

Editor-in-Chief Professor William G. Hill **Reviews Editor Professor Charles Godfray Publishing Editor** Claire Rawlinson

Editors: Professor Elizabeth Adkins-Regan

Professor Spencer Barrett Professor Nigel Bennett Professor Anne Magurran **Professor Paul Rainey** Professor Nils Chr. Stenseth

Editorial Board

W. G. Hill, Editor-in-Chief, School of Biological Sciences, University of Edinburgh E. Adkins-Regan, Editor, Department of Psychology, Cornell University S. Barrett, Editor, Department of Ecology

A. Magurran, Editor, Gatty Marine Laboratory, University of St Andrews

A. Magurran, Editor, Gatty Marine Laboratory, University of St Andrews

P. Rainey, Editor, School of Biological Sciences, University of Auckland N. Chr. Stenseth, Editor, Centre for Ecological and Evolutionary Synthesis (CEES), University

C. Godfray, Reviews Editor, Department of Zoology, University of Oxford

J. Avise, Department of Ecology and Evolutionary Biology, University of California M. Beaumont, School of Animal & Microbial

Sciences, University of Reading A. Bennett, School of Biological Sciences, University of Bristol

S. Bonhoeffer, Department of Ecology and Evolution, ETH Zurich

K. Boomsma, Department of Population

Ecology, University of Copenhagen P. Brakefield, Institute of Biology, Leiden University

R. Bshary, Institute of Zoology, University of Neuchâtel

P. Butler, School of Biological Sciences,

University of Birmingham
G. Carvalho, School of Biological Sciences,
University of Wales, Bangor
D. Charlesworth, Institute of Cell, Animal

and Population Biology, University of Edinburgh
M. Chase, Jodrell Laboratory, Royal Botanic

Gardens, Kew
R. L. Cifelli, Department of Zoology and
School of Geology and Geophysics, University of Oklahoma

N. S. Clayton, Department of Experimental Psychology, University of Cambridge

J. Cohen, Center for the Study of Brain, Mind and Behavior, Princeton University

T. Collett, Sussex Centre for Neuroscience, University of Sussex

D. Coltman, Department of Biological Sciences, University of Alberta

T. Coulson, Department of Biological Sciences,

Imperial College at Silwood Park

G. Cowlishaw, Institute of Zoology,

University of Cambridge

M. Dawkins, Department of Zoology, University of Oxford

M. Doebeli, Department of Zoology, University of British Columbia

R. Dunbar, School of Biological Sciences,

University of Liverpool
C. G. Faulkes, School of Biological Sciences,
Queen Mary, University of London
N. Franks, School of Biological Sciences,

University of Bristol

M. Gage, School of Biological Sciences, University of East Anglia

K. Gaston, Department of Animal and Plant Sciences, University of Sheffield A. Grafen, Department of Zoology, University of Oxford R. Gray, Psychology Department, University of Auckland

L. Harder, Department of Biological Sciences, University of Calgary
J. A. P. Heesterbeek, Department of Farm Animal Health, University of Utrecht
R. Hoelzel, Department of Biological Sciences, University of Durham

P. Holland, Department of Zoology,

University of Oxford

J. Koella, Faculty of Life Sciences,
Imperial College London

L. Kruuk, Institute of Cell, Animal and Population Biology, University of Edinburgh K. Lessells, Department of Animal Population

Biology, Netherlands Institute of Ecology B. Levin, Department of Biology, **Emory University**

S. P. Long, Department of Plant Biology, University of Illinois

E. Martins, Center for the Integrative Study of Animal Behavior, Indiana University

N. Metcalfe, Division of Environmental & Evolutionary Biology, University of Glasgow

A. Minetti, Institute of Human Physiology I, University of Milan B. Neff, Department of Biology, University

of Western Ontario

B. Okamura, School of Animal and Microbial Sciences, University of Reading

A. Orr, Department of Biology, University of Rochester

I. Owens, Department of Biological Sciences, Imperial College at Silwood Park
M. Pagel, School of Animal and Microbial Sciences, University of Reading
A. Read, Institute of Cell, Animal and

Population Biology, University of Edinburgh

M. Rees, Department of Animal and Plant Sciences, University of Sheffield

J. Robson, College of Optometry, University of Houston

L. Rowe, Department of Zoology, University of Toronto

B. Sheldon, Department of Zoology, University of Oxford

M. Siva-Jothy, Department of Animal and Plant Sciences, University of Sheffield

A. Smith, Department of Molecular Palaeontology, The Natural History Museum, London

L. Sundström, Department of Ecology and Systematics, University of Helsinki E. Svensson, Section for Animal Ecology,

Lund University C. Thomas, Department of Biology,

University of York R. Thornhill, Department of Biology,

Publishing Editor: Claire Rawlinson

(tel: +44 (0)20 7451 2602; fax: +44 (0)20 7976 1837; Claire.Rawlinson@royalsoc.ac.uk)

Editorial Coordinator: Helen Braysher

(tel: +44 (0)20 7451 2629; proceedingsb@royalsoc.ac.uk)

Senior Production Editor: Siân Roderick

6-9 Carlton House Terrace, London SW1Y 5AG, UK www.pubs.royalsoc.ac.uk

AIMS AND SCOPE

Research papers. Proc. R. Soc. B welcomes articles of high quality in all aspects of biology. Currently, it is particularly strong in ecology in the widest sense, and behavioural and evolutionary biology. Proc. R. Soc. B has also published significant numbers of papers in epidemiology, human biology, neuroscience, palaeontology and biomechanics. Authors are encouraged to submit articles not only in these fields, but in all branches of biology. The criteria for selection are scientific excellence, originality and potential interest to a wide spectrum of biologists.

University of New Mexico

Review papers. The journal also publishes topical reviews in emerging areas of biological science that will be of interest to non-specialists. Topical reviews are commissioned but unsolicited submissions will be considered.

Comment papers. Short additions to, or criticisms of, papers already published will also be considered. At the discretion of the editors, the authors of the original paper may be invited to reply. Comment papers should be short, interesting and conform to the rules of good manners.

Copyright © 2006 The Royal Society

Except as otherwise permitted under the Copyright, Designs and Patents Act, 1988, this publication may only be reproduced, stored or transmitted, in any form or by any other means, with the prior permission in writing of the publisher, or in the case of reprographic reproduction, in accordance with the terms of a licence issued by the Copyright Licensing Agency. In particular, the Society permits the making of a single photocopy of an article from this issue (under Sections 29 and 38 of this Act) for an individual for the purposes of research or private study.

SUBSCRIPTIONS

In 2007 Proc. R. Soc. B (ISSN 0962-8452) will be published twice a month. Full details of subscriptions may be obtained on request from the Subscription Sales Department, The Royal Society, 6–9 Carlton House Terrace, London SW1Y 5AG. Tel +44 (0)20 7451 2646; fax +44 (0)20 7976 1837; email: sales@royalsoc.ac.uk. The Royal Society is Registered Charity No 207043.

Subscription prices 2007 calendar year	Europe	USA & Canada	All other countries
Printed version plus electronic access	£930/US\$1720	£998/US\$1845	£1035/US\$1915

Typeset in Europe by the Alden Group, Oxfordshire. Printed by Latimer Trend, Plymouth.

This paper meets the requirements of ISO 9706:1994(E) and ANSI/NISO Z39.48-1992 (Permanence of Paper) effective with volume 247, issue 1318, 1992.

Proceedings of the Royal Society B (ISSN No: 0962-8452) is published twice a month by the Royal Society and distributed in the USA by DSW, 75 Aberdeen Road, Emigsville, PA 17318-0437, Periodicals postage paid at Emigsville PA. POSTMASTER: send address changes to Proceedings of the Royal Society B, c/o PO BOX 437, Emigsville, PA 17318-0437.