

Published in final edited form as:

Nature. 2011 March 24; 471(7339): . doi:10.1038/nature09831.

Inclusive fitness theory and eusociality

Patrick Abbot¹, Jun Abe², John Alcock³, Samuel Alizon⁴, Joao A. C. Alpedrinha⁵, Malte Andersson⁶, Jean-Baptiste Andre⁷, Minus van Baalen⁷, Francois Balloux⁸, Sigal Balshine⁹, Nick Barton¹⁰, Leo W. Beukeboom¹¹, Jay M. Biernaskie⁵, Trine Bilde¹², Gerald Borgia¹³, Michael Breed¹⁴, Sam Brown⁵, Redouan Bshary¹⁵, Angus Buckling⁵, Nancy T. Burley¹⁶, Max N. Burton-Chellew⁵, Michael A. Cant¹⁷, Michel Chapuisat¹⁸, Eric L. Charnov¹⁹, Tim Clutton-Brock²⁰, Andrew Cockburn²¹, Blaine J. Cole²², Nick Colegrave²³, Leda Cosmides²⁴, Iain D. Couzin²⁵, Jerry A. Coyne²⁶, Scott Creel²⁷, Bernard Crespi²⁸, Robert L. Curry²⁹, Sasha R. X. Dall¹⁷, Troy Day³⁰, Janis L. Dickinson³¹, Lee Alan Dugatkin³², Claire El Mouden⁵, Stephen T. Emlen³³, Jay Evans³⁴, Regis Ferriere³⁵, Jeremy Field³⁶, Susanne Foitzik³⁷, Kevin Foster⁵, William A. Foster²⁰, Charles W. Fox³⁸, Juergen Gadau³⁹, Sylvain Gandon⁴⁰, Andy Gardner⁵, Michael G. Gardner⁴¹, Thomas Getty⁴², Michael A. D. Goodisman⁴³, Alan Grafen⁵, Rick Grosberg⁴⁴, Christina M. Grozinger⁴⁵, Pierre-Henri Gouyon⁴⁶, Darryl Gwynne⁴⁷, Paul H. Harvey⁵, Ben J. Hatchwell⁴⁸, Jürgen Heinze⁴⁹, Heikki Helanterä⁵⁰, Ken R. Helms⁵¹, Kim Hill⁵², Natalie Jiricny⁵, Rufus A. Johnstone²⁰, Alex Kacelnik⁵, E. Toby Kiers⁵³, Hanna Kokko²¹, Jan Komdeur⁵⁴, Judith Korb⁵⁵, Daniel Kronauer⁵⁶, Rolf Kümmerli⁵⁷, Laurent Lehmann¹⁵, Timothy A. Linksvayer⁵⁸, Sébastien Lion⁵⁹, Bruce Lyon⁶⁰, James A. R. Marshall⁶¹, Richard McElreath⁶², Yannis Michalakis⁴, Richard E. Michod⁶³, Douglas Mock⁶⁴, Thibaud Monnin⁷, Robert Montgomerie⁶⁵, Allen J. Moore¹⁷, Ulrich G. Mueller⁶⁶, Ronald Noë⁶⁷, Samir Okasha⁶⁸, Pekka Pamilo⁶⁹, Geoff A. Parker⁷⁰, Jes S. Pedersen⁵⁸, Ido Pen⁷¹, David Pfennig⁷², David C. Queller⁷³, Daniel J. Rankin⁷⁴, Sarah E. Reece²³, Hudson K. Reeve³³, Max Reuter⁷⁵, Gilbert Roberts⁷⁶, Simon K. A. Robson⁷⁷, Denis Roze⁷⁸, Francois Rousset⁷⁹, Olav Rueppell⁸⁰, Joel L. Sachs⁸¹, Lorenzo Santorelli⁵, Paul Schmid-Hempel⁸², Michael P. Schwarz⁴¹, Tom Scott-Phillips⁸³, Janet Shellmann-Sherman³³, Paul W. Sherman³³, David M. Shuker⁸⁴, Jeff Smith⁷³, Joseph C. Spagna⁸⁵, Beverly Strassmann⁸⁶, Andrew V. Suarez⁸⁷, Liselotte Sundström⁵⁰, Michael Taborsky⁸⁸, Peter Taylor³⁰, Graham Thompson⁸⁹, John Tooby⁹⁰, Neil D. Tsutsui⁹¹, Kazuki Tsuji⁹², Stefano Turillazzi⁹³, Francisco Úbeda⁹⁴, Edward L. Vargo⁹⁵, Bernard Voelkl⁹⁶, Tom Wenseleers⁹⁷, Stuart A. West⁵, Mary Jane West-Eberhard⁹⁸, David F. Westneat⁹⁹, Diane C. Wiernasz²², Geoff Wild¹⁰⁰, Richard Wrangham¹⁰¹, Andrew J. Young¹⁷, David W. Zeh¹⁰², Jeanne A. Zeh¹⁰², and Andrew Zink¹⁰³

¹Vanderbilt University, Nashville, Tennessee 37235, USA ²Laboratory of Applied Entomology, Faculty of Agriculture, Shizuoka University, Sizuoka 422-8529, Japan ³School of Life Sciences, PO Box 874501, Arizona State University, Tempe, Arizona 85287-4501, USA ⁴UMR CNRS-IRD 2724, Genetics and Evolution of Infectious Diseases, IRD, 911 Avenue Agropolis, B.P. 64501, 34394 Montpellier Cedex 5, France ⁵Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK ⁶Department of Zoology, University of Gothenburg, SE 405 30 Gothenburg, Sweden ⁷CNRS, Université Pierre et Marie Curie, Ecole Normale Supérieure, UMR 7625, Ecologie and Evolution, 75005 Paris, France ⁸MRC Centre for Outbreak Analysis and Modelling, Department of Infectious Disease Epidemiology, Faculty of Medicine, Imperial College,

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Author Contributions All authors contributed to the planning, writing and/or revising of this paper. Several others who contributed significantly are not listed because they are named on separate comments.

Stuart.West@zoo.ox.ac.uk

Competing financial interests: declared none.

St Mary's Campus, Norfolk Place, London W2 1PG, UK ⁹Department of Psychology, Neuroscience and Behaviour, McMaster University, 1280 Main St West, Hamilton, Ontario L8S 4K1, Canada ¹⁰IST Austria, Am Campus 1, Klosterneuburg 3400, Austria ¹¹Evolutionary Genetics, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, NL-9750 AA Haren, The Netherlands ¹²Aarhus University, Department of Biological Sciences, Ny Munkegade 1540, 8000 Aarhus C, Denmark ¹³Department of Biology, University of Maryland, College Park, Maryland 20742-4415, USA ¹⁴Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309-0334, USA ¹⁵Faculté des sciences, Rue Emile-Argand 11, Case postale 158, 2000 Neuchâtel, Switzerland ¹⁶Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall, Irvine, California 92697-2525, USA ¹⁷Centre for Ecology and Conservation, University of Exeter, Cornwall, Tremough, Penryn TR10 9EZ, UK ¹⁸Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland ¹⁹Department of Biology, 167 Castetter Hall, MSC03 2020, 1 University of New Mexico, Albuquerque, New Mexico 87131-000, USA ²⁰Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK ²¹Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia ²²Department of Biology and Biochemistry, University of Houston, Houston, Texas 77204-5001, USA ²³Institutes of Evolution, Immunology and Infection Research, School of Biological Sciences, Ashworth Laboratories, University of Edinburgh, Edinburgh EH9 3JT, UK ²⁴Department of Psychology, University of California, Santa Barbara, Santa Barbara, California 93106-9660, USA ²⁵Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, USA ²⁶Department of Ecology and Evolution, The University of Chicago, 1101 E. 57 Street, Chicago, Illinois 60637, USA ²⁷Department of Ecology, Montana State University, Bozeman, Montana 59717, USA ²⁸Department of Biosciences, 8888 University Drive, Simon Fraser University, Burnaby, British Columbia V5A1S6, Canada ²⁹Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA ³⁰Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada ³¹The Cornell Laboratory of Ornithology, Cornell University — The Johnson Center, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA ³²Department of Biology, University of Louisville, Louisville, Kentucky 40292, USA ³³Seeley G. Mudd Hall, Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA ³⁴USDA-ARS Bee Research Laboratory, BARC-E Bldg 476, Beltsville, Maryland 20705, USA ³⁵Laboratoire Ecologie and Evolution, CNRS UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75005 Paris, France; Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA ³⁶School of Life Sciences, John Maynard Smith Building, University of Sussex, Brighton BN1 9QG, UK ³⁷Department Biologie II Behavioral Ecology (Verhaltensökologie), Ludwig-Maximilians-Universität, München Großhaderner Str. 2 D - 82152 Planegg/Martinsried, Germany ³⁸Department of Entomology, University of Kentucky, Lexington, Kentucky 40546-0091, USA ³⁹School of Life Sciences, Arizona State University, PO Box 874501, Tempe, Arizona 85287-4501, USA ⁴⁰CEFE - UMR 5175, 1919 route de Mende, F-34293 Montpellier Cedex 5, France ⁴¹School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia ⁴²Kellogg Biological Station and Department of Zoology, Michigan State University, Hickory Corners, Michigan 49060, USA ⁴³School of Biology and Petit Institute for Bioengineering and Bioscience, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, Georgia 30332-0230, USA ⁴⁴Department of Evolution and Ecology, College of Biological Sciences, 1 Shields Avenue, UC Davis, Davis, California 95616, USA ⁴⁵Center for Pollinator Research, Huck Institutes of the Life Sciences, Pennsylvania State University, Chemical Ecology Lab 4A, University Park, Pennsylvania 16802, USA ⁴⁶Muséum National d'Histoire Naturelle, CP39, 12 rue Buffon, 75005 Paris, France ⁴⁷Biology Department, University of Toronto, 3359 Mississauga Road, Mississauga, Ontario L5L 1C6, Canada ⁴⁸Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK ⁴⁹Biologie I, Universität

Regensburg, D-93040 Regensburg, Germany ⁵⁰Department of Biosciences, PL 65 (Viikinkaari 1), FI-00014 University of Helsinki, Finland ⁵¹Department of Biology, University of Vermont, Burlington, Vermont 05405, USA ⁵²School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona 85287-2402, USA ⁵³Department of Animal Ecology, Institute of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit, De Boelelaan 1085, NL-1081 HV Amsterdam, The Netherlands ⁵⁴Animal Ecology Group, Centre for Evolutionary and Ecological Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands ⁵⁵University of Osnabrueck, Barbarastr.11, D-49076 Osnabrueck, Germany ⁵⁶Harvard University, Museum of Comparative Zoology, 26 Oxford St, Cambridge, Massachusetts 02138, USA ⁵⁷Environmental Microbiology, Swiss Federal Institute of Aquatic Research and Technology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland ⁵⁸Centre for Social Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark ⁵⁹School of Biological Sciences, Royal Holloway, University of London, Egham TW20 0EX, UK ⁶⁰Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064, USA ⁶¹Department of Computer Science, University of Sheffield, Sheffield S1 4DP, UK ⁶²Department of Anthropology and Center for Population Biology, UC Davis, Davis, California 95616, USA ⁶³Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA ⁶⁴Department of Zoology, 730 Van Vleet Oval, University of Oklahoma, Norman, Oklahoma 73019, USA ⁶⁵Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada ⁶⁶Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, Texas 78712, USA ⁶⁷Psychologie — Université de Strasbourg, Ethologie des Primates — DEPE (IPHC CNRS UMR 7178), 23 rue Becquerel — Strasbourg 67087, Cedex, France ⁶⁸Department of Philosophy, University of Bristol, Bristol BS8 1TB, UK ⁶⁹Biocenter Oulu and Department of Biosciences, University of Helsinki, Box 65, 00140 University of Helsinki, Finland ⁷⁰Institute of Integrative Biology, Biosciences Building, Crown Street, University of Liverpool, Liverpool L69 7ZB, UK ⁷¹Theoretical Biology group, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands ⁷²Department of Biology, CB#3280, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280, USA ⁷³Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005-1892, USA ⁷⁴Department of Biochemistry, University of Zurich, Building Y27, Office J-46, Winterthurstrasse 190, CH-8057 Zurich, Switzerland; Swiss Institute of Bioinformatics, Quartier Sorge Bâtiment Génopode, CH-1015 Lausanne, Switzerland ⁷⁵Research Department of Genetics, Evolution and Environment, Faculty of Life Sciences, University College London, 4 Stephenson Way, London NW1 2HE, UK ⁷⁶Centre for Behaviour and Evolution, Institute of Neuroscience, Faculty of Medical Sciences, Newcastle University, Henry Wellcome Building, Framlington Place, Newcastle upon Tyne NE2 4HH, UK ⁷⁷School of Marine and Tropical Biology, James Cook University, Queensland 4811, Australia ⁷⁸Station Biologique de Roscoff, CNRS-UPMC UMR 7144, 29680 Roscoff, France ⁷⁹Institut des Sciences de l'Evolution, University of Montpellier 2, Montpellier 34095, France ⁸⁰Department of Biology, University of North Carolina at Greensboro, 312 Eberhart Building, Greensboro, North Carolina 27403, USA ⁸¹Department of Biology, 3314 Spieth Hall, University of California — Riverside, Riverside, California 92521, USA ⁸²ETH Zurich, Institute of Integrative Biology (IBZ), Universitätsstrasse 16, CH.8092 Zürich, Switzerland ⁸³School of Philosophy, Psychology and Language Sciences, University of Edinburgh, 3 Charles Street, Edinburgh EH8 9AD, UK ⁸⁴School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK ⁸⁵William Paterson University of New Jersey, 300 Pompton Road, Wayne, New Jersey 07470, USA ⁸⁶Department of Anthropology, 101 West Hall, University of Michigan, Ann Arbor, Michigan 48109, USA ⁸⁷Department of Entomology and Department of Animal Biology, University of Illinois, Urbana, Illinois 61801, USA ⁸⁸Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland ⁸⁹Department of Biology, University of Western Ontario, 1151 Richmond Street North, London, Ontario N6A 5B7, Canada ⁹⁰Department of Anthropology, University of California,

Santa Barbara, California 93106-3210, USA ⁹¹Department of Environmental Science, Policy and Management, 130 Mulford Hall, 3114, University of California Berkeley, Berkeley, California 94720-3114, USA ⁹²Faculty of Agriculture, University of the Ryukyus, Okinawa 903-0213, Japan ⁹³Dipartimento di Biologia Evoluzionistica, Università degli Studi di Firenze, via Romana 17, 50125 Firenze, Italy ⁹⁴Department of Ecology and Evolutionary Biology, University of Tennessee Knoxville, Knoxville, Tennessee 37902, USA ⁹⁵Department of Entomology, Box 7613, North Carolina State University, Raleigh, North Carolina 27695-7613, USA ⁹⁶Institute for Theoretical Biology, Humboldt University zu Berlin, Invalidenstr. 43, D-10115 Germany ⁹⁷Department of Biology, Zoological Institute, K.U. Leuven, Naamsestraat 59, B-3000 Leuven, Belgium ⁹⁸Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panamá ⁹⁹Department of Biology, 101 Morgan Building, University of Kentucky, Lexington, Kentucky 40506-0225, USA ¹⁰⁰Department of Applied Mathematics, University of Western Ontario, 1151 Richmond Street North, London, Ontario N6A 5B7, Canada ¹⁰¹Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA ¹⁰²Department of Biology and Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Nevada 89557, USA ¹⁰³Department of Biology, San Francisco State University, San Francisco, California 94132, USA

Nowak *et al.*¹ argue that inclusive fitness theory has been of little value in explaining the natural world, and that it has led to negligible progress in explaining the evolution of eusociality. However, we believe that their arguments are based upon a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature. We will focus our comments on three general issues.

First, Nowak *et al.*¹ are incorrect to suggest a sharp distinction between inclusive fitness theory and “standard natural selection theory”. Natural selection explains the appearance of design in the living world, and inclusive fitness theory explains what this design is for. Specifically, natural selection leads organisms to become adapted as if to maximize their inclusive fitness²⁻⁴. Inclusive fitness theory is based upon population genetics, and is used to make falsifiable predictions about how natural selection shapes phenotypes, and so it is not surprising that it generates identical predictions to those obtained using other methods^{2,5-7}.

Second, Nowak *et al.*¹ are incorrect to state that inclusive fitness requires a number of “stringent assumptions” such as pairwise interactions, weak selection, linearity, additivity and special population structures. Hamilton’s original formulations did not make all these assumptions, and generalizations have shown that none of them is required^{3,5,6,8}. Inclusive fitness is as general as the genetical theory of natural selection itself. It simply partitions natural selection into its direct and indirect components.

Nowak *et al.*¹ appear to have confused the completely general theory of inclusive fitness with models of specific cases. Yes, researchers often make limiting assumptions for reasons of analytical tractability when considering specific scenarios^{5,7}, as with any modelling approach. For example, Nowak *et al.*¹ assume a specific form of genetic control, where dispersal and helping are determined by the same single locus, that mating is monogamous, and so on. However, the inclusive fitness approach has facilitated, not hindered, empirical testing of evolutionary theory⁹⁻¹¹. Indeed, an advantage of inclusive fitness theory is that it readily generates testable predictions in situations where the precise genetic architecture of a phenotypic trait is unknown.

Third, we dispute the claim of Nowak *et al.*¹ that inclusive fitness theory “does not provide any additional biological insight”, delivering only “hypothetical explanations”, leading only

to routine measurements and “correlative studies”, and that the theory has “evolved into an abstract enterprise largely on its own”, with a failure to consider multiple competing hypotheses. We cannot explain these claims, which seem to overlook the extensive empirical literature that has accumulated over the past 40 years in the fields of behavioural and evolutionary ecology⁹⁻¹¹ (Table 1). Of course, studies must consider the direct consequences of behaviours, as well as consequences for relatives, but no one claims otherwise, and this does not change the fact that relatedness (and lots of other variables) has been shown to be important in all of the above areas.

We do not have space to detail all the advances that have been made in the areas described in Table 1. However, a challenge to the claims of Nowak *et al.*¹ is demonstrated with a single example, that of sex allocation (the ratio of investment into males versus females). We choose sex allocation because: (1) Nowak *et al.*¹ argue that inclusive fitness theory has provided only “hypothetical explanations” in this field; (2) it is an easily quantified social trait, which inclusive fitness theory predicts can be influenced by interactions between relatives; and (3) the study of sex allocation has been central to evolutionary work on the eusocial insects. In contrast to the claims of Nowak *et al.*¹, recent reviews of sex allocation show that the theory explains why sex allocation varies with female density, inbreeding rate, dispersal rate, brood size, order of oviposition, sib-mating, asymmetrical larval competition, mortality rate, the presence of helpers, resource availability and nest density in organisms such as protozoan parasites, nematodes, insects, spiders, mites, reptiles, birds, mammals and plants^{5,12,13}.

The quantitative success of this research is demonstrated by the percentage of the variance explained in the data. Inclusive fitness theory has explained up to 96% of the sex ratio variance in across-species studies and 66% in within-species studies¹³. The average for all evolutionary and ecological studies is 5.4%. As well as explaining adaptive variation in behaviour, inclusive fitness theory has even elucidated when and why individuals make mistakes (maladaptation), in response to factors such as mechanistic constraints¹³. It is not clear how Nowak *et al.*¹ can characterize such quantifiable success as “meagre”. Their conclusions are based upon a discussion in the Supplementary Information of just three papers (by authors who disagree with the interpretations of Nowak *et al.*¹), out of an empirical literature of thousands of research articles. This would seem to indicate a failure to engage seriously with the body of work that they recommend we abandon.

The same points can be made with regard to the evolution of the eusocial insects, which Nowak *et al.*¹ suggest cannot be explained by inclusive fitness theory. It was already known that haplodiploidy itself may have only a relatively minor bearing on the origin of eusociality, and so Nowak *et al.*¹ have added nothing new here. Inclusive fitness theory has explained why eusociality has evolved only in monogamous lineages, and why it is correlated with certain ecological conditions, such as extended parental care and defence of a shared resource^{14,15}. Furthermore, inclusive fitness theory has made very successful predictions about behaviour in eusocial insects, explaining a wide range of phenomena (Table 2).

Ultimately, any body of biological theory must be judged on its ability to make novel predictions and explain biological phenomena; we believe that Nowak *et al.*¹ do neither. The only prediction made by their model (that offspring are favoured to help their monogamously mated mother if this provides a sufficient benefit) merely confirms, in a less general way, Hamilton’s original point: if the fitness benefits are great enough, then altruism is favoured between relatives.

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Table 1
Inclusive fitness theory has been important in understanding a range of behavioural phenomena

Research area	Correlational?	Experimental?	Theory–data interplay
Sex allocation	Yes	Yes	Yes
Policing	Yes	Yes	Yes
Conflict resolution	Yes	Yes	Yes
Cooperation	Yes	Yes	Yes
Altruism	Yes	Yes	Yes
Spite	Yes	Yes	Yes
Kin discrimination	Yes	Yes	Yes
Parasite virulence	Yes	Yes	Yes
Parent–offspring conflict	Yes	Yes	Yes
Sibling conflict	Yes	Yes	Yes
Selfish genetic elements	Yes	Yes	Yes
Cannibalism	Yes	Yes	Yes
Dispersal	Yes	Yes	Yes
Alarm calls	Yes	Yes	Yes
Eusociality	Yes	Yes	Yes
Genomic imprinting	Yes	Yes	Yes

Data are taken from refs 9–11. Correlational studies test predictions using natural variation in key variables, whereas experimental studies involve their experimental manipulation. Interplay between theory and data means that theory has informed empirical study, and vice versa. Inclusive fitness is not the only way to model evolution, but it has already proven to be an immensely productive and useful approach for studying eusociality and other social behaviours.

Table 2
Areas in which inclusive fitness theory has made successful predictions about behaviour in eusocial insects

Trait examined	Explanatory variables	Correlational studies?	Experimental studies?	Interplay between theory and data?
Altruistic helping	Haplodiploidy versus diploidy	Yes	No	Yes
Worker egg laying	Worker policing	Yes	Yes	Yes
Policing	Relatedness	Yes	Yes	Yes
Level of cooperation	Costs, benefits and relatedness	Yes	Yes	Yes
Intensity of work	Need for work and probability of becoming queen	Yes	Yes	Yes
Sex allocation	Relatedness asymmetries due to variation in queen survival, queen number and mating frequency	Yes	Yes	Yes
Sex allocation	Resource availability	Yes	Yes	Yes
Sex allocation	Competition for mates between related males	Yes	Yes	Yes
Number of individuals trying to become reproductive	Presence of old queens	Yes	Yes	Yes
Workers killing queens	Presence of workers, reproductives or other queens	Yes	No	No
Exclusion of non-kin	Colony membership	Yes	Yes	Yes

Data are taken from refs 12–16.