

# PROCEEDINGS OF THE ROYAL SOCIETY B

**Editor-in-Chief**  
Professor Michael P. Hassell  
**Reviews Editor**  
Professor Mike T. Siva-Jothy  
**Publishing Editor**  
Victoria Millen

**Editors:**  
Professor Suzanne H. Alonzo  
Professor Gary R. Carvalho  
Professor Innes C. Cuthill  
Professor Hans A. P. Heesterbeek

## Editorial Board

**Michael P. Hassell, Editor-in-Chief**, Imperial College London

**Suzanne H. Alonzo, Editor**, Yale University

**Gary R. Carvalho, Editor**, Bangor University

**Innes C. Cuthill, Editor**, University of Bristol

**Hans A. P. Heesterbeek, Editor**, University of Utrecht

**Mike T. Siva-Jothy, Reviews Editor**, University of Sheffield

**Peter Aerts**, University of Antwerp

**Fred W. Allendorf**, University of Montana

**W. Scott Armbruster**, University of Portsmouth

**Roland J. Baddeley**, University of Bristol

**Michael D. Beecher**, University of Washington

**Michael Begon**, University of Liverpool

**Mike Bonsall**, University of Oxford

**Paul M. Brakefield**, University of Cambridge and Leiden University

**Lindell Bromham**, Australian National University

**Redouan Bshary**, University of Neuchatel

**Neil Burgess**, University College London

**Michel Chapuisat**, University of Lausanne

**Lars Chittka**, Queen Mary London

**Steven Chown**, Stellenbosch University

**Richard L. Cifelli**, University of Oklahoma

**Nicky S. Clayton**, University of Cambridge

**Andrew Cockburn**, The Australian National University

**Dan P. Costa**, University of California, Santa Cruz

**Guy Cowlishaw**, University of Cambridge

**Sasha Dall**, University of Exeter

**Marian S. Dawkins**, University of Oxford

**Troy Day**, Queen's University

**Luc De Meester**, Katholieke Universiteit Leuven

**Christl A. Donnelly**, Imperial College London

**Greg Edgecombe**, Natural History Museum

**Santiago Elena**, CSIC-UPV

**Jonathan Evans**, University of Western Australia

**Chris G. Faulkes**, Queen Mary, University of London

**Russell Foster**, University of Oxford

**Takema Fukatsu**, National Institute of Advanced Industrial Science and Technology

**Deborah Gordon**, Stanford University

**Russell Gray**, The University of Auckland

**Richard G. Harrison**, Cornell University

**Fangliang He**, University of Alberta

**Sue Healy**, University of St Andrews

**Jeffrey Hutchings**, Dalhousie University

**Mark Kirkpatrick**, The University of Texas at Austin

**Rosemary Knapp**, University of Oklahoma

**Jacob C. Koella**, Imperial College London

**Bruce R. Levin**, Emory University

**Stephen P. Long**, University of Illinois

**Irby Lovette**, Cornell University

**Bobbi Low**, University of Michigan

**Per Lundberg**, Lund University

**Zhe-Xi Luo**, Carnegie Museum of Natural History

**Joah Madden**, University of Exeter

**Lynn Martin**, University of South Florida

**Norman Macleod**, Natural History Museum

**Daniel Nettle**, Newcastle University

**Ken Norris**, University of Reading

**Dan Nussey**, University of Edinburgh

**Daniel Osorio**, University of Sussex

**Karin S. Pfennig**, University of North Carolina at Chapel Hill

**Catherine A. Pfister**, University of Chicago

**Tom Pizzari**, University of Oxford

**Trevor Price**, University of Chicago

**Daniel Promislow**, University of Georgia

**Andy Purvis**, Imperial College London

**Lars Råberg**, Lund University

**Andy Radford**, University of Bristol

**Jacek Radwan**, Jagiellonian University

**Mark Rees**, University of Sheffield

**Susanne Renner**, University of Munich

**Mike G. Ritchie**, University of St Andrews

**Locke Rowe**, University of Toronto

**Dustin R. Rubenstein**, Columbia University

**Howard Rundle**, University of Ottawa

**Daniel Ruzzante**, Dalhousie University

**Wolfram Schultz**, University of Cambridge

**Leigh W. Simmons**, University of Western Australia

**Jennifer Smith**, Scripps Institution of Oceanography

**Max Telford**, University College London

**Hirokazu Tsukaya**, University of Tokyo

**Johan L. van Leeuwen**, Wageningen University

**Philip C. Withers**, University of Western Australia

**Patricia J. Wittkopp**, University of Michigan

**Da-Yong Zhang**, Beijing Normal University

### Publishing Editor: Victoria Millen

(tel: +44 (0)20 7451 2631; fax: +44 (0)20 7976 1837;

[victoria.millen@royalsociety.org](mailto:victoria.millen@royalsociety.org))

### Editorial Coordinator: Buchi Okerefor

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

### Production Editor: Siân Roderick

**6–9 Carlton House Terrace, London SW1Y 5AG, UK**

[rspb.royalsocietypublishing.org](http://rspb.royalsocietypublishing.org)

Copyright © 2011 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 2011 *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](mailto:sales@portland-services.com) or by visiting our website at [royalsocietypublishing.org/info/subscriptions](http://royalsocietypublishing.org/info/subscriptions). The Royal Society is a Registered Charity No. 207043.

### AIMS AND SCOPE

**Research papers.** *Proc. R. Soc. B* welcomes articles of outstanding 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* also publishes significant numbers of papers in health and disease, palaeontology and biomechanics, as well as molecular biology, neuroscience and cognition, where these bear upon organismal biology. Authors are encouraged to submit articles not only in these fields, but in all branches of biology. The criteria for selection are: work of outstanding importance, 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 in this journal 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 2011 calendar year	Europe	USA & Canada	All other countries
Electronic access	£1106/€1437	US\$2128	£1231/US\$2207
Printed version plus electronic access	£1327/€1724	US\$2553	£1477/US\$2648

Typeset in India by Techset Composition Limited, Salisbury, UK. 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 0962-8452) is published twice a month for \$2128 per year by the Royal Society, and is distributed in the USA by Agent named Air Business, C/O Worldnet Shipping USA Inc., 149-35 177th Street, Jamaica, New York, NY11434, USA. US Postmaster: Send address changes to *Proceedings of the Royal Society B*, C/O Air Business Ltd, C/O Worldnet Shipping USA Inc., 149-35 177th Street, Jamaica, New York, NY11414.