

The American Naturalist

Volume 135, Number 1
January 1990
Established 1867

QH
1
A5

THE AMERICAN NATURALIST

ISSN 0003-0147

Marcus W. Feldman, *Editor*

Paul R. Ehrlich, *Senior Associate Editor*

Harold A. Mooney, *Senior Associate Editor*

Jonathan Roughgarden, *Senior Associate Editor*

Peter M. Vitousek, *Senior Associate Editor*

Ward B. Watt, *Senior Associate Editor*

Jean Doble McIntosh, *Managing Editor*

The American Naturalist is published monthly by The University of Chicago Press, 5720 S. Woodlawn Avenue, Chicago, Illinois 60637. Manuscripts and editorial correspondence should be addressed to The Editor, *The American Naturalist*, Department of Biological Sciences, Stanford University, Stanford, California 94305. A page of advice to authors may be found in this issue. Copy editor: Teresa Carson; editorial assistant: Leanne Grega Simmons.

Subscription to the journal does not require membership in the American Society of Naturalists. Subscriptions to *The American Naturalist* may be ordered from, and remittance should be made payable to, *The American Naturalist*, The University of Chicago Press, Journals Division, P.O. Box 37005, Chicago, Illinois 60637. Subscription rates, U.S.A.: institutions, 1 year \$130.00; individuals, 1 year \$50.00; students, 1 year \$37.00 (letter from professor must accompany subscription). Other countries: add \$12.00 for each year's subscription to cover postage. Single-copy rates: institutions, \$11.00; individuals, \$4.75. Japanese subscription agent: Kinokuniya Company Ltd. Reprinted volumes 1–10 available from Walter J. Johnson, Inc., 355 Chestnut Street, Norwood, New Jersey 07648. Volumes available in microfilm from University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106; in microfiche from Johnson Associates, P.O. Box 1017, Greenwich, Connecticut 06830.

For change of address, please notify the Press and local postmaster immediately, providing both the old and new addresses. Allow four weeks for change. Postmaster: send address changes to *The American Naturalist*, The University of Chicago Press, Journals Division, P.O. Box 37005, Chicago, Illinois 60637.

Copying beyond fair use: The code on the first page of an article in this journal indicates the copyright owner's consent that copies of the article may be made beyond those permitted by Sections 107 or 108 of the U.S. Copyright Law provided that copies are made only for personal or internal use, or for the personal or internal use of specific clients, and provided that the copier pay the stated per-copy fee through the Copyright Clearance Center, Inc., Operations Center, 27 Congress Street, Salem, Massachusetts 01970. To request permission for other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale, kindly write to Permissions Department, The University of Chicago Press, 5801 S. Ellis Avenue, Chicago, Illinois 60637.

Articles appearing in this journal are indexed in *Environmental Periodicals Bibliography*.

The paper used in this publication meets the minimum requirements of American National Standard for Information Sciences—Permanence of Paper for Printed Library Materials. ANSI Z39.48-1984. ©™

Second-class postage paid at Chicago, Illinois, and at additional mailing office.
© 1990 by The University of Chicago. All rights reserved. PRINTED IN U.S.A.

AMERICAN SOCIETY OF NATURALISTS

The American Naturalist is the official journal of the American Society of Naturalists. It is the Society's objective to advance and diffuse the knowledge of organic evolution and other broad biological principles so as to enhance the conceptual unification of the biological sciences. Membership in the Society is open to persons who have shown interest in its purposes by continued publication of papers of scholarly value. Inquiries regarding new membership should be addressed to Dr. Barbara Bentley, Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794.

All inquiries regarding current journal subscriptions or American Society of Naturalists dues should be directed to The University of Chicago Press, Journals Subscription Department, P.O. Box 37005, Chicago, Illinois 60637, (312) 753-3347.

Executive Committee, 1990

	Years to Serve*
Dr. Lee Ehrman, President Division of Natural Sciences State University of New York, Purchase	1990
Dr. John A. Endler, Vice-President Department of Biological Sciences University of California, Santa Barbara	1990
Dr. Barbara Bentley, Secretary Department of Ecology and Evolution State University of New York, Stony Brook	1989-1991
Dr. Victoria L. Sork, Treasurer Department of Biology, University of Missouri-St. Louis	1990-1992
Dr. James H. Brown, President-Elect Department of Biology, University of New Mexico	1991
Dr. Leslie Real, Vice-President-Elect Department of Zoology, North Carolina State University	1991
Dr. David Wake, Past President Museum of Vertebrate Zoology, University of California, Berkeley	1989
Dr. Thomas Eisner, Past President Section of Neurobiology and Behavior, Cornell University	1988
Dr. Wyatt W. Anderson, Past President Department of Genetics, University of Georgia	1987
Dr. Philip W. Hedrick, Past Secretary Department of Biology, Pennsylvania State University	1986-1988
Dr. Henry M. Wilbur, Past Treasurer Department of Zoology, Duke University	1987-1989
Dr. Marcus W. Feldman, Editor Department of Biological Sciences, Stanford University	1984-1990

* Indicates years of tenure of principal office, not of membership in executive committee.