 1970s this changed with the publication of Wilson's *Sociobiology*. The orienting attitudes of ethology continued but the motivational models disappeared and many of the old concepts fell into disuse. Behavioral ecology came to the fore, and new theoretical approaches made possible the study of function in a quantitative fashion. Data on foraging behavior were compared with the behavior to be expected (on certain assumptions that were not always made fully explicit) from an organism foraging with maximal efficiency. Later, attention turned to such issues as sperm competition and the role of fluctuating asymmetry. Hamilton's work on kin selection, first published in 1964 but neglected for much of the next decade, made possible a new approach to social behavior.

Game theory was recruited, and mathematical modeling came to be a much used tool in studies of behavior.

At the same time, the influence of ethology started to penetrate into a number of other disciplines. Lehrman and Rosenblatt, as well as Beach and his many students, adopted the orienting attitudes of ethology in their work on behavioral endocrinology. Von Holst had already studied the elicitation of fixed action patterns by brain stimulation through implanted electrodes, and the importance of using unconfined animals where possible was recognized by neurophysiologists. Bowlby, a psychoanalyst concerned with the effects of maternal deprivation in children, realized that what had been called the “irrational fears of childhood” (fear of falling, being alone, etc.) would have been highly adaptive in the environments in which early hominids lived, and an ethological element was incorporated in the “attachment theory” which he elaborated, an approach that was to become central in studies of child development. The study of human nonverbal communication profited from the input of ethologists, such as Eibl Eibesfeldt. The techniques of the behavioral ecologists were applied in studies of preindustrial human groups. An ethological influence is to be seen in studies of human personal relationships, and even in studies of religion and morality. Thus, while ethology as a set of concepts or as a theory of animal behavior has been largely superseded, the influence of its orienting attitudes has increased and is potent in other disciplines.

While behavioral ecology took center stage in the study of animal behavior, many felt it to be impoverished by the neglect of problems of development and causation. This book will go a long way toward setting the balance straight. Each of the four problems is covered, and the chapters

introduce the growing points in the study of animal behavior at the start of the twenty-first century.