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978-0-521-02211-8 - Animal Traditions: Behavioural Inheritance in Evolution

Eytan Avital and Eva Jablonka

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Animal Traditions

Behavioural Inheritance in Evolution

Animal Traditions maintains that the assumption that the selection of genes supplies both a sufficient explanation of the evolution of behaviour and a true description of its course is, despite its almost universal acclaim, wrong. Eytan Avital and Eva Jablonka contend that evolutionary explanations must take into account the well-established fact that, in mammals and birds, the transfer of learnt information across generations is both ubiquitous and indispensable. The introduction of the behavioural inheritance system into the Darwinian explanatory scheme enables the authors to offer new interpretations for common behaviours such as maternal behaviours, behavioural conflicts within families, adoption and helping. This approach offers a richer view of heredity and evolution, integrates developmental and evolutionary processes, suggests new lines for research and provides a constructive alternative to both the selfish gene and meme views of the world. It will make stimulating reading for all those interested in evolutionary biology, sociobiology, behavioural ecology and psychology.

EYTAN AVITAL is a lecturer in Zoology in the Department of Natural Sciences at David Yellin College of Education in Jerusalem. He is a highly experienced field biologist, and has written one zoology text and edited several others on zoology and evolution for the Israel Open university.

EVA JABLONKA is a senior lecturer in the Cohn Institute for the History and Philosophy of Science and Ideas, at Tel-Aviv University. She is the author of three books on heredity and evolution, most recently *Epigenetic Inheritance and Evolution* with Marion Lamb.

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CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press

The Edinburgh Building, Cambridge CB2 2RU, UK

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

www.cambridge.org

Information on this title: www.cambridge.org/9780521662734

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First published 2000

This digitally printed first paperback version 2005

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

Library of Congress Cataloguing in Publication data

Avital, Eytan, 1951–

Animal traditions: behavioural inheritance in evolution / Eytan Avital and
Eva Jablonka.

p. cm.

Includes bibliographical reference.

ISBN 0 521 66273 7

1. Animal behavior. 2. Behavior evolution. 3. Behavior genetics I. Jablonka, Eva II.

Title

QL751 .A94 2000

591.5–dc21 00-037819

ISBN-13 978-0-521-66273-4 hardback

ISBN-10 0-521-66273-7 hardback

ISBN-13 978-0-521-02211-8 paperback

ISBN-10 0-521-02211-8 paperback

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To Marion and Silvi with love and gratitude

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Preface

This book is about the way in which the evolution of birds and mammals is affected by social learning and by the traditions formed by social learning. From observation and experiment, we know that higher animals can acquire information from or through the behaviour of others, and through their own behaviour they can transmit this information to the next generation. Variations in such socially acquired and transmitted behaviour-influencing information cannot be under direct genetic control, since animals with very similar genes can have, and pass on, very different behaviours and traditions. There is clearly another inheritance system, a behavioural system of information transmission, which is superimposed on the genetic system. Some years ago we decided that the evolutionary consequences of this additional tier of variation and inheritance were worth exploring, and set out to see how our view of the evolution of higher animals is altered by incorporating non-genetic behavioural inheritance and the traditions that it produces. This book is the outcome of that endeavour.

We found that adding the behavioural system of information transmission has some radical implications for the current gene-centred view of evolution. For example, the classical distinctions between development and evolution become very blurred. An animal tradition is the product of a historical, evolutionary process, yet it can be formed and transmitted only if it is actively constructed during the behavioural development of individuals and groups. Unlike genetic information, behavioural information must be used and displayed for it to be transmitted. The generation and transmission of learnt behaviours are therefore not independent of their development, since any change acquired during the development of a behaviour can be passed on. Consequently, evolutionary adaptations are not shaped exclusively by selective processes; the evolution of behavioural adaptations involves the inheritance of acquired characters.

In acknowledging the importance of behavioural inheritance, we reject the rigid gene-centred sociobiological view of evolution, which ignores the influence of habits and traditions. As we see it, any evolutionary interpretation of social behaviour requires a consideration of

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both genetic and 'cultural' factors. Variations in socially transmitted behaviours affect evolution in two ways: first, the variant behaviours are an additional source of raw material for selection; second, social behaviour forms part of the selective regime in which individuals live, learn and reproduce. Therefore, habits and traditions are not merely the products of evolution – they are also one of its major constructing agents.

In presenting our ideas, we have not attempted to provide a comprehensive review of animal social learning and cultural evolution, since they are subjects which, much to our delight, are reaching vast, textbook dimensions. Instead, we have explored the consequences of the two-tier thinking that we believe is necessary for the evolutionary interpretation of various types of behaviour – thinking that includes both the behavioural and the genetic inheritance systems. In most chapters, we start our discussion by presenting a description of real-life behaviour based on our own observations of animals, because we feel that such descriptions make the reading more enjoyable and introduce a social and ecological framework that makes the subsequent discussion easier to follow. To avoid the inevitable stumbling over unfamiliar Latin names, we use common species names throughout the book, but provide a detailed index of species at the end. We present many examples that portray the scope and breadth of animal traditions, and explain our reasons for believing that this is merely the tip of a large iceberg. We show that when we consider the exchange and the sharing of learnt information in an evolutionary framework, we are often compelled to change previous assumptions about the costs and benefits of the behaviour for the interacting partners, and hence change established evolutionary interpretations. We also illustrate how the different ways that information can be transmitted by the behavioural inheritance system – through two parents, through a single parent or through non-parents – may alter the manner and the direction in which evolution proceeds. We go on to argue that social learning and the establishment of traditions may lead to a shift in the level at which selection occurs, and sometimes to rapid and effective speciation. Finally, we examine the intricate and subtle ways in which learning and traditions affect the evolution of the genetic basis of learning and of morphological characters. The overall result is a picture of the evolution of animal behaviour that is driven and shaped by habits and traditions.

Although this book is mainly about birds and mammals, some aspects

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of the developmental approach we advocate are also relevant to invertebrates. The implications of the view we present also bear on how one sees the structure of the human mind, and how the developmental and evolutionary relationships between genes and behaviour are understood. These two problems are related, and are at present hotly debated. Our position, which we explain in the introductory chapters and return to in the final chapter, is that the facile assumption that many animal and human behaviours are underlain by pre-existing, specifically selected mental modules is often unfounded. The relationship between mind, behaviour and genes is usually a lot more subtle and circuitous than is assumed by most sociobiologists and evolutionary psychologists. The structure, the limits and the possibilities of the wide behavioural plasticity of birds and mammals have hardly been explored, and, although all behaviour has a genetic basis, the attempt to derive behaviours or mental states solely from pre-existing genetic programs is at best problematical, and at worse absurd.

Writing this book has been a very gratifying experience. We were encouraged by colleagues from our home institutions and from elsewhere. We are very grateful to the Wissenschaftskolleg in Berlin, which enabled E. J. to spend a year in a stimulating and challenging environment, and provided ideal working conditions. The discussions in the biology group, the excellent library services and the encouragement provided by the fellows and the staff of the Kolleg have been invaluable.

We were, in fact, extremely fortunate to encounter the scientific community at its best. Almost all of the very many individuals to whom we turned for material or advice have been enormously generous, often without knowing us previously. They devoted much of their time to our questions and requests, sent us papers and even books that we could not obtain, corresponded with us and helped us in every conceivable way. In this cynical age, it was a heart-warming experience. We have learnt and benefited enormously from the flood of material we received, although because of lack of space we could not incorporate all of it into the final manuscript. We are very grateful to all of them. In particular, we would like to thank the following friends, colleagues, students and former teachers for various forms of help, advice and encouragement: Israel Avital, Orit Avital, Zvi Atzmon, Carol Berman, Sharmila Choudhury, Yehuda Elkana, Rachel Galun, Lilach Gang, Dani Golani, J. Lee Kavanau, Mikhal Lederer, Yaron Lehavi, Alicia F. Lieberman, Shlomit Magen, Yoram Okhanuna, Laor Orshan, Craig Packer, Meir P. Pener,

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Frederick D. Provenza, Alexander F. Skutch, Iddo Tavory, Timothy H. Tear and Amotz Zahavi.

Special thanks are due to our colleagues and friends Evelyn Fox Keller, Simona Ginzburg, Claudia Goebel, Rainer Goebel, James Griesemer, Peter Hammerstein, Dan-Eric Nilsson, Ekkehart Schlicht and Eric Warrant, who each read one or more chapters of the book and gave us invaluable criticism, penetrating comments and a lot of encouragement. We thank our editor, Tracey Sanderson, for her help and patience through the gestation and delivery periods of this book. We also thank our mothers for the very valuable and long-lasting legacies they have transmitted to us. Silvi Fridman-Avital deserves special thanks for her competent editorial assistance, useful criticism of some of the chapters, and for the construction (along with Dror and Shakhaf) of a long-term, loving writing-niche for E. A. The greatest thanks go to our friend and colleague, Marion Lamb, without whom this book would never have seen the light of day. She read the whole book, scrutinised and sharpened our arguments, pointed out numerous inconsistencies and contradictions, and improved the English. It is to Marion and to Silvi that we dedicate this book.

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Acknowledgements

We are grateful to the following publishers, institutions and authors for permission to quote from their books or papers: Academic Press, for the quotation (p. 94) from C. M. Heyes' paper in *Animal Behaviour*, 1993; Bloomsbury for the quotation (p. 96) from R. Wrangham & D. Peterson's 1995 book, *Demonic Males*; Cambridge University Press for the quotation (pp. 320–1) from *Darwin's Biological Work* (ed. P. R. Bell, J. B. S. Haldane, P. Marler, H. L. K. Whitehouse & J. S. Wilkie, 1959); Sigmund Freud © Copyrights, the Institute of Psychoanalysis and the Hogarth Press for the quotation (p. 299) from the Standard Edition of *The Complete Psychological Works of Sigmund Freud*, 1952; Houghton Mifflin Company for the definition (p. 22) taken from *The American Heritage® Dictionary*, 3rd Edition, 1992; Oxford University Press for the quotations (pp. 248 and 369) from S. Asch's *Social Psychology* (1952), and the quotation (p. 181) from D. W. Mock & G. A. Parker's *The Evolution of Sibling Rivalry* (1997); Princeton University Press for the quotation (p. 227) from H. Kummer's (1995) book *In Quest of the Sacred Baboon*; Routledge for the quotation (p. 61) from H. Hendrichs's paper in *Evolution, Order and Complexity* (ed. E. L. Khalil & K. E. Boulding, 1996); the Royal Society of Medicine for the quotation (pp. 264–5) taken from J. B. Calhoun's paper in *Proceedings of the Royal Society of Medicine*, (1973); Robert Trivers for the quotation (p. 183), from his book *Social Evolution* (1985, Benjamin Cummings: Menlo Park, California); W. H. Freeman for the quotations (p. 25 and p. 358) from R. Dawkins' (1982) *The Extended Phenotype*; W. W. Norton & Co. Inc. for the quotation (p. 48) from J. B. Watson's 1924 book, *Behaviorism*.