



Preface

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One contribution of 18 to a theme issue 'The evolution of cooperation based on direct fitness benefits'.

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Author for correspondence:

Michael Taborsky
e-mail: michael.taborsky@iee.unibe.ch

The evolution of cooperation based on direct fitness benefits

Michael Taborsky¹, Joachim G. Frommen¹ and Christina Riehl²

¹Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

²Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

MT, 0000-0002-1357-4316

The evolution of cooperation remains a central paradox in biology. As Charles Darwin remarked in *On the Origin of Species* [1], "Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each". An operation harming the actor at the benefit of somebody else cannot be easily explained by the theory of natural selection. For this reason, Darwin regarded sterility in female insects to be "by far the most serious special difficulty, which my theory has encountered" [1]. When dealing with human evolution in *The Descent of Man* [2], Darwin further expounded "He who was ready to sacrifice his life... rather than betray his comrades, would often leave no offspring to inherit his noble nature... Therefore, it seems scarcely possible... that the number of men gifted with such virtues... could be increased through natural selection, that is, by the survival of the fittest".

Much progress has been made on the paradox of cooperation since the publication of Darwin's epochal work. Major advances include the development of kin selection theory [3] and the insight that all major transitions in biological evolution from simple to complex structures are characterized by some degree of cooperation and sacrifice [4]. But despite decades of study, the 125th anniversary issue of the journal *Science* still identified the question of 'how did cooperative behaviour evolve?' as one of the top 25 challenges scientists would be facing over the next quarter-century [5].

To take up this challenge, we organized two symposia on the evolution of cooperation based on direct fitness benefits in Arolla, Switzerland (supported by CUSO) and at the VIIth ECBB in Prague, Czech Republic. The current theme issue originated at these meetings because the stimulating discussions decidedly revealed that this subject has not received the scientific attention it deserves. Several of the contributors to these meetings have agreed to contribute to this special theme issue, in addition to other experts we invited to share their results, concepts and views on this topic with us. The resulting theme issue on 'The evolution of cooperation based on direct fitness benefits' combines 17 articles that are closely linked by a common question: what mechanisms promote cooperation between unrelated individuals, and how is such cooperation evolutionarily stable? This question is not new (cf. [6]), but it has received increased attention over the past several years, driven by new empirical data as presented in [7–11], as well as by novel theoretical and conceptual approaches [12–16]. Empirically, there is a growing realization that the direct fitness benefits of cooperation must be quantified as carefully as kin-selected benefits have been in the past [17]. Studies on human hunter–gatherer societies, for instance, as well as on natural groups of non-human primates and cooperatively breeding vertebrates have provided opportunities for direct measurements of reciprocity and negotiation [18,19]. Theoreticians have moved beyond the tit-for-tat models of reciprocity that held sway over this field for many years, and are now building more complex models to understand cooperation in larger, multi-level societies [20–22] and to consider the importance of individual variation in the evolution of such societies [23].

We have structured this theme issue in three main parts focusing on the evolution of cooperation based on direct fitness benefits at the levels of (i) theoretical models, (ii) animal societies and (iii) humans. We are confident that

the contributions to this theme issue will advance the research field by synthesizing our current understanding of cooperation between non-kin, and by pointing out problems that are still outstanding.

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