PERSPECTIVES IN ETHOLOGY

Volume 7

Alternatives

CONTRIBUTORS

Janis Antonovics

*Department of Botany
Duke University
Durham, North Carolina 27706*

Anne Barrett Clark

*Kellogg Biological Station
Michigan State University
Hickory Corners, Michigan 49060*

John L. Craig

*Department of Zoology
University of Auckland
Auckland, New Zealand*

Timothy J. Ehlinger

*Kellogg Biological Station
Michigan State University
Hickory Corners, Michigan 49060*

Deborah M. Gordon

*Museum of Comparative Zoology
and Society of Fellows
Harvard University
Cambridge, Massachusetts 02138*

Ian G. Jamieson

*Department of Zoology
University of Auckland
Auckland, New Zealand*

Andrew P. King

*Department of Psychology
Duke University
Durham, North Carolina 27706*

Robert W. Mitchell

*Department of Psychology
Clark University
Worcester, Massachusetts 01610*

Nadav Nur

*Department of Biological Science
University of Stirling
Stirling FK9 4LA, Scotland*

J. G. Ollason

*Culterty Field Station
University of Aberdeen
Newburgh, Ellon
Aberdeenshire AB4 0AA, Scotland*

H. Ronald Pulliam

*Department of Zoology
University of Georgia
Athens, Georgia 30602*

Nicholas S. Thompson

*Departments of Psychology and Biology
Clark University
Worcester, Massachusetts 01610*

Marcy K. Uyenoyama

*Department of Zoology
Duke University
Durham, North Carolina 27706*

Meredith J. West

*Department of Psychology
University of North Carolina
Chapel Hill, North Carolina 27514*

A Continuation Order Plan is available for this series. A continuation order will bring delivery of each new volume immediately upon publication. Volumes are billed only upon actual shipment. For further information please contact the publisher.

PERSPECTIVES IN ETHOLOGY

Volume 7

Alternatives

Edited by

P. P. G. Bateson

*Sub-Department of Animal Behaviour
University of Cambridge
Cambridge, England*

and

Peter H. Klopfer

*Department of Zoology
Duke University
Durham, North Carolina*

PLENUM PRESS • NEW YORK AND LONDON

The Library of Congress has cataloged this title as follows:

Perspectives in ethology. — Vol. 1 — New York: Plenum Press, 1973–
v.: ill.; 24 cm.

Irregular.

Includes bibliographies and indexes.

Editors: v. 1— P.P.G. Bateson and P. H. Klopfer.

ISSN 0738-4394 = Perspectives in ethology.

1. Animal behavior—Collected works. I. Bateson, P. P. G. (Paul Patrick Gordon), 1938– . II. Klopfer, Peter H. [DNLM: W1 PE871AN]

QL750.P47

591.5'1—dc19

86-649219

AACR 2 MARC-S

Library of Congress

[8610]

ISBN-13: 978-1-4612-9015-5 e-ISBN-13: 978-1-4613-1815-6

DOI: 10.1007/978-1-4613-1815-6

© 1987 Plenum Press, New York

Softcover reprint of the hardcover 1st edition 1987

A Division of Plenum Publishing Corporation

233 Spring Street, New York, N.Y. 10013

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted
in any form or by any means, electronic, mechanical, photocopying, microfilming,
recording, or otherwise, without written permission from the Publisher

PREFACE

This volume is subtitled “Alternatives” because we wanted to devote at least a part of it to the alternative ways in which members of the same species behave in a given situation. Not so very long ago the supposition among many ethologists was that if one animal behaved in a particular way, then all other members of the same age and sex would do the same. Any differences in the ethogram between individuals were to be attributed to “normal biological variation.” Such thinking is less common nowadays after the discovery of dramatic differences between members of the same species which are of the same age and sex. Alternative modes of behavior, though now familiar, raise particularly interesting questions about current function, evolutionary history, and mechanism. Do the differences represent equally satisfactory solutions to a given problem? Are some of the solutions the best that those animals can do, given their body size and general condition? Is an alternative solution adopted because so many other individuals have taken the first? If so, do the frequencies reached at equilibrium depend on differential survival of genetically distinct types or do they result from decisions taken by individual animals? If the alternatives are induced during development, as are the castes of social insects, what is required for such triggering?

The questions about alternative ways of behaving are addressed in some of the chapters in this volume. However, other chapters have moved away from this theme and represent alternative modes of thinking about behavioral biology. In keeping with our intention, announced in the Preface to Volume 6 of *Perspectives in Ethology*, we have reverted to a more eclectic editorial policy. We have welcomed original essays that explored distinctive and even unpopular approaches to the subject. The

mathematician Anatole Holt used to declare that the duty of scientists was to create distorting lenses so that the world could be viewed from many different perspectives. We think he was right and believe that our subject, like others, can only benefit from the airing of heterodox views.

Perhaps the most contentious issue discussed by different authors in this volume is the approach to the current function of behavior and the implication that when a job is well done by an animal it represents "good design." In Chapter 1 Clark and Ehlinger examine functional explanations for individual differences, arguing that nonadaptive explanations cannot be tested. They proceed to develop a framework in which the occurrence or nonoccurrence of differences can be related to the life history and ecology of the species. Nur examines alternative functional explanations for variation in the clutch size of birds in Chapter 2. He favors the view that these differences represent the outcome of year-to-year fluctuations in selection pressure. Jamieson and Craig also consider an aspect of parental behavior in birds in Chapter 3. In dealing with parent-helping behavior, they reject direct functional explanations and suggest that the feeding of nestlings in communal breeders is maintained by the same mechanism that results in parents feeding their own young.

The next two chapters are concerned explicitly with evolutionary issues. In Chapter 4 Pulliam reexamines the old problem of whether population density is regulated by the behavior of individuals. He argues that such cases exist and do not present such a problem for evolutionary explanations in terms of individual selection as has sometimes been supposed in the past; they may be interpreted in terms of the benefits derived by each of the active agents in the population. In Chapter 5 Uyenoyama and Antonovics examine another controversial issue, namely the extent to which inbreeding may have certain benefits. In the zoological literature it is commonly supposed that inbreeding should be avoided under all circumstances. Yet many plants self-pollinate and others (along with some animals) cope well when practicing biparental inbreeding. A history of being purged of deleterious recessive genes may greatly reduce or even eliminate the costs of inbreeding while simultaneously enhancing the relative costs of outbreeding.

Chapters 6 and 7 are primarily concerned with developmental issues. King and West draw on their own extensive studies of the social development of cowbirds and consider the various ways in which behavior can be inherited. After examining the dynamics of development they are led by their evidence to reject Ernst Mayr's famous dichotomizing of behavior as being driven by either "open" or "closed" programs. Many similarities between offspring and parent may depend on imitation, which is the topic discussed by Mitchell in Chapter 7. He considers the approaches to the

subject by some great figures of the past and suggests that the differences between them can be reconciled within a scheme of nested levels. At the lowest level imitations are based on evolution and morphogenesis alone; at the next level they depend on perception and action. At the third level they depend on learning, at the fourth on self-awareness, and, finally, at the fifth on the awareness of another's awareness.

The last three chapters deal specifically with different approaches to the study of behavior. In Chapter 8 Gordon points out that, conventionally, group behavior has been inferred from the actions of individuals. Drawing on her own work on the group behavior of harvester ants, she suggests that it is both possible and desirable to measure the behavior of a group as an entity in its own right. In Chapter 9 Ollason adopts a line that will be unpopular among many behavioral ecologists since he attacks the optimal design approach, which has been so fashionable in the last few years. He argues that its application to animal behavior depends on circular reasoning. By contrast, Thompson makes a case for objective teleological approaches to function and "design," which he refers to as "teleonomic." However, he suggests that, in order to break the circularity in much current thinking, the evidence must be clearly distinguished from the evolutionary interpretations that are used to explain such evidence. We believe these last two chapters will perform a valuable service in sharpening thought about teleological approaches in the study of behavior.

The contributions to this volume deal with the alternative ways in which animals may behave and the alternative ways in which scientists seek to explain what they do. As for the future, we shall be happy to hear from those who have completed manuscripts and also those who have proposals for articles. Though we shall continue to develop particular themes through invited contributions, we believe that the strength of this series often lies in the chapters we had not anticipated.

P. P. G. Bateson
Sub-Department of Animal Behavior
University of Cambridge
Madingley, Cambridge CB 3 8AA
England

Peter H. Klopfer
Department of Zoology
Duke University
Durham, North Carolina 27706

CONTENTS

Chapter 1
PATTERN AND ADAPTATION IN INDIVIDUAL BEHAVIORAL DIFFERENCES
Anne Barrett Clark and Timothy J. Ehlinger

I.	Abstract	1
II.	Introduction	2
III.	Semantic Issues	5
IV.	The Occurrence and Form of Individuality	7
	A. Social Behavior	8
	B. Foraging Behavior	22
	C. Advantages and Disadvantages of Being Different	29
V.	Adaptation and the Process of Differentiation	31
	A. Introduction	31
	B. Stages and Shifting Characteristics	35
	C. Covert Differences and Threshold Effects	36
VI.	Acknowledgments	39
VII.	References	39

Chapter 2
ALTERNATIVE REPRODUCTIVE TACTICS IN BIRDS: INDIVIDUAL VARIATION IN CLUTCH SIZE
Nadav Nur

I.	Abstract	49
----	--------------------	----

II.	Introduction	50
	A. Individual Variation in Clutch Size	51
	B. Clutch Size: Proximal Influences	53
III.	Hypotheses to Account for Clutch Size Variation	54
IV.	Evaluation of the Evidence	57
	A. The Individual Optimization Hypothesis	57
	B. The Tradeoff Hypothesis	61
	C. The Fluctuating Selection Pressures Hypothesis	64
V.	Conclusions Regarding the Three Hypotheses	67
VI.	Discussion	70
	A. Why Should Selection Pressures Fluctuate?	70
	B. Implications: Life in a Fluctuating Environment	72
VII.	Acknowledgments	75
VIII.	References	76

Chapter 3

CRITIQUE OF HELPING BEHAVIOR IN BIRDS: A DEPARTURE FROM FUNCTIONAL EXPLANATIONS

Ian G. Jamieson and John L. Craig

I.	Abstract	79
II.	Introduction	80
III.	Criticisms and Alternatives	81
	A. How Is Helping Behavior Perceived?	81
	B. Control of Provisioning Behavior	82
	C. In What Contexts Is Provisioning Behavior Observed?	83
	D. Provisioning Behavior in Communal Breeders	85
	E. Development and Evolution of Communal Breeding	89
	F. How Is Provisioning Behavior Maintained in Communal Breeders?	91
IV.	Discussion	93
V.	Acknowledgments	95
VI.	References	96

Chapter 4

ON THE EVOLUTION OF DENSITY-REGULATING BEHAVIOR

H. Ronald Pulliam

I.	Abstract	99
II.	Introduction	100
	A. The Controversy over Group Selection	101

	B. Individual Selection and Individual Preferences	103
III.	The Haystack Model	104
IV.	Breeding Site Limitation	105
V.	Habitat Selection in the Nonbreeding Season	108
	A. Random Assignment	108
	B. Ideal Avoidance	111
	C. Ideal Assessment	112
	D. Ideal Dominance	113
	E. The Assessment Dominance Distribution (ADD)	114
VI.	Population Dynamics	115
	A. Density Dependence in Two Seasons	115
	B. Nest Site Selection and Geographic Range	117
VII.	Discussion of Model Assumptions	119
VIII.	Wynne Edwards Theory Reconsidered	121
IX.	Acknowledgment	122
X.	References	122

Chapter 5

THE EVOLUTIONARY DYNAMICS OF MIXED MATING SYSTEMS: ON THE ADAPTIVE VALUE OF SELFING AND BIPARENTAL INBREEDING

Marcy K. Uyenoyama and Janis Antonovics

I.	Abstract	125
II.	Introduction	126
III.	Determination of the Adaptive Value of Selfing	127
	A. Response of Characters Correlated with Selection	127
	B. Modification to Accommodate the Evolution of Transmission	128
	C. Inbreeding Depression and Reproductive Mode of Origin As Determinants of Tradeoffs in Offspring Number	132
	D. The Effect of Uniparental and Biparental Inbreeding on the Selective Advantage of Selfing	133
IV.	Three Regular Systems of Biparental Inbreeding	134
	A. Regular Systems of Inbreeding	134
	B. The Effect of Prior Inbreeding on the Condition Permitting the Increase of Selfing under Negligible Inbreeding Depression	135
	C. The Effect of Biparental Inbreeding on the Adaptive Value of Selfing in the Presence of Significant Inbreeding Depression	135

D.	A Summary of the Qualitative Effects of Biparental Inbreeding on the Evolution of Selfing	136
V.	Discussion	137
A.	Toward a Predictive Theory of Mating System Dynamics	137
B.	Genetic Variation in Reproductive Mode	138
C.	The Resemblance between Parents and Their Offspring	138
D.	Empirical Estimates of Tradeoffs in Offspring Number	139
E.	Long-Term and Short-Term Effects of Selfing on Progeny Variance	141
F.	The Effect of Selfing on Male Success	141
G.	Implications of Biparental Inbreeding for the Adaptive Value of Selfing	142
H.	Consequences of Environmentally Imposed Shifts in the Breeding System	142
I.	Summary	144
VI.	Appendix A	146
VII.	Appendix B	147
VIII.	Appendix C	148
IX.	Acknowledgments	149
X.	References	149

Chapter 6

THE EXPERIENCE OF EXPERIENCE: AN EXOGENETIC PROGRAM FOR SOCIAL COMPETENCE

Andrew P. King and Meredith J. West

I.	Abstract	153
II.	Introduction: The Bird of Paradox	154
III.	Methods of Inquiry: Functional Metrics of Communication	155
IV.	Male Inheritance: An Embarrassment of Riches?	159
V.	Female Cowbirds: Like Mother, Like Daughter	160
VI.	Male Modifiability: Behind Closed Doors	162
VII.	The Female: A Connoisseur of Fine Song	169
VIII.	Population Comparisons: The Perspective from the Prairie	171

IX. General Perspectives: Exogenetic Programs for Development	173
X. A Final Perspective: The Cowbird's Place in Nature's Gallery	178
XI. Acknowledgments	179
XII. References	179

Chapter 7

A COMPARATIVE-DEVELOPMENTAL APPROACH TO UNDERSTANDING IMITATION

Robert W. Mitchell

I. Abstract	183
II. Introduction	184
III. Baldwin, Morgan, Guillaume, and Piaget on Imitation	186
A. James Mark Baldwin	186
B. Conwy Lloyd Morgan	187
C. Paul Guillaume	189
D. Jean Piaget	191
E. Similarities and Differences	193
IV. The Definition of "Imitation"	194
V. The Levels of Imitation	200
A. First-Level Imitation	202
B. Second-Level Imitation	203
C. Third-Level Imitation	205
D. Fourth-Level Imitation	206
E. Fifth-Level Imitation	209
F. Clarifications	211
VI. Conclusion	211
VII. Acknowledgments	212
VIII. References	212

Chapter 8

THE DYNAMICS OF GROUP BEHAVIOR

Deborah M. Gordon

I. Abstract	217
II. Introduction	217
A. What Is Group Behavior?	217
B. Why Study Group Behavior?	219

III.	Investigating Group Behavior: An Example of the Approach	221
A.	The Daily Round As a Unit of Group Behavior	221
B.	The Individual in Group Context	223
C.	Dynamics of Group Behavior	224
IV.	Extending the Approach	227
V.	Acknowledgments	230
VI.	References	230

Chapter 9

ARTIFICIAL DESIGN IN NATURAL HISTORY: WHY IT'S SO EASY TO UNDERSTAND ANIMAL BEHAVIOR

J. G. Ollason

I.	Abstract	234
II.	Introduction: The Design Argument in Natural Theology	234
III.	Natural Selection As a Designer	240
IV.	Artificial Design: Synthesis and Analysis	244
V.	Apparent Design in Behavior: Optimal Foraging Theory	249
VI.	Conclusion	255
VII.	Acknowledgments	256
VIII.	References	256

Chapter 10

THE MISAPPROPRIATION OF TELEONOMY

Nicholas S. Thompson

I.	Abstract	259
II.	Introduction	259
III.	Teleonomy As an Antidote to Circular Reasoning	260
IV.	Psychology and the Concept of Objective Teleology	263
A.	Tolman's Purposive Behaviorism	263
B.	Hofstadter's Objective Teleology	264
V.	Biological Interpreters of Teleonomy	266
A.	Huxley and the Openbill's Open Bill	266
B.	Mayr and Determination by a Program	267
C.	George Williams's Natural Selection and Adaptation	268

Contents**xv**

D. Curio's Teleonomic Methodology	270
E. Pittendrigh, Reprise	271
F. Conclusion: The Biological Interpreters	271
VI. The Appropriate Use for "Teleonomy"	272
VII. Acknowledgments	273
VIII. References	273
 INDEX	 275