

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. C. H. Barrett, Editor, Department of Ecology & Evolutionary Biology, University of Toronto
N. C. Bennett, Editor, Department of Zoology and Entomology, University of Pretoria
A. E. Magurran, Editor, Gatty Marine Laboratory, University of St Andrews
P. Rainey, Editor, New Zealand Institute for Advanced Study, Massey University
N. Chr. Stenseth, Editor, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo
M. T. Siva-Jothy, Reviews Editor, Department of Animal & Plant Sciences, University of Sheffield

F. W. Allendorf, Division of Biological Sciences, University of Montana
S. H. Alonzo, Department of Ecology and Evolutionary Biology, Yale University
J. Altmann, Department of Ecology and Evolutionary Biology, Princeton University
M. A. Beaumont, School of Animal & Microbial Sciences, University of Reading
M. W. Blows, Evolutionary Quantitative Genetics Group, University of Queensland
A. T. D. Bennett, School of Biological Sciences, University of Bristol
S. L. Bonhoeffer, Department of Ecology and Evolution, ETH Zurich
J. J. Boomsma, Department of Population Ecology, University of Copenhagen
R. Boyd, Department of Anthropology, University of California, Los Angeles
P. M. Brakefield, Institute of Biology, Leiden University
R. Bshary, Institute of Zoology, University of Neuchâtel
N. Burgess, Institute of Cognitive Neuroscience and Department of Anatomy, University College London
G. R. Carvalho, School of Biological Sciences, University of Wales, Bangor
M. Chase, Jodrell Laboratory, Royal Botanic Gardens, Kew
R. L. Cifelli, Department of Zoology and School of Geology and Geophysics, University of Oklahoma
T. S. Clare, Marine Science and Technology, University of Newcastle upon Tyne

N. S. Clayton, Department of Experimental Psychology, University of Cambridge
J. D. Cohen, Center for the Study of Brain, Mind and Behavior, Princeton University
T. S. Collett, Sussex Centre for Neuroscience, University of Sussex
D. P. Costa, Center for Ocean Health University of California, Santa Cruz
G. Cowlshaw, Institute of Zoology, University of Cambridge
I. C. Cuthill, School of Biological Sciences, University of Bristol
M. S. Dawkins, Department of Zoology, University of Oxford
T. Day, Departments of Mathematics & Biology, Queen's University
L. De Meester, Laboratory of Aquatic Ecology, Katholieke Universiteit Leuven
M. Doebeli, Department of Zoology, University of British Columbia
C. G. Faulkes, School of Biological Sciences, Queen Mary, University of London
N. R. Franks, School of Biological Sciences, University of Bristol
T. Fukatsu, National Institute of Advanced Industrial Science and Technology (AIST), Japan
K. J. Gaston, Department of Animal and Plant Sciences, University of Sheffield
A. Grafen, Department of Zoology, University of Oxford
R. O. Gray, Psychology Department, University of Auckland
L. O. Harder, Department of Biological Sciences, University of Calgary
R. G. Harrison, Department of Ecology and Evolutionary Biology, Cornell University
J. A. P. Heesterbeek, Department of Farm Animal Health, University of Utrecht
P. W. H. Holland, Department of Zoology, University of Oxford
M. Kirkpatrick, College of Natural Sciences, University of Texas at Austin
J. C. Koella, Faculty of Life Sciences, Imperial College London
L. E. B. Kruuk, Institute of Cell, Animal and Population Biology, University of Edinburgh

K. C. M. Lessells, Department of Animal Population Biology, Netherlands Institute of Ecology
B. R. Levin, Department of Biology, Emory University
S. P. Long, Department of Plant Biology, University of Illinois
P. Lundberg, Department of Theoretical Ecology, Lunds University
E. P. Martins, Center for the Integrative Study of Animal Behavior, Indiana University
N. B. Metcalfe, Division of Environmental & Evolutionary Biology, University of Glasgow
A. E. Minetti, Institute of Human Physiology I, University of Milan
B. D. Neff, Department of Biology, University of Western Ontario
I. P. F. Owens, Department of Biological Sciences, Imperial College at Silwood Park
J. Radwan, Institute of Environmental Sciences, Jagiellonian University
A. F. Read, Center for Infections Disease Dynamics, Departments of Biology and Entomology, The Pennsylvania State University
M. Rees, Department of Animal and Plant Sciences, University of Sheffield
J. G. Robson, College of Optometry, University of Houston
L. Rowe, Department of Zoology, University of Toronto
B. C. Sheldon, Department of Zoology, University of Oxford
L. W. Simmons, Centre for Evolutionary Biology, University of Western Australia
A. Smith, Department of Molecular Palaeontology, The Natural History Museum, London
L. Sundström, Department of Ecology and Systematics, University of Helsinki
E. I. Svensson, Section for Animal Ecology, Lund University
R. Thornhill, Department of Biology, University of New Mexico
J. L. van Leeuwen, Experimental Zoology Group, Wageningen University
M. Wikelski, Department of Ecology and Evolutionary Biology, Princeton University
J. T. Wootton, Department of Ecology & Evolution, The University of Chicago
X. Xing, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
D.-Y. Zhang, Beijing Normal University

Publishing Editor: Claire Rawlinson

(tel: +44 (0)20 7451 2602; fax: +44 (0)20 7976 1837;
Claire.Rawlinson@royalsociety.org)

Editorial Coordinator: Helen Braysher

(tel: +44 (0)20 7451 2629; proceedingsb@royalsociety.org)

Senior Production Editor: Siân Roderick

6–9 Carlton House Terrace, London SW1Y 5AG, UK
publishing.royalsociety.org

Copyright © 2007 & 2008 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 2008 *Proc. R. Soc. B* (ISSN 0962-8452) will be published twice a month. Full details on how to subscribe can be obtained either by contacting our journal fulfilment agent, Portland Customer Services, Commerce Way, Colchester CO2 8HP. Tel: +44 (0)1206 796351; fax: +44 (0)1206 799331; email: sales@portland-services.com or by visiting our website at www.publishing.royalsociety.org/subscribers. The Royal Society is a Registered Charity No. 207043.

Typeset in India 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.

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.

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.

Subscription prices 2008 calendar year	Europe	USA & Canada	All other countries
Printed version plus electronic access	£985/US\$1822/ €1477	£1057/US\$1955	£1096/US\$2025