

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

©2022 John Wiley & Sons, Inc.

*Edition History*

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

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by law. Advice on how to obtain permission to reuse material from this title is available at <http://www.wiley.com/go/permissions>.

The right of Johan J. Bolhuis, Luc-Alain Giraldeau, and Jerry A. Hogan to be identified as the author(s) of the editorial material in this work has been asserted in accordance with law.

*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](http://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.

*Limit of Liability/Disclaimer of Warranty*

The contents of this work are intended to further general scientific research, understanding, and discussion only and are not intended and should not be relied upon as recommending or promoting scientific method, diagnosis, or treatment by physicians for any particular patient. In view of ongoing research, equipment modifications, changes in governmental regulations, and the constant flow of information relating to the use of medicines, equipment, and devices, the reader is urged to review and evaluate the information provided in the package insert or instructions for each medicine, equipment, or device for, among other things, any changes in the instructions or indication of usage and for added warnings and precautions. While the publisher and authors have used their best efforts in preparing this work, they make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives, written sales materials, or promotional statements for this work. The fact that an organization, website, or product is referred to in this work as a citation and/or potential source of further information does not mean that the publisher and authors endorse the information or services the organization, website, or product may provide or recommendations it may make. This work is sold with the understanding that the publisher is not engaged in rendering professional

services. The advice and strategies contained herein may not be suitable for your situation. You should consult with a specialist where appropriate. Further, readers should be aware that websites listed in this work may have changed or disappeared between when this work was written and when it is read. Neither the publisher nor authors shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

*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

[Cover](#)

[Title page](#)

[Copyright](#)

[List of Contributors](#)

[Foreword by Robert A. Hinde](#)

[Preface](#)

[1. The Study of Animal Behavior](#)

[2. Stimulus Perception](#)

[3. Motivation and Emotion](#)

[4. Biological Rhythms and Behavior](#)

[5. Brain and Behavior](#)

[6. Hormones and Behavior](#)

[7. Development of Behavior](#)

[8. Learning and Memory](#)

[9. Animal Cognition](#)

[10. Applied Animal Behavior and Animal Welfare](#)

[11. The Function of Behavior](#)

[12. Mate Choice, Mating Systems, and Sexual Selection](#)

[13. Animal Personality, the Study of Individual Behavioral Differences](#)

[14. Animal Communication](#)

[15. Evolution of Behavior](#)

[16. The Evolution of Hominin Behavior](#)

[17. Evolutionary Approaches to Human Behavior](#)

[Name Index](#)

[Subject Index](#)

[End User License Agreement](#)

## List of Illustrations

### Chapter 2

[Figure 2.1 \(A\) The “reflection experiment.”...](#)

[Figure 2.2 Looking into a “black-box”:](#)...

[Figure 2.3 Configurational features in sign-stimuli....](#)

[Figure 2.4 The prey \(a, c\) vs. threat \(b, d\) configuration...](#)

[Figure 2.5 \(a\) Common toad displaying anti-predator behavior...](#)

[Figure 2.6 Male silk moth in alerted position, with combed...](#)

[Figure 2.7 Principles of scent detection in moths by...](#)

[Figure 2.8 Prey-feature analysis in common toads....](#)

[Figure 2.9 Neuroimaging toad’s visual system...](#)

[Figure 2.10 “Window hypothesis” of...](#)

[Figure 2.11 Visual processing streams in the...](#)

### Chapter 3

[Figure 3.1 Conception of behavior systems. Stimuli from the...](#)

[Figure 3.2 Lorenz’ model of motivation. The tap \(T\)...](#)

[Figure 3.3 Results of an experiment on guppy courtship.,...](#)

[Figure 3.4 Courtship and mating behavior of the...](#)

[Figure 3.5 Genetically featherless chicks...](#)

[Figure 3.6 Upright postures of the herring gull:...](#)

[Figure 3.7 "Waltzing" in a male...](#)

[Figure 3.8 Facial expressions of fear and aggression...](#)

## Chapter 4

[Figure 4.1 Rest-activity records from...](#)

[Figure 4.2 \(A\) Daily rhythm of core body...](#)

[Figure 4.3 Plasticity of rest-activity...](#)

[Figure 4.4 A phase-response curve \(PRC\)...](#)

[Figure 4.5 The rat brain and some areas...](#)

[Figure 4.6 The molecular basis of...](#)

## Chapter 5

[Figure 5.1 The facial ruff of the barn owl...](#)

[Figure 5.2 Acoustic measurements taken from microphones...](#)

[Figure 5.3 \(a\) Auditory neurons and neurons in the...](#)

[Figure 5.4 Electron micrograph of the head...](#)

[Figure 5.5 \(a\) The brain of the honeybee...](#)

[Figure 5.6 \(a\) Schematic sagittal view of the...](#)

[Figure 5.7 Juvenile zebra finch males were injected at...](#)

## Chapter 6

[Figure 6.1 Simplified metabolic pathway...](#)

[Figure 6.2 Schematic view of the endocrine...](#)

[Figure 6.3 Schematic model illustrating how a...](#)

[Figure 6.4 Reciprocal interactions between...](#)

[Figure 6.5 Schematic representation of the...](#)

## Chapter 7

[Figure 7.1 "Epigenetic landscape"...](#)

[Figure 7.2 Schematic illustration of two...](#)

[Figure 7.3 Zebra finch \(left\) and...](#)

[Figure 7.4 Stages in song development in...](#)

[Figure 7.5 Three ways in which experience,...](#)

[Figure 7.6 Mean preference scores...](#)

[Figure 7.7 Schematic drawings of the...](#)

## Chapter 8

[Figure 8.1 \(a\) Associative connections in...](#)

[Figure 8.2 \(a\) A typical color-based...](#)

[Figure 8.3 A serial position curve...](#)

[Figure 8.4 An experiment on chunking in...](#)

[Figure 8.5 A schematic of the experiment...](#)

[Figure 8.6 The effect of electroconvulsive...](#)

## Chapter 9

[Figure 9.1 \(a\) \*Ammophiia sabulosa\*,...](#)

[Figure 9.2 Greylag goose retrieving an egg. \(a\)...](#)

[Figure 9.3 Supernormal stimulus. Herring gull...](#)

[Figure 9.4 \(a\) Computational framework for the...](#)

[Figure 9.5 The lifetime of an engram. The formation...](#)

[Figure 9.6 Observational learning in doves...](#)

[Figure 9.7 Bumblebee using a string to...](#)

[Figure 9.8 Young capuchin monkey using a stick to...](#)

[Figure 9.9 \(a\) Female \*Portia fimbriata\*...](#)

[Figure 9.10 Neural encoding of regret in...](#)

## Chapter 10

[Figure 10.1 A dog in the Australian...](#)

[Figure 10.2 A moose \(\*Alces alces\*\)...](#)

[Figure 10.3 A serval \(\*Felis serval\*\)...](#)

[Figure 10.4 The price that caged American mink...](#)

[Figure 10.5 Calf demand for two types of...](#)

[Figure 10.6 Facial expressions of a newborn...](#)

[Figure 10.7 Cognitive bias in dairy calves...](#)

## Chapter 11

[Figure 11.1 The power expressed as multiples...](#)

[Figure 11.2 The results of Krebs et...](#)

[Figure 11.3 Results of Giraldeau and Kramer...](#)

[Figure 11.4 Red knots \(\*Calidris canutus\*\)...](#)

[Figure 11.5 The payoff functions of the...](#)

[Figure 11.6 The value of two habitats...](#)

[Figure 11.7 The university ducks experiment...](#)

## Chapter 12

[Figure 12.1 Mating system described as a...](#)

[Figure 12.2 Polygyny threshold model with...](#)

[Figure 12.3 Male mating success in...](#)

[Figure 12.4 Egg survival \(%\) in relation to...](#)

[Figure 12.5 Survival rate of male barn...](#)

[Figure 12.6 Sex ratio of zebra...](#)

## Chapter 13

[Figure 13.1 Representation of personality...](#)

[Figure 13.2 Illustration of the distribution...](#)

[Figure 13.3 The broccoli model of...](#)

[Figure 13.4 A\) Fitness increases with...](#)

[Figure 13.5 The relative importance...](#)

## Chapter 14

[Figure 14.1 Non-informational and...](#)

[Figure 14.2 A taxonomy in which signals...](#)

[Figure 14.3 Representative flight paths...](#)

[Figure 14.4 A graphical version of the handicap mechanism...](#)

[Figure 14.5 A graphical version of a differential benefits model...](#)

[Figure 14.6 Spectrograms of three...](#)

## Chapter 15

[Figure 15.1 \(\*left\*\) Darwin predicted that...](#)

[Figure 15.2 In the hypothetical phylogeny...](#)

[Figure 15.3 Mean body hue of males and...](#)

[Figure 15.4 \(\*top\*\) The dose-dependent...](#)

[Figure 15.5 \(left\)\(a\) Several ecological \(beak depth...](#)

[Figure 15.6 \(A\) The relationship between two...](#)

[Figure 15.7 \(top\) Weber's Law predicts...](#)

## Chapter 16

[Figure 16.1 Graphic representation of encephalization...](#)

[Figure 16.2 Reconstruction by the paleoartist Jay...](#)

[Figure 16.3 Side views of the toothrows of \(from top to bottom\):...](#)

[Figure 16.4 Highly approximate tentative genealogical...](#)

[Figure 16.5 Diorama at the American Museum of...](#)

[Figure 16.6 The "Nariokotome Boy"...](#)

[Figure 16.7 Two Acheulean implements from the type...](#)

[Figure 16.8 Three-quarter view of the most...](#)

[Figure 16.9 Reconstruction of the largest of the...](#)

[Figure 16.10 Comparison between a reconstructed...](#)

[Figure 16.11 The best preserved of the small...](#)

[Figure 16.12 Monochrome rendering of a...](#)

## Chapter 17

[Figure 17.1 Charles Darwin \(from Wikimedia Commons\)...](#)

[Figure 17.2 Frontispiece of Thomas...](#)

[Figure 17.3 John B. Watson \(from Wikimedia Commons\)...](#)

[Figure 17.4 Field studies have shown that...](#)

[Figure 17.5 Sarah Hrdy \(courtesy of Dan Hrdy\)...](#)

[Figure 17.6 The human archaeological record...](#)

[Figure 17.7 A\) In most mammals, the individuals...](#)

[Figure 17.8 In an experimental study, the...](#)

[Figure 17.9 Capuchin monkeys...](#)

## List of Tables

### Chapter 2

[Table 2.1 Invariance in Gestalt perception...](#)

[Table 2.2 From heterogeneous summation...](#)

[Table 2.3 Feature discrimination causes dishabituation.](#)

[Table 2.4 Command neuron hypothesis.](#)

[Table 2.5 Constants  \$\alpha\$  and  \$\beta\$ ...](#)

[Table 2.6 Minimum number of cell types...](#)

### Chapter 8

[Table 8.1 Experimental designs in classical conditioning](#)

### Chapter 10

[Table 10.1 Three Conceptions of Animal...](#)

### Chapter 11

[Table 11.1 Payoffs to the row player...](#)

## **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.

*Taeniopygia guttata*, [130](#), [151](#), [177](#), [358](#)

*Tamiasciurus hudsonicus*, [357](#)

*Tamias sibiricus*, [357](#)

*Tamias striatus*, [292](#)

taxonomy, [402](#)

testosterone, [137](#)

*Thamnophis sirtalis*, [161](#)

theory of mind, [244](#), [429](#), [479](#)–481

thermoreception, [13](#)

three-spined sticklebacks (*Gasterosteus aculeatus*), [358](#)

tonic immobility, [267](#)

tonotopical, [117](#)

topi (*Damaliscus lunatus*), [382](#)

topographic maps, [40](#)

túngara frogs (*Engystomops pustulosus*), [382](#)

túngara frogs (*Physalaemus pustulosus*), [418](#)

*Tyto alba*, [112](#)

ubiquitin, [125](#)

ultradian rhythmicity, [105](#)–106

“ultradian” rhythms, [79](#)

unconditional (or unconditioned) response, [199](#)

unconditioned stimulus (US), [121](#), [199](#)

*Uria lomvia*, [86](#)

vacuum activity, [58](#)

Vandenbergh effect, [153](#)

variable interval schedule, [201](#)

variable ratio schedule, [201](#)

variables correlations, [413](#)-416

ventral processing stream, [38](#)

vervet monkeys (*Cercopithecus aethiops*), [242](#)

visual cortex, [40](#), [187](#)

visual feature detection, [29](#)-37

- in amphibians, [29](#)-37
- brain structures, feature detection, [32](#)-33
- configurational object perception, [33](#)-34
- eye and brain, [31](#)-32
- features-relating-algorithm, configurational perception, [30](#)-31
- multimethodological analysis, [29](#)-37
- sensorimotor codes, [36](#)-37
- size constancy phenomenon, [34](#)-35
- species-specific feature detection, learning, [36](#)
- toad's visual system, [37](#)
- visuomotor access, [35](#)

visual imagination, [39](#), [40](#)

visual perception

- imagination, [39](#)-40

primate cortex, [37](#)-41

visual signals, [367](#), [381](#), [475](#)

vocal learning, [386](#)-387

vocal motor control, [126](#)-129

vocal motor memory, [130](#)-132

voles (*Microtus ochrogaster*), [347](#)

  

waggle dance, [87](#), [373](#), [385](#)

wasp, [223](#)-225

water striders (*Aquarius remigis*), [357](#)

waveform, [84](#), [115](#)

Weber's Law, [419](#), [420f](#)

well-being, [271](#)

Whitten effect, [153](#)

wild chimpanzees (*Pan troglodytes*), [261](#)

willow tits (*Poecile montanus*), [388](#)

working memory, [209](#)-211

- forgetting of items in, [211](#)-213
- versus* reference memory, [217](#)

  

*Xanthopan morganni praedicta*, [399](#)

*Xenopus laevis*, [159](#)

*Xiphophorus helleri*, [418](#)

zebra finches (*Taeniopygia guttata*), [130](#), [151](#), [177](#),  
[177f](#), [358](#)

zebrafish (*Danio rerio*), [269](#)

Zeitgeber, [82](#)

Zeitgedächtnis, [87](#)

*Zenaida macroura*, [239](#)

Zugunruhe, [238](#)