The Cambridge Handbook of Animal Cognition

This handbook lays out the science behind how animals think, create, calculate, and remember. It provides concise overviews on major areas of study, such as animal communication and language, memory and recall, social cognition, social learning and teaching, and numerical and quantitative abilities, as well as innovation and problem-solving. The chapters also explore more nuanced topics in greater detail, showing how the research was conducted and how it can be used for further study. The authors range from academics working in renowned university departments to those from research institutions and practitioners in zoos. The volume encompasses a wide variety of species, ensuring the breadth of the field is explored.

Allison B. Kaufman is a research scientist for the Department of Ecology and Evolutionary Biology at University of Connecticut, USA, and holds a Ph.D. in Neuroscience from the University of California at Riverside. She currently has a research program based at the University of Connecticut, where her main interests are in communication and innovative abilities in animals. She has written or edited five books, including Animal Cognition 101 with Erin Colbert-White.

Josep Call is a comparative psychologist specializing in primate cognition, Wardlaw Professor of Evolutionary Origins of Mind in the School of Psychology and Neuroscience at University of St Andrews, UK, and Director of the Budongo Research Unit at Edinburgh Zoo. He has also been an elected fellow of the American Psychological Association, the Cognitive Science Society, the Royal Society of Edinburgh, and the British Academy.

James C. Kaufman is Professor of Educational Psychology at the University of Connecticut, USA. He is the author or editor of more than forty-five books, including The Cambridge Handbook in Creativity, 2nd edition (Cambridge University Press, 2019). He has also published more than 400 papers and won many awards, including from Mensa, the American Psychological Association, and the National Association for Gifted Children.
For our boys, Jacob and Asher, who have tolerated and even enjoyed the
dogs, cats, parrot, millipedes, rabbits, iguana, chameleons, toad, hairless
rats, and hissing cockroaches over the years.

No, we’re not getting another dog.

—ABK and JCK
Contents

List of Figures, Tables, and Boxes  page x
List of Contributors  xiii
Acknowledgments  xviii

Introduction  1

Part I Communication and Language  3
1 Animal Communication Overview  5
FEDERICO ROSSANO AND STEPHAN P. KAUFHOLD
2 Communication in Ant Societies  36
BAPTISTE PIQUERET AND PATRIZIA D’ETTORRE
3 Symbolic Communication in the Grey Parrot  56
IRENE M. PEPPERBERG
4 Communication in Dogs and Wolves  74
KATALIN OLAH, JÓZSEF TOPÁL, AND ANNA GERGELY
5 Semantic Communication in Primates  100
KLAUS ZUBERBÜHLER

Part II Memory and Recall  115
6 Memory and Recall Overview  117
GEMA MARTÍN-ORDÁS
7 A Fish Memory Tale: Memory and Recall in Fish and Sharks  140
CATARINA VILA POUCA, LOUISE TOSETTO, AND CULUM BROWN
8 Memory in Hummingbirds  174
MARIA CRISTINA TELLO-RAMOS AND DAVID J. PRITCHARD
9 Event Memory in Rats  190
JONATHON D. CRYSTAL
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Authors</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Primate Recall Memory</td>
<td>Molly Flessert and Michael J. Beran</td>
<td>210</td>
</tr>
<tr>
<td></td>
<td><strong>Part III Social Cognition</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>11 Social Cognition Overview</td>
<td>Juan C. Gómez</td>
<td>223</td>
</tr>
<tr>
<td></td>
<td>12 Proximate and Ultimate Mechanisms of Cooperation in Fishes</td>
<td>Joachim G. Frommen and Stefan Fischer</td>
<td>225</td>
</tr>
<tr>
<td></td>
<td>13 Evolutionary and Neural Bases of the Sense of Animacy</td>
<td>Elena Lorenzi and Giorgio Vallortigara</td>
<td>272</td>
</tr>
<tr>
<td></td>
<td>14 Raven Social Cognition and Behavior</td>
<td>Thomas Bugnyar</td>
<td>295</td>
</tr>
<tr>
<td></td>
<td>15 Reciprocal cooperation – Norway rats ((\text{Rattus norvegicus})) as an example</td>
<td>Manon K. Schweinfurth</td>
<td>322</td>
</tr>
<tr>
<td></td>
<td>16 Exploring the Social Minds of Elephants</td>
<td>Elizabeth A. Krisch Pirutinsky and Joshua M. Plotnik</td>
<td>343</td>
</tr>
<tr>
<td></td>
<td>17 Dolphin Social Cognition</td>
<td>Adam A. Pack</td>
<td>362</td>
</tr>
<tr>
<td></td>
<td>18 Mirror Self-Recognition: Five Decades of Primate Research</td>
<td>James R. Anderson and David L. Butler</td>
<td>383</td>
</tr>
<tr>
<td></td>
<td><strong>Part IV Social Learning and Teaching</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 Social Learning and Teaching Overview</td>
<td>Rachel L. Kendal</td>
<td>415</td>
</tr>
<tr>
<td></td>
<td>20 Tandem Running Recruitment by (\text{Temnothorax}) Ants as a Model System for Social Learning</td>
<td>Takao Sasaki and Stephen C. Pratt</td>
<td>434</td>
</tr>
<tr>
<td></td>
<td>21 Fish Social Networks</td>
<td>Matthew J. Hasenjager and William Hoppitt</td>
<td>457</td>
</tr>
<tr>
<td></td>
<td>22 Social Learning in Birds</td>
<td>Victoria E. Lee, Alison L. Greggor, and Alex Thornton</td>
<td>486</td>
</tr>
<tr>
<td></td>
<td>23 Social Learning in Chimpanzees</td>
<td>Rachel S. Nelson, Erin C. Connelly, and Lydia M. Hopper</td>
<td>503</td>
</tr>
<tr>
<td></td>
<td><strong>Part V Numerical and Quantitative Abilities</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>24 Numerical and Quantitative Abilities Overview</td>
<td>Sarah T. Boysen</td>
<td>534</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chapter</td>
<td>Title</td>
<td>Authors</td>
<td>Page</td>
</tr>
<tr>
<td>---------</td>
<td>----------------------------------------------------------------------</td>
<td>----------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>25</td>
<td>Numerical Competence in Fish</td>
<td>Christian Agrillo and Maria Elena Mileto Petrazzini</td>
<td>580</td>
</tr>
<tr>
<td>26</td>
<td>Spatial–Numerical Association in Nonhuman Animals</td>
<td>Rosa Rugani and Orsola Rosa-Salva</td>
<td>602</td>
</tr>
<tr>
<td>27</td>
<td>Perceptual Categorization in Pigeons</td>
<td>Olga F. Lazareva</td>
<td>621</td>
</tr>
<tr>
<td><strong>Part VI Innovation and Problem-Solving</strong></td>
<td></td>
<td></td>
<td>637</td>
</tr>
<tr>
<td>28</td>
<td>Innovation and Problem-Solving Overview</td>
<td>Daniel Sol</td>
<td>639</td>
</tr>
<tr>
<td>29</td>
<td>General Intelligence (g) in Mice</td>
<td>Charles Locurto</td>
<td>653</td>
</tr>
<tr>
<td>30</td>
<td>Bowerbird Innovation and Problem-Solving</td>
<td>Jason Keagy</td>
<td>667</td>
</tr>
<tr>
<td>31</td>
<td>Parrot Innovation</td>
<td>Theresa Rössler, Berenika Mioduszewska, and Alice M. I. Auersperg</td>
<td>690</td>
</tr>
<tr>
<td>32</td>
<td>Innovation in Marine Mammals</td>
<td>Allison B. Kaufman</td>
<td>710</td>
</tr>
<tr>
<td>33</td>
<td>Innovation in Capuchin Monkeys</td>
<td>Eduardo B. Ottoni</td>
<td>721</td>
</tr>
<tr>
<td>34</td>
<td>Innovation and Problem-Solving in Orangutans</td>
<td>Anne E. Russon</td>
<td>733</td>
</tr>
<tr>
<td>35</td>
<td>Do Apes and Monkeys Know What They (Don’t) Know?</td>
<td>Heidi L. Marsh</td>
<td>755</td>
</tr>
<tr>
<td>36</td>
<td>Decision Making in Animals: Rational Choices and Adaptive Strategies</td>
<td>Francesca de Petrillo and Alexandra G. Rosati</td>
<td>770</td>
</tr>
</tbody>
</table>

*Index* 792
Figures, Tables, and Boxes

Figures

2.1 Simplified phylogenetic tree of the insect order *Hymenoptera*. page 37
2.2 The stridulatory organ of the ant *Neoponera apicalis*. 41
2.3 Trophallaxis and antennal boxing between two ants. 45
2.4 Gas-chromatogram showing the cuticular hydrocarbon profile of a *Lasius niger* queen. 48
3.1 (a) Occluded shapes (amodal completion) and (b) subjective (Kanizsa, illusory) shapes (modal completion). 58
3.2 Samples of Kanizsa figures, occluded figures, and probes presented to Griffin. Numbers are expected “x-corner” response. 61
5.1 The triangle of reference where a symbol is defined as “a thing that represents or stands for something else.” 101
7.1 Main mechanisms of regulation of memory investigated in fish. 151
8.1 A male rufous hummingbird feeding from an artificial flower. 177
8.2 To the left there is a four-panel graph representing the percentage of first visits made to each patch over five days by eight birds; to the right there is a diagram of the flower array. 183
9.1 Source memory is documented by a higher revisit rate to the chocolate replenishment location than to the nonreplenishment chocolate location. 193
9.2 A hypothetical representation of unbound features. 195
9.3 Bound episodic memories function to disambiguate multiple, interleaved study episodes. 196
9.4 Dissociating episodic item-in-context memory from familiarity cues. 198
9.5 Rats replay a stream of multiple episodic memories. 201
12.1 Examples for multifaceted cooperative interactions in fishes. 276
12.2 Typical helping behaviors in cooperatively breeding cichlids. 277
13.1 Schematic representation of the experimental procedure used to test spontaneous preference for face-like stimuli in chicks. 296
13.2 Examples of simple moving stimuli used for studying axis alignment. 301
13.3 Schematic representation of a point-light display with a person standing and shaking his left hand. 302
13.4 Schematic representation of the subcortical visual pathway
supposed to be involved in directing attention toward biologically
relevant stimuli in different vertebrates. 306
15.1 The three different decision rules involved in reciprocal help. 344
15.2 Food-exchange apparatus. 347
16.1 Asian elephant cooperation during a collaborative task
depicted from ground (1), aerial (2), and side (3) views. 365
16.2 An Asian elephant female at the Golden Triangle Asian
Elephant Foundation in Chiang Rai, Thailand touches a
nearby conspecific. 372
20.1 A tandem running pair, with the leader at the right and the
follower at the left, of *T. rugatulus*. 474
20.2 Part of a tandem running path by a leader (black) and
a follower (gray) (top) and their speed during the trip (bottom). 475
20.3 CCE in homing pigeons and ants. 478
21.1 Networks are composed of multiple nodes (often representing
individuals) that are connected by edges. 488
21.2 The core assumption underlying NBDA is that if a novel
behavioral trait, such as an extractive foraging technique or
knowledge of a profitable foraging patch, spreads through
social transmission, then this spread is expected to follow a
social network that reflects social learning opportunities. 492
21.3 An interaction network from Rosenthal et al. (2015). 495
25.1 Experimental apparatuses used to observe the spontaneous
behavior of *fish* in the presence of biologically relevant stimuli
differing in numerosity. 582
25.2 Experimental apparatuses used to study numerical abilities in
trained *fish*. 587
25.3 Blind Somalian cavefish can distinguish between two groups
of sticks that differ in numerosity in order to find food. 590
25.4 The solitaire illusion. 593
25.5 The future of numerical cognition studies in trained *fish*. 596
26.1 (a) Birds eye view of the apparatus used for training and testing.
(b) Representation of the test series in the orientation used for
the fronto-parallel test. 605
26.2 Birds eye view of the apparatus used for training and testing,
showing disposition of the elements with respect to the chick’s
starting position. 607
26.3 Schematic representation of the training set up. 612
26.4 Schematic representation of the training setup, with a single
central panel depicting twenty elements. 613
27.1 A schematic representation of a go/no-go task (left) and
forced-choice task (right). 623
27.2 Proportion of change from baseline rate to training rate during
extinction training. 626
27.3 Schematic representation of superordinate-level categorization through association with a common response. 630
28.1 The use of tools is one of the most sophisticated forms of innovation. 644
28.2 Innovations open the window to new ecological opportunities. 646
30.1 Bowers. 669
30.2 Bowerbird problem-solving tasks. 678
30.3 Bowerbird problem-solving ability predicts mating success and represents extreme selection on cognitive ability. 682
31.1 Cockatoo Figaro uses his tongue in a thumb-like fashion against his flexible upper beak. 692
34.1 Sif’s “tripod” hanging structure and rake use. 744
36.1 Measuring animal rationality. 774

Tables

4.1 Summary of the most important aspects of canine communication. 80
7.1 Summary information of studies testing memory retention in fish and elasmobranchs. 142
15.1 Overview of studies on reciprocal cooperation in Norway rats. 348
18.1 Summary of major research developments across five decades of research on mirror-image responses and MSR in nonhuman primates. 421
27.1 Studies of basic-level categorization in pigeons. 624
27.2 Experimental approaches used to establish features controlling pigeons’ categorical behavior. 627
29.1 Positive manifold in school performance, from Spearman (1904). 654
29.2 Correlation matrix for multidimensional aptitude battery. 655
29.3 Correlations for F2S & CD-1 mice. 657
29.4 First principal component characteristics for studies of individual differences in mice. 659
34.1 Provisional wild orangutan innovations. 737
35.1 Summary of empirical research conducted with primate species, investigating metacognitive abilities using the “uncertain” response, information-seeking method, or another method. References in bold indicate that the authors concluded that their subjects had shown evidence of metacognitive-like behavior. 761

Box

12.1 Cooperation in a nutshell 274
Contributors

CHRISTIAN AGRILLO
Department of General Psychology, University of Padova, Italy; and Padua Neuroscience Center, University of Padova, Italy

JAMES R. ANDERSON
Department of Psychology, Kyoto University Graduate School of Letters, Kyoto, Japan

ALICE M. I. AUERSPERG
Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

MICHAEL J. BERAN
Department of Psychology and Language Research Center, Georgia State University

SARAH T. BOYSEN
Comparative Cognition Project, Sunbury, OH; and Center for Animal Welfare Science, Department of Comparative Pathobiology, College of Veterinary Medicine, Purdue University, West Lafayette, IN

CULUM BROWN
Department of Biological Sciences, Macquarie University, 2109 NSW Australia

THOMAS BUGNYAR
Department of Behavioral and Cognitive Biology, University of Vienna

DAVID L. BUTLER
Cairnmillar Institute, Melbourne, Australia

ERIN CONNELLY
Lester E Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL, 60614
JONATHON D. CRYSTAL
Department of Psychological & Brain Sciences, Indiana University, Bloomington, IN, 47405-7007, USA

FRANCESCA DE PETRILLO
Institute for Advance Study in Toulouse, Université Toulouse 1 Capitole, Espanade de l’Université, 31080 Toulouse Cedex 06, France; and Department of Psychology, University of Michigan, 530 Church St, Ann Arbor, MI, 48109, USA

PATRIZIA D’ETTORRE
Laboratory of Experimental and Comparative Ethology (LEEC), University of Paris XIII, Sorbonne Paris Nord; and Institut Universitaire de France (IUF)

STEFFAN FISCHER
Mammalian Behaviour and Evolution Group, Institute of Integrative Biology, University of Liverpool, Leahurst Campus, Neston CH64 7TE, UK; Konrad Lorenz Institute for Ethology, University of Veterinary Medicine, Savoyenstrasse 1, 1160 Vienna, Austria; and Department of Behavioural and Cognitive Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

MOLLY FLESSERT
Department of Psychology and Language Research Center, Georgia State University

JOACHIM G. FROMMEN
Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland; and Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester, M15GD, UK

ANNA GERGELY
Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences, Budapest

ALISON L. GREGGOR
Institute for Conservation Research, San Diego Zoo Global, USA

MATTHEW J. HASENJAGER
Department of Biological Sciences, Royal Holloway, University of London

LYDIA M. HOPPER
Lester E Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL 60614

WILLIAM HOPPITT
Department of Biological Sciences, Royal Holloway, University of London
ALLISON B. KAUFMAN
Department of Ecology and Evolutionary Biology, University of Connecticut

JASON KEAGY
Department of Ecosystem Science and Management and , The Pennsylvania State University, University Park, PA, USA

RACHEL L. KENDAL
Durham Cultural Evolution Research Centre, Department of Anthropology, Durham University, UK

ELIZABETH A. KRISCH PIRUTINSKY
Department of Psychology, Hunter College, City University of New York, New York, NY 10065, USA

OLGA F. LAZAREVA
Department of Psychology and Neuroscience, Drake University

VICTORIA E. LEE
Centre for Ecology and Conservation, University of Exeter, UK

CHARLES LOCURTO
Department of Psychology, College of the Holy Cross, Worcester, MA 01610

ELENA LORENZI
Centre for Mind/Brain Sciences - University of Trento

HEIDI L. MARSH
George Brown College, Toronto, Canada

GEMA MARTIN-ORDAS
Division of Psychology, Faculty of Natural Sciences, University of Stirling, Scotland, FK9 4LA

MARIA ELENA MILETTO PETRAZZINI
School of Biological and Chemical Science, Queen Mary University of London, UK

BERENIKA MIODUSZEWSKA
Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria; and Max Planck Institute for Ornithology, Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany

RACHEL NELSON
Lester E Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL 60614; and The Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington DC 20052
List of Contributors

KATALIN OLÁH
MTA-Momentum Social Minds Research Group, Eötvös Loránd University, Budapest, Hungary

EDUARDO B. OTTONI
University of São Paulo, Institute of Psychology - Dept. of Experimental Psychology

ADAM A. PACK
Departments of Psychology and Biology, University of Hawaii at Hilo, Hilo, Hawaii; and The Dolphin Institute, Hilo, Hawaii

IRENE M. PEPPERBERG
Department of Psychology, Harvard University

BAPTISTE PIQUERET
Laboratory of Experimental and Comparative Ethology (LEEC), University of Paris XIII, Sorbonne Paris Nord

JOSHUA M. PLOTNIK
Department of Psychology, Hunter College, City University of New York, New York, NY 10065, USA

STEPHEN C. PRATT
School of Life Sciences, Arizona State University, Tempe AZ 85287, USA; and Center for Social Dynamics and Complexity, Arizona State University, Tempe AZ 85287, USA

DAVID J. PRITCHARD
School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK

ORSOLA ROSA-SALVA
Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy

ALEXANDRA G. ROSATI
Departments of Psychology and Anthropology, University of Michigan, 530 Church St, Ann Arbor, MI 48109, USA

THERESA RÖSSLER
Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria; and Department of Cognitive Biology, University of Vienna, Vienna, Austria

ROSA RUGANI
Department of General Psychology, University of Padova, Padova, Italy; and Department of Psychology, University of Pennsylvania, Philadelphia, PA, United States
ANNE E. RUSSON
York University, Toronto, Canada

TAKAO SASAKI
Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

MANON K. SCHWEINFURTH
School of Psychology and Neuroscience, University of St Andrews, KY16 9JP
St Andrews, Scotland

DANIEL SOL
CREAF-CSIC (Centre for Ecological Research and Applied Forestries),
Cerdanyola del Vallès, Catalonia E-08193, Spain

MARIA CRISTINA TELLO-ROMAS
School of Biology, University of St Andrews, Harold Mitchell Building,
St Andrews, Fife KY16 9TH, UK

ALEX THORNTON
Centre for Ecology and Conservation, University of Exeter, UK

JÓZSEF TOPÁL
Institute of Cognitive Neuroscience and Psychology, Research Centre for
Natural Sciences, Hungarian Academy of Sciences, Budapest

LOUISE TOSETTO
Department of Biological Sciences, Macquarie University, 2109 NSW
Australia

GIOVANNO VALLORTIGARA
Centre for Mind/Brain Sciences - University of Trento

CATARINA VILA POUCA
Department of Zoology, Stockholm University SE-106 91 Stockholm,
Sweden; and Behavioural Ecology Group, Wageningen University &
Research, Wageningen, The Netherlands

KLAUS ZUBERBUEHLER
Institute of Biology, University of Neuchatel, Switzerland & School of
Psychology and Neuroscience, University of St Andrews, Scotland (UK)
Acknowledgments

We are eternally grateful for the endless patience and understanding of Stephen Acerra, David Repetto, Matthew D. Bennett, and Emily Watton at Cambridge University Press. This book would never have happened without their guidance. We are also grateful to Alan S. Kaufman, Clare Mazur, and Genet Tulgetske for their help.