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Inclusive fitness theory and eusociality

Nowak et al. (hereafter “NTW”) argue that inclusive fitness (IF) 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, their arguments are based on a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature. We do not have space to go into all their specific errors, and so we will focus upon three general issues.

First, is there a sharp distinction between IF theory and “standard natural selection theory”? No. Natural selection explains the appearance of design in the living world, and IF theory explains what this design is for. Specifically, natural selection leads organisms to become adapted as if to maximize their IF¹⁻³. IF theory is based on 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^{1,4-6}.

Second, does IF require a number of “stringent assumptions” such as pairwise interactions, weak selection, linearity, additivity and special population structures? No. Hamilton’s original formulations did not make all these assumptions, and generalisations have shown that none of them are required^{2,4,5,7}. IF is as general as the genetical theory of natural selection itself. It is simply a partition of natural selection into its direct and indirect components.

NTW’s error is to have confused the completely general theory of IF with models of specific cases. Yes, researchers often make limiting assumptions for reasons of analytical tractability when considering specific scenarios^{4,6}, as with any modelling approach. For example, NTW 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 general IF approach has facilitated, not hindered, empirical testing of IF theory⁸⁻¹⁰. Indeed, an advantage of IF theory is that it readily generates testable predictions in situations where the precise genetic architecture of a phenotypic trait is unknown.

Third, NTW claim that IF theory “does not provide any additional biological insight”. They argue that it has delivered only “hypothetical explanations”, leading only to “routine” measurements and “correlative studies”, and that the theory has “evolved into an abstract enterprise on its own”, with a “failure to consider multiple competing hypotheses”. We cannot explain these puzzling claims, which completely neglect the extensive empirical literature that has accumulated over the past 40 years in the fields of behavioural and evolutionary ecology⁸⁻¹⁰ (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 a load of other variables) has been shown to be important in all 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, the falseness of NTW’s claims is easily demonstrated with a single example, that of sex allocation (the ratio of investment into males versus females). We choose sex allocation because: (a) NTW argue that IF theory has provided only “hypothetical explanations” in this field; and (b) it is an easily

quantified social trait, which IF theory predicts can be influenced by interactions between relatives; (3) the study of sex allocation has been central to evolutionary work on the eusocial insects. In undeniable contrast to NTW's claims, recent reviews of sex allocation show that the theory has provided strong explanation for why sex allocation varies with variables such as female density, inbreeding rate, dispersal rate, brood size, order of oviposition, sibmating, asymmetrical larval competition, mortality rate, the presence of helpers, resource availability and nest density in organisms such as protozoan parasites, worms, insects, spiders, mites, reptiles, birds, mammals and plants^{4,11,12}.

The quantitative success of this research can be summarized in one statistic: the percentage of the variance explained in the data. IF theory has explained up to 96% of the sex ratio variance in across-species studies and 66% in within-species studies¹². The average for evolutionary and ecological studies is 5.4%. In addition, as well as explaining adaptive variation in behaviour, IF theory has even elucidated when and why individuals make mistakes (maladaptation), in response to factors such as mechanistic constraints¹². It is not clear how NTW can characterize such quantifiable ringing success as "meagre". Their conclusions are based upon a selection of just three papers (by authors who all strongly disagree with NTW's interpretations), out of an empirical literature of thousands of research articles. This betrays a failure to seriously engage with the body of work that they would have us abandon.

The same points can be made with regard to the evolution of the eusocial insects, which NTW suggest cannot be explained by IF theory. Haplodiploidy itself may have only a relatively minor bearing on the origin of eusociality, but by impugning the value of IF theory as well, Nowak et al. discard the baby with the bathwater. IF 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^{13,14}. Furthermore, IF 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. The most striking fact about NTW's offering is that it does neither. The only prediction made by their model (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 and immensely important point: if the fitness benefits are great enough, then altruism can be favoured between relatives.

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Author information: The authors declare no competing interests. Correspondence should be addressed to SAW (Stuart.West@zoo.ox.ac.uk).

Research Area	Correlational studies?	Experimental studies?	Interplay between theory and data?
Sex allocation	✓	✓	✓
Policing	✓	✓	✓
Conflict resolution	✓	✓	✓
Cooperation	✓	✓	✓
Altruism	✓	✓	✓
Spite	✓	✓	✓
Kin discrimination	✓	✓	✓
Parasite virulence	✓	✓	✓
Parent-offspring conflict	✓	✓	✓
Sibling conflict	✓	✓	✓
Selfish genetic elements	✓	✓	✓
Cannibalism	✓	✓	✓
Dispersal	✓	✓	✓
Alarm calls	✓	✓	✓
Eusociality	✓	✓	✓
Genomic imprinting	✓	✓	✓

Table 1. Some example areas (non-exhaustive) in which IF theory has been vitally important in understanding a range of behavioural phenomena⁸⁻¹⁰. We are not suggesting that IF is the only way to model evolution, just that it has already proven an immensely productive and useful approach for studying eusociality and other social behaviours.

Trait examined	Explanatory variables	Correlational studies?	Experimental studies?	Interplay between theory and data?
Altruistic helping	Haplodiploidy vs diploidy	✓		✓
Worker egg laying	Worker policing	✓	✓	✓
Policing	Relatedness	✓	✓	✓
Level of cooperation	Costs, benefits and relatedness	✓	✓	✓
Intensity of work	Need for work and probability of becoming queen	✓	✓	✓
Sex allocation	Relatedness asymmetries due to variation in queen survival, queen number, and mating frequency	✓	✓	✓
Sex allocation	Resource availability	✓	✓	✓
Sex allocation	Competition for mates between related males	✓	✓	✓
Number of individuals trying to become reproductive	Presence of old queens	✓	✓	✓
Workers killing queens	Presence of workers, reproductives or other queens	✓		
Exclusion of non-kin	Colony membership	✓	✓	✓

Table 2. Example areas (non-exhaustive) in which IF theory has made very successful predictions about behaviour in eusocial insects¹¹⁻¹⁵.

Patrick Abbot, Jun Abe, John Alcock, Samuel Alizon, Joao A.C. Alpedrinha, Malte Andersson, Jean-Baptiste Andre, Minus van Baalen, Francois Balloux, Sigal Balshine, Nick Barton, Leo W. Beukeboom, Jay M. Biernaskie, Trine Bilde, Gerald Borgia, Michael Breed, Sam Brown, Redouan Bshary, Angus Buckling, Nancy T. Burley, Max N. Burton-Chellew, Michael A. Cant, Michel Chapuisat, Eric L. Charnov, Tim Clutton-Brock, Andrew Cockburn, Blaine J. Cole, Nick Colegrave, Leda Cosmides, Iain D. Couzin, Jerry A. Coyne, Scott Creel, Bernard Crespi, Robert L. Curry, Sasha R.X. Dall, Troy Day, Janis L. Dickinson, Lee Alan Dugatkin, Claire El Mouden, Stephen T. Emlen, Jay Evans, Regis Ferriere, Jeremy Field, Susanne Foitzik, Kevin Foster, William A. Foster, Charles Fox, Juergen Gadau, Sylvain Gandon, Andy Gardner, Michael G. Gardner, Thomas Getty, Michael A. D. Goodisman, Alan Grafen, Rick Grosberg, Christina M. Grozinger, Pierre-Henri Gouyon, Darryl Gwynne, Paul Harvey, Ben J. Hatchwell, Jürgen Heinze, Heikki Helanterä, Ken R. Helms, Kim Hill, Natalie Jiricny, Rufus A. Johnstone, Alex Kacelnik, E. Toby Kiers, Hanna Kokko, Jan Komdeur, Judith Korb, Daniel Kronauer, Rolf Kümmerli, Laurent Lehmann, Timothy A. Linksvayer, Sébastien Lion, Bruce Lyon, James A. R. Marshall, Richard McElreath, Yannis Michalakis, Richard E. Michod, Douglas Mock, Thibaud Monnin, Robert Montgomerie, Allen J. Moore, Ulrich G. Mueller, Ronald Noë, Samir Okasha, Pekka Pamilo, Geoff A. Parker, Ido Pen, Jes S. Pedersen, David Pfennig, David C. Queller, Daniel J. Rankin, Sarah E. Reece, Hudson K. Reeve, Max Reuter, Gilbert Roberts, Simon K. A. Robson, Denis Roze, Francois Rousset, Olav Rueppell, Joel Sachs, Lorenzo Santorelli, Paul Schmid-Hempel, Michael P. Schwarz, Tom Scott-Phillips, Paul W. Sherman, David M. Shuker, Jeff Smith, Joseph C. Spagna, Andrew Suarez, Liselotte Sundström, Michael Taborsky, Peter Taylor, Graham Thompson, John Tooby, Neil D. Tsutsui, Kazuki Tsuji, Stefano Turillazzi, Francisco Úbeda, Edward L. Vargo, Bernard Voelkl, Tom Wenseleers, Stuart A. West, Mary Jane West-Eberhard, David F. Westneat, Diane C. Wiernasz, Geoff Wild, Richard Wrangham, Andrew J. Young, David W. Zeh, Jeanne A. Zeh, Andrew Zink.

PA
Vanderbilt University
Nashville, TN 37235 USA

JA
Laboratory of Applied Entomology
Faculty of Agriculture
Shizuoka University
Shizuoka 422-8529
Japan

JA
Arizona State University [retired]

SA + YM
UMR CNRS-IRD 2724, Genetics and Evolution of Infectious Diseases
IRD, 911 Avenue Agropolis, B.P. 64501
34394 Montpellier Cedex 5, France

JACA, JB, SB, AB, MB-C, PH, NJ, AK, LS, CEM, AG, SAW

Department of Zoology
University of Oxford
South Parks Road
Oxford, OX1 3PS, UK

MA
Department of Zoology
University of Gothenburg
SE 405 30 Gothenburg, Sweden

MvB
Ecole Normale Supérieure, UMR 7625
« Ecologie et Evolution », Paris, F-75005, France; Université
Pierre et Marie Curie, UMR 7625
« Ecologie et Evolution », Paris, F-75005, France; CNRS, UMR
7625 « Ecologie et Evolution », Paris, F-75005, France. Bâtiment A
7ème Etage CC237, 7 quai St.-Bernard, F-75252
Paris cedex 05, France.

FB
MRC Centre for Outbreak Analysis and Modelling,
Department of Infectious Disease Epidemiology,
Faculty of Medicine,
Imperial College,
St Mary's Campus,
Norfolk Place,
London W2 1PG,
United Kingdom

SB
Department of Psychology, Neuroscience & Behaviour
McMaster University
1280 Main St. West
Hamilton, ON L8S 4K1 Canada

NB
IST Austria
Am Campus 1
Klosterneuburg 3400

RB+LL
Faculté des sciences
Rue Emile-Argand 11,
Case postale 158
2000 Neuchâtel, Switzerland
Australia

LB
Evolutionary Genetics
Centre for Ecological and Evolutionary Studies

University of Groningen
P.O. Box 14, NL-9750 AA Haren
The Netherlands

TB
Aarhus University
Department of Biological Sciences
Ny Munkegade 1540
8000 Aarhus C
Denmark

GB
Professor
Department of Biology
University of Maryland
College Park, MD 20742-4415 USA

MB
Ecology and Evolutionary Biology
University of Colorado,
Boulder CO, USA

NB
Dept Ecology and Evolutionary Biology
University of California
321 Steinhaus Hall
Irvine, CA 92697-2525 USA

MAC + SRXD + +AJM + AY
Centre for Ecology and Conservation
University of Exeter, Cornwall
Tremough
Penryn TR10 9EZ
Cornwall
UK

MC
Department of Ecology and Evolution
Biophore
University of Lausanne
1015 Lausanne
Switzerland

TCB + WF + RJ
Department of Zoology
University of Cambridge
Downing Street
Cambridge
CB2 3EJ UK

AC+HK
Evolution, Ecology and Genetics
Research School of Biology
Australian National University
Canberra, ACT 0200, Australia

BJC+DW
Dept of Biology & Biochemistry
University of Houston
Houston TX 77204-5001 USA

NC+SR
Institutes of Evolution, Immunology and Infection Research,
School of Biological Sciences,
Ashworth Laboratories,
University of Edinburgh,
Edinburgh EH9 3JT
Scotland, UK

LC
Department of Psychology
University of California, Santa Barbara
Santa Barbara, CA 93106-9660 USA

BC
Department of Biosciences
8888 University Drive
Simon Fraser University, Burnaby BC V5A1S6 Canada

IC
Department of Ecology and Evolutionary Biology,
Princeton University,
Princeton, 08540, USA

RC
Department of Biology
Villanova University
800 Lancaster Avenue
Villanova, PA 19085 USA

JAC
Department of Ecology and Evolution
The University of Chicago
1101 E. 57 Street
Chicago, IL 60637 USA

Scott Creel
Department of Ecology
Montana State University
Bozeman MT 59717 USA

TD+PT
Dept Math&Stats
Queen's University
Kingston ON K7L 3N6

JLD
The Cornell Lab of Ornithology
Cornell University - The Johnson Center
159 Sapsucker Woods Road
Ithaca, NY 14850

LAD
Department of Biology
University of Louisville
Louisville, KY, 40292 USA

HKR + PWS + JSS + SE
Seeley G. Mudd Hall
Department of Neurobiology and Behavior
Cornell University
Ithaca, New York 14853 USA

JE
USDA-ARS Bee Research Lab
BARC-E Bldg 476
Beltsville, MD 20705 USA

RF
Laboratoire Ecologie & Evolution, CNRS UMR 7625, Ecole Normale Supérieure, 46
rue d'Ulm, 75005 Paris, France and
2. Department of Ecology & Evolutionary Biology, University of Arizona, Tucson
AZ 85721, USA.

JF
School of Life Sciences
John Maynard Smith Building
University of Sussex
Brighton BN1 9QG,
UK

SF
Department Biologie II Behavioral Ecology (Verhaltensökologie)
Ludwig-Maximilians-Universität
München Großhaderner Str. 2 D - 82152 Planegg / Martinsried Germany

KRF
Center for Systems Biology
Harvard University
Cambridge, MA 02138

CF
Department of Entomology
University of Kentucky
Lexington, KY 40546-0091 USA

JG
School of Life Sciences
Arizona State University
PO Box 874501
Tempe, AZ, 85287-4501 USA

MS + MGG
School of Biological Sciences,
Flinders University,
GPO Box 2100,
Adelaide, SA 5001,
Australia

SG
CEFE - UMR 5175
1919 route de Mende
F-34293 Montpellier cedex 5
France

TG
Kellogg Biological Station & Department of Zoology
Michigan State University
Hickory Corners, MI 49060 USA

MADG
School of Biology and Petit Institute for Bioengineering and Bioscience
Georgia Institute of Technology
310 Ferst Drive
Atlanta, GA 30332-0230
USA

RG
Department of Evolution & Ecology
College of Biological Sciences
1 Shields Avenue
UC Davis
Davis, CA 95616
USA

CMG
Center for Pollinator Research
Huck Institutes of the Life Sciences
Pennsylvania State University
Chemical Ecology Lab 4A

University Park, PA 16802 USA

P-HG

Muséum National d'Histoire Naturelle, CP39, 12 rue Buffon 75005 Paris France

DG

Biology Department
University of Toronto
3359 Mississauga Road
Mississauga ON L5L 1C6 Canada

BH

Department of Animal & Plant Sciences
University of Sheffield
Western Bank
Sheffield S10 2TN
UK

HH+LS

University of Helsinki
Department of Biosciences POB 65, FI-00014
University of Helsinki, Finland

JH

Biologie I
Universität Regensburg
D-93040 Regensburg, Germany

KH

Department of Biology
University of Vermont
Burlington, VT 05405, USA

KH

School of Human Evolution and Social Change
Arizona State University
Tempe, Arizona 85287-2402 USA

ETK

Department of Animal Ecology, Institute of Ecological Science
Faculty of Earth and Life Sciences, Vrije Universiteit
De Boelelaan 1085
NL-1081 HV Amsterdam
The Netherlands

HK

Evolution, Ecology and Genetics, Research School of Biology (Banks
Building 44), Australian National University, Canberra, ACT 0200,
Australia

JK
Animal Ecology Group, Centre for Evolutionary and Ecological Studies
University of Groningen, PO Box 14
9750 AA Haren
The Netherlands.

JK
University of Osnabrueck
Barbarastr.11
D-49076 Osnabrueck
Germany

DK
Harvard University
Museum of Comparative Zoology
26 Oxford St
Cambridge, MA 02138
USA

RK
Environmental Microbiology
Swiss Federal Institute of Aquatic Research and Technology
Überlandstrasse 133
CH-8600 Dübendorf
Switzerland

SL
School of Biological Sciences
Royal Holloway, University of London
Egham TW20 0EX, UK

BL
Department of Ecology and Evolutionary Biology
University of California
Santa Cruz, CA 95064, USA

JARM
Department of Computer Science
University of Sheffield
Sheffield UK

RMc
Department of Anthropology and Center for Population Biology
UC Davis, Davis CA 95616 USA

REM
Dept. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721

DM
Dept. of Zoology

730 Van Vleet Oval
University of Oklahoma
Norman, OK 73019 USA

TM
Laboratoire Écologie & Évolution CNRS UMR 7625
Université Pierre et Marie Curie
7 quai St Bernard, Bâtiment A 7ème étage, Case 237
75 252 Paris Cedex 05, France

RM
Dept Biology
Queen's University
Kingston
Ontario K7L 3N6
Canada

UGM
Integrative Biology
University of Texas at Austin
1 University Station #C0930
Austin, TX 78712, USA

RN
Psychologie - Université de Strasbourg
Ethologie des Primates - DEPE (IPHC CNRS UMR 7178) 23 rue Becquerel -
Strasbourg 67087 CEDEX - France

SO
Department of Philosophy,
University of Bristol,
Bristol BS8 1TB, U.K.

PP
Biocenter Oulu and Department of Biosciences
University of Helsinki
Box 65
00140 University of Helsinki
Finland

GP
Institute of Integrative Biology
Biosciences Building
Crown Street
University of Liverpool
LIVERPOOL L69 7ZB UK

IP
Theoretical Biology group
University of Groningen

PO Box 14, 9750 AA Haren, The Netherlands

JP + TL
Centre for Social Evolution
Department of Biology
University of Copenhagen
Universitetsparken 15
DK-2100 Copenhagen
Denmark

DP
Department of Biology
CB#3280, Coker Hall
University of North Carolina
Chapel Hill, NC 27599-3280 USA

DQ
Department of Ecology and Evolutionary Biology
Rice University
Houston TX, USA

DJR
Department 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)

GR
Centre for Behaviour & Evolution, Institute of Neuroscience
Faculty of Medical Sciences, Newcastle University
Henry Wellcome Building, Framlington Place
Newcastle upon Tyne, NE2 4HH

SKAR
School of Marine & Tropical Biology
James Cook University QLD 4811
Australia

DR
Station Biologique de Roscoff, CNRS-UPMC UMR 7144, 29680 Roscoff, France

FR
Institut des Sciences de l'Evolution
University of Montpellier 2
Montpellier, France

MR

Research Department of Genetics, Evolution and Environment
Faculty of Life Sciences
University College London
4 Stephenson Way
London NW1 2HE, UK

OR

Department of Biology
Univ. North Carolina at Greensboro
312 Eberhart Bldg.
Greensboro, NC 27403, USA

JS

Department of Biology
3314 Spieth Hall
University of California - Riverside
Riverside, CA 92521

PS-H

ETH Zurich
Institute of Integrative Biology (IBZ)
Universitätsstrasse 16
CH.8092 Zürich
Switzerland

TS-P

School of Philosophy, Psychology and Language Sciences
University of Edinburgh
3 Charles Street
Edinburgh
EH8 9AD

DMS

School of Biology
University of St Andrews
Harold Mitchell Building
St Andrews
Fife KY16 9TH
UK

JCS

Assistant Professor of Biology
William Paterson University of New Jersey
300 Pompton Rd., Wayne NJ 07470

BS

Department of Anthropology
101 West Hall
University of Michigan
Ann Arbor Michigan 48109

AS

Department of Entomology and Department of Animal Biology
University of Illinois, Urbana, IL 61801

MT

Behavioural Ecology
Institute of Ecology and Evolution
University of Bern
Wohlenstrasse 50a
CH-3032 Hinterkappelen
Switzerland

GT

Department of Biology
University of Western Ontario
1151 Richmond Street North
London, Ontario N6A 5B7
Canada

JT

Department of Anthropology
University of California
Santa Barbara CA 93106-3210 USA

NDT

Department of Environmental Science, Policy and Management
130 Mulford Hall, #3114
University of California Berkeley
Berkeley CA, US

KT

Faculty of Agriculture
University of the Ryukyus
Okinawa 903-0213, Japan

ST

Dipartimento di Biologia Evoluzionistica
Università degli Studi di Firenze,
via Romana 17, 50125 Firenze, Italy

FU

Department of Ecology and Evolutionary Biology
University of Tennessee Knoxville
Knoxville, TN 37902, USA

BV

Institute for Theoretical Biology
Humboldt University zu Berlin
Invalidenstr. 43, D-10115 Germany

ELV
Department of Entomology
Box 7613
North Carolina State University
Raleigh, NC 27695-7613, U.S.A.

MJW-E
Smithsonian Tropical Research Institute
Apartado 0843-03092
Balboa, Panamá

TW
Dept. of Biology, Zoological Institute, K.U.Leuven,
Naamsestraat 59, B-3000 Leuven, Belgium

DW
Department of Biology
101 Morgan Building
University of Kentucky
Lexington, KY 40506-0225 USA

RW
Department of Human Evolutionary Biology
Harvard University
Cambridge MA, USA

DZ + JZ
Department of Biology & Program in Ecology
Evolution & Conservation Biology
University of Nevada
Reno, NV 89557 USA

AZ
Department of Biology
San Francisco State University
San Francisco, CA 94132

(Authors in alphabetical order)