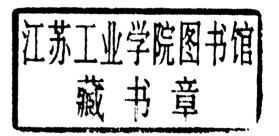


Keywords in Evolutionary Biology

EDITED BY

Evelyn Fox Keller and Elisabeth A. Lloyd



HARVARD UNIVERSITY PRESS
CAMBRIDGE, MASSACHUSETTS
LONDON, ENGLAND

Copyright © 1992 by the President and Fellows of Harvard College All rights reserved Printed in the United States of America Fourth printing, 1999

First Harvard University Press paperback edition, 1994

Library of Congress Cataloging-in-Publication Data

Keywords in evolutionary biology / edited by Evelyn Fox Keller and Elisabeth A. Lloyd.

p. cm.
Includes bibliographical references and index.

ISBN 0-674-50312-0 (cloth) ISBN 0-674-50313-9 (pbk.)

ISBN 0-674-50313-9 (pbk.)
1. Evolution (Biology)—Terminology.

I. Keller, Evelyn Fox, 1936 - . II. Lloyd, Elisabeth Anne.

QH360.6.K49 1992 575'.0014—dc20 92-8283

CIP

Designed by Gwen Frankfeldt

KEYWORDS IN EVOLUTIONARY BIOLOGY

ACKNOWLEDGMENTS

BY ITS very nature, the realization of this project has depended entirely on the good will and cooperation of our colleagues in evolutionary biology and the history and philosophy of science who agreed to write essays for it. Our first and primary debt is therefore to the contributors, especially for their patience with and responsiveness to our many requests. We are also indebted to Renee Courey for her good-humored, diligent, and vast help in compiling the bibliography; to Howard Boyer, Lindsay Waters, and Elizabeth Gretz at Harvard University Press for their unfailingly generous support and assistance in organizing and editing this manuscript; and to Jennifer Culbert for her help in the final stages of editing.

Permission has been granted by the University of California Press to reprint in "Competition: Current Usages" and "Fitness: Reproductive Ambiguities" portions of Evelyn Fox Keller, "Language and Ideology in Evolutionary Biology," in The Boundaries of Humanity: Humans, Animals, and Machines, ed. James Sheehan and Morton Sosna, pp. 90-95, 97-99, copyright © 1991 The Regents of the University of California; by Princeton University Press to reprint in "Natural Selection: Current Usages" material from chapters 1 and 2 of John A. Endler, Natural Selection in the Wild, copyright © 1986 Princeton University Press; by the American Statistical Association to reproduce in "Heritability: Some Theoretical Ambiguities" Figure 1 from Sewall Wright, "Statistical Methods in Biology," Journal of the American Statistical Association 26:155-163 (1931); by W. H. Freeman to reproduce in "Genotype and Phenotype" Figure 1-7 from D. T. Suzuki, A. J. F. Griffiths, J. H. Miller, and R. C. Lewontin, An Introduction to Genetic Analysis (New York: W. H. Freeman, 1981); and by the director of the Bancroft Library to quote in "Macromutation" from Sewall Wright's letter to Richard Goldschmidt, August 12, 1949, Goldschmidt Papers, Bancroft Library, University of California, Berkeley. Michael J. Donoghue acknowledges the grant support of the NSF (BSR-8822658) in the preparation of "Homology."

CONTRIBUTORS

PETER ABRAMS
Department of Ecology and
Behavioral Biology
University of Minnesota
Minneapolis, Minnesota

JOHN BEATTY Department of Ecology and Behavioral Biology University of Minnesota Minneapolis, Minnesota

DOUGLAS H. BOUCHER Appalachian Environmental Laboratory University of Maryland Frostburg, Maryland

PETER J. BOWLER
Department of Social Anthropology
The Queen's University of Belfast
Belfast, Northern Ireland

ROBERT N. BRANDON Department of Philosophy Duke University Durham, North Carolina

RICHARD M. BURIAN Department of Philosophy Virginia Polytechnic and State University Blacksburg, Virginia ROBERT K. COLWELL Department of Ecology and Evolutionary Biology University of Connecticut Storrs, Connecticut

HELENA CRONIN
Department of Philosophy
London School of Economics
London, England

JAMES F. CROW Genetics Department University of Wisconsin Madison, Wisconsin

JOHN DAMUTH Department of Biological Sciences University of California, Santa Barbara Santa Barbara, California

LINDLEY DARDEN Department of Philosophy University of Maryland College Park, Maryland

RICHARD DAWKINS Department of Zoology University of Oxford Oxford, England MICHAEL R. DIETRICH
Department of Philosophy, History and
Philosophy of Science Program
University of California, Davis
Davis, California

MICHAEL J. DONOGHUE Department of Ecology and Evolutionary Biology University of Arizona Tucson, Arizona

LEE A. DUGATKIN
Department of Biology
Mt. Allison University
Sackville, New Brunswick
Canada

JOHN DUPRÉ
Department of Philosophy
Stanford University
Stanford, California

JOHN A. ENDLER Department of Biological Sciences University of California, Santa Barbara Santa Barbara, California

MARCUS W. FELDMAN
Department of Biological Sciences
Stanford University
Stanford, California

KURT FRISTRUP Biology Department Woods Hole Oceanographic Institution Woods Hole, Massachusetts

DEBORAH M. GORDON Department of Biological Sciences Stanford University Stanford, California

STEPHEN JAY GOULD Museum of Comparative Zoology Harvard University Cambridge, Massachusetts JAMES R. GRIESEMER Department of Philosophy and Center for Population Biology University of California, Davis Davis, California

M. J. S. HODGE Philosophy Department Leeds University Leeds, England

DAVID L. HULL Department of Philosophy Northwestern University Evanston, Illinois

EVELYN FOX KELLER Program in Science, Technology, and Society Massachusetts Institute of Technology Cambridge, Massachusetts

DANIEL J. KEVLES Department of History California Institute of Technology Pasadena, California

MOTOO KIMURA National Institute of Genetics Mishima, Japan

PHILIP KITCHER
Philosophy Department
University of California, San Diego
La Jolla, California

JAMES G. LENNOX Department of History and Philosophy of Science University of Pittsburgh Pittsburgh, Pennsylvania

RICHARD C. LEWONTIN Museum of Comparative Zoology Harvard University Cambridge, Massachusetts

ELISABETH A. LLOYD Department of Philosophy University of California, Berkeley Berkeley, California JANE MAIENSCHEIN Department of Philosophy Arizona State University Tempe, Arizona

JUDITH C. MASTERS College of Science University of the Witwatersrand Wits. South Africa

ROBERT McINTOSH Biology Department University of Notre Dame Notre Dame, Indiana

DIANE PAUL
Department of Political Science
University of Massachusetts
Boston, Massachusetts

ROBERT J. RICHARDS Committee on the Conceptual Foundations of Science University of Chicago Chicago, Illinois

ALEXANDER ROSENBERG Department of Philosophy University of California, Riverside Riverside, California

MICHAEL RUSE
Departments of History
and Philosophy
University of Guelph
Guelph, Ontario
Canada

ELLIOTT SOBER Department of Philosophy University of Wisconsin Madison, Wisconsin HAMISH G. SPENCER Department of Zoology University of Otago Dunedin, New Zealand

PETER F. STEVENS
The Gray Herbarium of
Harvard University
Harvard University
Cambridge, Massachusetts

PETER TAYLOR
Program on Science, Technology
and Society
Cornell University
Ithaca, New York

MARCY K. UYENOYAMA Department of Zoology Duke University Durham, North Carolina

MICHAEL J. WADE Department of Biology University of Chicago Chicago, Illinois

MARY JANE WEST-EBERHARD Smithsonian Tropical Research Institute Balboa, Panama

MARY B. WILLIAMS Center for Science and Culture University of Delaware Newark, Delaware

DAVID SLOAN WILSON Department of Biological Sciences State University of New York Binghamton, New York

KEYWORDS IN EVOLUTIONARY BIOLOGY

Contents

Acknowledgments ix	
Contributors xi	
Introduction Evelyn Fox Keller and Elisabeth A. Lloyd	1
ADAPTATION: Historical Perspectives Richard M. Burian	7
ADAPTATION: Current Usages Mary Jane West-Eberhard	13
ALTRUISM: Theoretical Contexts Alexander Rosenberg	19
ALTRUISM: Contemporary Debates David Sloan Wilson and Lee A. Dugatkin	29
ALTRUISM: Some Theoretical Ambiguities Marcy K. Uyenoyama and Marcus W. Feldman	34
CHARACTER: Historical Perspectives Lindley Darden	41
CHARACTER: Current Usages Kurt Fristrup	45
COMMUNITY Peter Taylor	52

COMPETITION: Historical Perspectives Robert McIntosh	61
COMPETITION: Current Usages Evelyn Fox Keller	68
DARWINISM Michael Ruse	74
ENVIRONMENT Robert N. Brandon	8 1
EPISTASIS Michael J. Wade	87
EUGENICS Daniel J. Kevles	92
EVOLUTION Robert J. Richards	95
EXTINCTION John Damuth	106
FITNESS: Historical Perspectives Diane Paul	112
FITNESS: Theoretical Contexts John Beatty	115
FITNESS: Reproductive Ambiguities Evelyn Fox Keller	120
GENE: Historical Perspectives Jane Maienschein	122
GENE: Current Usages Philip Kitcher	128
GENETIC LOAD James F. Crow	132
GENOTYPE AND PHENOTYPE Richard C. Lewontin	137

GROUP SELECTION David Sloan Wilson	145
HERITABILITY: Historical Perspectives Michael J. Wade	149
HERITABILITY: Some Theoretical Ambiguities Marcus W. Feldman	151
HETEROCHRONY Stephen Jay Gould	158
HETEROSIS Diane Paul	166
HOMOLOGY Michael J. Donoghue	170
INDIVIDUAL David L. Hull	180
LAMARCKISM Peter J. Bowler	188
MACROMUTATION Michael R. Dietrich	194
MONOPHYLY Elliott Sober	202
MUTUALISM AND COOPERATION Douglas H. Boucher	208
NATURAL SELECTION: Historical Perspectives M. J. S. Hodge	212
NATURAL SELECTION: Current Usages John A. Endler	220
NEUTRALISM Motoo Kimura	225
NICHE: Historical Perspectives	231

NICHE: A Bifurcation in the Conceptual Lineage of the Term Robert K. Colwell	241
PARSIMONY Elliott Sober	249
PHENOTYPIC PLASTICITY Deborah M. Gordon	255
PROGRESS Richard Dawkins	263
RANDOM DRIFT John Beatty	273
RESOURCE Peter Abrams	282
SEXUAL SELECTION: Historical Perspectives Helena Cronin	286
SEXUAL SELECTION: Contemporary Debates Hamish G. Spencer and Judith C. Masters	294
SPECIES: Historical Perspectives Peter F. Stevens	302
SPECIES: Theoretical Contexts John Dupré	312
SPECIES: Current Usages Mary B. Williams	318
TELEOLOGY James G. Lennox	324
UNIT OF SELECTION Elisabeth A. Lloyd	334
References 343	
Index 395	

Introduction

Evelyn Fox Keller and Elisabeth A. Lloyd

UNLIKE poets, and even unlike most speakers of ordinary prose, scientists expect and indeed generally assume that their language is (or at least ought to be) both precise and clear. Scientific terms are intended to mean neither more nor less than what they say, and to say neither more nor less than what they mean. In the traditional model for scientific language, at least since Leibniz, Condillac, and Pascal, terminological ambiguity, uncertainty, and double entendre are generally seen as evidence of scientific inadequacy—as impediments simultaneously to progress and to truth and, accordingly, as impurities requiring removal. In the writings of the early positivists of this century, insistence on the univocality and unireferentiality of scientific language reached a new height. It might even be said that escape from the vagaries, opacity, and imprecision of ordinary language has become one of the primary functions of technical vocabulary.

The reality, of course, is somewhat different. It would be difficult to find or even to construct a sentence composed strictly of technical terms; in practice, scientific discourse is entirely suffused with ordinary language, with terms that bring with them all varieties of the imprecision scientists seek to avoid. More distressing yet, even technical terms turn out, far more often than we had hoped, to be plagued by the unruliness of ordinary language. By virtue of their dependence on ordinary language counterparts, technical terms carry, along with their ties to the natural world of inanimate and animate objects, indissoluble ties to the social world of ordinary language speakers. In this way, even carefully delineated technical

1. Gillian Beer cites the work of Leonard Bloomfield's Linguistic Aspects of Science (1939) as an instance of the linguistic positivism of the earlier part of this century. Bloomfield wrote, "It is our task to discover which of our terms are undefined or partially defined or draggled with fringes of connotation, and to catch our hypotheses and exhibit them by clear statements, instead of letting them haunt us in the dark" (quoted in Beer, 1987, p. 44).

terms are bedeviled by semantic shadows that insistently blur their borders. Words, even technical terms, have insidious ways of traversing the boundaries of particular theories, of historical periods, and of disciplines—in the process contaminating the very notion of a pure culture. They serve as conduits for unacknowledged, unbidden, and often unwelcome traffic between worlds. Words also have memories; they can insinuate a theoretical or cultural past into the present. Finally, they have force. Upon examination, their multiple shadows and memories can be seen to perform real conceptual work, in science as in ordinary language.² They help to hold worldviews together, to bridge disparate (even contradictory) concepts, to insulate us from problems we cannot solve. They work to help make arguments persuasive, even to turn arguments into "proofs." It is words that take us from the logic of a predicate calculus to the logos of scientific reasoning.

Over the past thirty years, the traditional model of scientific language so hopefully aspired to by working scientists has come under a barrage of criticism. Not only is the practice remote from the ideal, but significant challenges to even the possibility of such an ideal language have recently been posed by scholars in the history, philosophy, and sociology of science (see, e.g., Kuhn, 1962, 1979; Black, 1962, 1979; Hesse, 1966, 1980, 1985; Rorty, 1985; Beer, 1983). Early on, Thomas Kuhn focused attention on the importance of (generally unconscious) changes in the meaning of scientific terms and showed how such changes can signal the profound shifts in worldviews that we associate with scientific revolutions. For Kuhn, as for others, this recognition provided a starting point for more intensive subsequent investigations into the complex (even tortured) relations between language and "nature." The possibility of the traditional goal of univocality and precision for scientific language recedes yet further if one believes that meanings do not simply change, but, in a certain sense, accumulate—"carry[ing] the mark of the historical (sedimented) circumstances of their origin and use in ever new ways" (Edie, 1976, pp. 154-158; see also Carlisle, 1980).

In parallel (and virtual synchrony) with Kuhn, Max Black made an important contribution from a somewhat different perspective to the view of scientific language as "open rather than closed." By calling philosophi-

2. See, e.g., the discussion of the concept of "normal" in Ian Hacking, The Taming of Chance (1990). Hacking writes: "The word [normal] is also like a faithful retainer, a voice from the past. It uses a power as old as Aristotle to bridge the fact/value distinction, whispering in your ear that what is normal is also right. But also . . . , it has become a soothsayer, teller of the future, of progress and ends . . ." (pp. 160–161). And finally, "The normal stands indifferently for what is typical, the unenthusiastic objective average, but it also stands for what has been, good health, and for what shall be, our chosen destiny. That is why the benign and sterile-sounding word 'normal' has become one of the most powerful ideological tools of the twentieth century" (p. 169).

cal attention to the similarities between models and metaphors, Black (1962) provided a basis for regarding the use of metaphor in the construction of scientific theories as beneficial. This initial argument for the scientific value of linguistic "open-endedness" (such as that found in the use of metaphors) has since been considerably extended by others, especially by Mary Hesse (1966, 1980, 1985). Finally, and most recently, the influence of critical theory (or deconstruction) has become detectable in discussions of language and science as authors such as Gillian Beer and Richard Rorty have tentatively begun to argue for the same kind of conceptual productivity for ambiguity (or semantic polysemy)³ in scientific texts as was earlier argued for in literary texts.

Yet throughout all such efforts to undermine our traditional conception of a clear demarcation between scientific and ordinary or literary language. one crucial distinction remains relatively intact. Although it may not be possible, or even wholly desirable, to achieve a fixed meaning for scientific terms, the effort to "control and curtail the power of language" remains a significant feature of scientific activity (Beer, 1987, p. 42). The very extent to which scientists (far more than speakers of ordinary language) aim at a language of fixed and unambiguous meanings constitutes, in itself, one of the most distinctive features of their enterprise. And even though never quite realizable, this effort to control the vicissitudes of language, like the commitment to objectivity, reaps distinctive cognitive benefits. The same effort also reaps distinctive social benefits, on which at least some of the cognitive benefits depend. It especially serves to delineate a disciplinary and theoretical community, a community whose participants can be identified by their tacit agreement to abide by local conventions that restrict the range of possible meanings and, hence, stabilize the discourse. Because of the abiding commitment of working scientists to precision and clarity. to fixed meaning, the elaboration of prevailing instabilities (or multiplicities) of meaning attempted here will be of value to scientists themselves. We have chosen to concentrate on evolutionary biology for the simple reason that the borders between subdisciplines in this field are less well drawn than in many other disciplines, and the conventions necessary to stabilize meaning are correspondingly less clearly established. It is because of their commitment to restabilizing their own discourse that scientists working in this field need to be able to identify the domains where meanings are unstable.

Accordingly, our goal in this book has been to identify and explicate those terms in evolutionary biology that, though commonly used, are plagued in their usage by multiple concurrent and historically varying

^{3.} Arguments had earlier been extended for the rhetorical (rather than conceptual) productivity of ambiguity in scientific language (see, e.g., Robert Young's paper, "Darwin's Metaphor: Does Nature Select?" in Young, 1985), but just how sharply the distinction between rhetorical and conceptual can be maintained remains a question for consideration.

meanings. Our choice of the term "keywords" is thus indebted to Raymond Williams, for it was he who first used it in this particular sense and who first alerted us to the social, political, and intellectual value of exploring the multiple and shifting meanings of familiar terms. Williams' Keywords (1976) was intended primarily for social and intellectual historians; this book, by contrast, is intended as much for scientists and philosophers actually working in the field of evolutionary biology as it is for historians and sociologists of science. These two groups of readers, however, will surely use the book in different ways.

The relevance of this project to historians of science interested in the cognitive evolution of scientific theories (that is, in the history of ideas) will be evident. But it is as a resource for the social history of science that this project bears its closest resemblance to Williams' own work on "keywords." Williams' project grew out of what he saw as a problem of vocabulary: "the available and developing meanings of known words, which needed to be set down; and the explicit but as often implicit connections which people were making, in what seemed to me . . . particular formations of meaning." He wrote:

Keywords are significant, binding words in certain activities and their interpretation; they are significant, indicative words in certain forms of thought. Certain uses bound together certain ways of seeing culture and society, not least in these two most general words [i.e., culture and society]. Certain other uses seemed to me to open up issues and problems, in the same general area, of which we all needed to be very much more conscious.

Williams is a cultural historian; accordingly, he is primarily interested in "keywords" as fruitful indicators of social patterns and patterns of social change. As historians and philosophers of science, however, our interest in "keywords" is primarily as indicators of patterns of scientific meaning and of changes over time in the ways that particular scientific meanings have been structured. Attending to the multiple meanings of key terms provides a lens through which it is possible not only to understand better what is at issue in particular scientific debates but also to scrutinize the very structure of the arguments under debate. Such a lens enables an exploration of the historically evolving field of meanings from which these arguments draw and on which they depend. Gould's essay on "heterochrony," Damuth's on "extinction," Donoghue's on "homology," and Stevens' on "species" all provide good examples of such analyses.

In no case, however, and especially not in evolutionary biology, is the field of meanings on which scientific representations of nature draw strictly scientific. Indeed, it is precisely because of the large overlap between forms of scientific thought and forms of social thought that "keywords"—terms whose meanings chronically and insistently traverse the boundaries between ordinary and technical discourse—can serve not simply as indi-