

## COMMENTARY

## Much ado about nothing: Nowak *et al.*'s charge against inclusive fitness theory

F. ROUSSET\* &amp; S. LION†

\*Université Montpellier II, CNRS, Institut des Sciences de l'Évolution, Montpellier Cedex, France

†Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, CNRS, Montpellier, France

### Keywords:

altruism;  
 editorial policies;  
 eusociality;  
 evolutionary theory;  
 inclusive fitness.

### Abstract

In a recent article, Nowak *et al.* claim that the mathematical basis of inclusive fitness theory does not stand to scrutiny and to have found an alternative explanation for eusociality. We show that these claims are based on false premises, many of which have been exposed more than 25 years ago, such as misrepresentations of the basic components of inclusive fitness and fallacious distinctions between individual fitness and inclusive fitness. Moreover, some limitations ascribed to inclusive fitness are actually limitations of current evolutionary theory, for which Nowak *et al.* propose no new solution. Likewise, their assertedly 'common sense' empirical alternative to estimating inclusive fitness is not applicable in cases of interest. Finally, their eusociality model merely confirms the importance of all the components of inclusive fitness. We conclude by discussing how rhetorical devices and editorial practices can impede scientific endeavours.

Why would an individual sacrifice its own reproduction to the benefit of the reproduction of others is one of the central questions in evolutionary biology. Selection on a behavioural trait can be thought of at the level of the average reproductive success of all copies of an allele affecting the trait (the gene-centred view well popularized by Dawkins, 1989). Hamilton (1964) proposed to evaluate the effect of an allele on this average in the form  $-c + rb$ , where  $-c$  is a fitness cost of the alternative behaviour, and  $rb$  is the expected benefit to individuals, partitioned in terms of the benefit  $b$  received from an individual with deviant strategy, and of the relatedness coefficient  $r$  that measures how much this benefit is likely to be received by an individual with deviant strategy rather than by a random individual in the population. It then appears that individual sacrifice is favoured by selection only if  $rb - c > 0$  (Hamilton's rule), and in particular if relatives of the sacrificing individual preferentially recover benefits from the sacrifice, a fact known as kin selection. Evolutionary biologists have

built on such foundations to understand various forms of social evolution, ranging from the spectacular organization of ant societies to virtually any behaviour that involves interactions between individuals (e.g. Krebs & Davies, 1993).

A recent paper by Nowak *et al.* (2010) in *Nature* received much media coverage by claiming to have found a new and more general explanation for social behaviour. Our aim is to clarify some of the scientific issues raised by Nowak *et al.* (hereafter NTW). In particular, we show that the mathematical results underpinning their claim are neither new nor general and that their criticisms of the mathematical foundations of inclusive fitness theory are based on severe misrepresentations of the latter. Similar misrepresentations can be found in their rewriting of the history of inclusive fitness theory, as illustrated by the role of haplodiploidy. This role was actually described as 'central' in Wilson (1975), whereas it has been more critically assessed in the line of works that NTW criticize (e.g. Crozier & Pamilo, 1996; Queller & Strassmann, 1998; Foster *et al.*, 2006; Crozier, 2008; and notably Hamilton's (1972) own warning that this role 'must not be overemphasized'). We conclude that the paper owes its impact as much to the slow diffusion of modern ideas in inclusive fitness

Correspondence: François Rousset, CC065, ISEM, USTL, Pl. E. Bataillon, 34095 Montpellier Cedex, France.  
 Tel.: +33 4 67 14 36 22; fax: +33 4 67 14 36 28;  
 e-mail: francois.rousset@univ-montp2.fr

theory as to the use of rhetorical tricks that impede critical thinking and argue that the publication of this article illustrates more general concerns about the publishing process.

At this point, a disclaimer may be needed. Our aim is not to claim that Hamilton's rule solves all questions about social behaviour; indeed, our own work in this field has focused on issues that either were not fully addressed in Hamilton's original analysis or are not fully answered simply by applying Hamilton's rule, how correct it may be. Similarly, we do not doubt inclusive fitness has been misused (any valid idea is), nor would we want to argue that all theoreticians should abjure their favourite modelling approach and embrace inclusive fitness. But if taken seriously, the misrepresentations spread by NTW would bring us decades back in our understanding of social behaviour (Okasha, 2010). Indeed, many of their criticisms of inclusive fitness theory have been well answered more than 25 years ago (Grafen, 1982, 1984, 1985).

### Nothing new under the Sun

A key point of NTW's argument, exposed in their Appendices A4 and A5, is that Hamilton's rule  $br > c$  supposedly almost never holds. However, NTW's analysis is based on faulty premises, because the  $b$  and  $c$  parameters they use are not the *fitness* cost and benefit of Hamilton's rule, but only the cost and benefit in terms of some vital rates, such as juvenile production (i.e. the pay-offs, in the language of game theory). This is important, because when deriving Hamilton's rule, it is crucial to take into account all effects of the behaviour on the number of descendants after one full iteration of the life cycle (*fitness*) in the computation of the fitness cost ( $c$ ) and benefit ( $b$ ). This point was already clear to Hamilton (1964, 1970, 1975) and has been repeated in various forms since (e.g. Grafen, 1982; Taylor, 1992; Rousset, 2004; Lehmann & Keller, 2006). Hence, in contrast with NTW's claim that inclusive fitness theory is characterized by a 'narrow focus on relatedness,' inclusive fitness theory is actually rooted in ecology, because the cost and benefit of Hamilton's rule, when properly written, depend on demographic, ecological and genetic assumptions (Lion & van Baalen, 2008; Lehmann & Rousset, 2010). NTW's message is nevertheless seductive, as the distinction between pay-off and fitness is often left implicit in expositions of inclusive fitness theory. Yet, misrepresentations of the components of Hamilton's rule have been pointed out repeatedly (Grafen, 1982, 1984; Dawkins, 1989), and theoreticians have developed simple analytical techniques to avoid such fallacies. In particular, in the direct fitness formalism (Taylor & Frank, 1996),  $c$  and  $b$  can be expressed in terms of the individual fitness function (see Lehmann & Rousset, 2010 for a recent review), making explicit the meaning of these coefficients.

NTW also oppose the inclusive fitness and the neighbour-modulated perspectives both introduced by Hamilton (1964). In the neighbour-modulated view of individual fitness, effects on individual fitness ( $-c + rb$ ) are analysed by adding the expected benefits  $rb$  received from neighbours to the cost  $-c$  of the sacrifice. In the inclusive fitness perspective, the same effects  $-c + rb$  on individual fitness are analysed by adding the expected benefits received by genetically similar neighbours to the cost of the sacrifice (indeed this is only a 'verbal presentation' that comes after the mathematical argument in Hamilton's paper). NTW attempt to argue that 'inclusive fitness' is mathematically flawed, but as they misinterpret  $c$  and  $b$ , they have a basis neither to discuss whether the  $-c + rb$  formula is valid, nor more specifically whether the inclusive fitness interpretation of this formula is valid. Hamilton's rule is a representation of the average effect on the fitness of bearers of an allele and thus cannot be meaningfully opposed to individual fitness. When Hamilton's rule is valid, it is valid independently of its verbal interpretation. Consequently, theoreticians who use the neighbour-modulated derivation often call the result inclusive fitness (e.g. Taylor & Frank, 1996; Rousset & Billiard, 2000).

More generally, NTW oppose 'natural selection versus kin selection' (the title of their Appendix 1), a distinction already well criticized by Dawkins (1979). This distinction is void because all concepts of inclusive fitness theory aim at analysing natural selection (Abbot *et al.*, in press). NTW's argument also rests upon an artificial distinction between inclusive fitness theory and evolutionary game theory (EGT). This distinction ignores the specifics of EGT as developed and applied in the biological literature, compared to its traditional economic version. In biology, one more often considers traits with continuous sets of possible values (e.g. any sex ratio may be produced by some mutant) and one seeks a strategy that may evolve by successive allele replacements (this is known as convergence stability; Eshel, 1983, 1996; Geritz *et al.*, 1998). The direction of selection is given by the sign of the selection gradient, and potential unbeatable strategies are those where the selection gradient vanishes. The weak selection version of inclusive fitness provides an often efficient way to compute the selection gradient, which explains its widespread use to identify unbeatable strategies in the most successful applications of EGT such as sex ratio evolution (e.g. Hamilton, 1979; Boomsma & Grafen, 1991; Frank, 1998; Hardy, 2002; West, 2009). Here, weak selection means that mutational effects on expected individual fitness are small, whether they result from small allelic effects on individual phenotypes (as classically assumed to determine convergence stable strategies) or more generally from small differences in pay-offs of different sets of interacting genes or individuals as in Roze & Rousset (2003); Wild & Traulsen (2007), or Ohtsuki (2010). Clearly, the weak selection version of inclusive fitness

has the same limitations as the notion of the selection gradient itself. In particular, it is not sufficient to fully characterize evolutionary stability in continuous games, but again, this is a well-known point (Eshel, 1983; Day & Taylor, 1998; Ajar, 2003). As we show in the next section, NTW have nothing new to propose.

Finally, another old debate revisited by NTW is whether the  $r$ ,  $b$  and  $c$  in Hamilton's rule must be measured exactly under arbitrarily strong selection or only taken as approximations under weak selection. Each interpretation has a long history and different uses. A general exact version is based on an equally general linear regression formalism that handles nonadditive effects (e.g. Gardner *et al.*, in press). This general formalism can serve as a basis to support claims that intergroup selection works only if groups are made of related individuals (Hamilton, 1975; Grafen, 1984). However, an exact computation can in general only be achieved numerically (as in NTW's Appendix C). Furthermore, behavioural ecologists generally need a broad approximation for the direction of selection on a trait rather than an exact result for a precise set of segregating alleles, a point that has also long been made (Maynard Smith, 1982, p. 4; Grafen, 1982, 1985, p. 79). The aim of a theoretical analysis is then to provide general approximations rather than exact results, and such approximations have been derived from the weak selection version of inclusive fitness, where the different terms of the regression have narrower meaning and are tied to their most relevant determinants (e.g. genealogical ties for relatedness). In such respects, inclusive fitness is not different from selection gradient approximations classically used in quantitative genetics and artificial breeding. We do not claim that these are the only possible nor the best approaches, but NTW do not propose anything new to solve this issue.

It is easy to criticize the exact version as being a black box and the gradient version as not being exact, but these weaknesses are not specific to inclusive fitness *per se*. Besides, from a mathematical point of view, such criticisms are becoming increasingly obsolete as analytical tools from inclusive fitness theory can be used to compute approximations that are more accurate than the phenotypic gradient version, yet retain some of its ease of interpretation. These analytical tools have been used to investigate the consequences of different genetic architectures (e.g. Roze & Rousset, 2004; Lehmann *et al.*, 2009; Roze, 2009) and to more fully characterize different concepts of evolutionary stability (e.g. Ajar, 2003; Ladret & Lessard, 2007; Ohtsuki, 2010). In particular, the two assumptions (additivity and 'nongeneric' population structure) that the authors affirm to have identified as 'necessary for inclusive fitness theory to be defined and to work' have already been addressed by inclusive fitness theory. Approximations have been derived to account for nonadditive interactions between individuals (or between genes, as per Mendelian dominance relation-

ships). Ohtsuki (2010) provides a clear recent account of this issue. As for 'nongeneric' population structures, they can be handled by the class-structured version of inclusive fitness (Taylor, 1990; Taylor & Frank, 1996), which generalizes the  $rb - c$  formula and also allows to take into account more complex population dynamics (Rousset & Ronce, 2004; Alizon & Taylor, 2008; Wild *et al.*, 2009; Lehmann & Rousset, 2010). We are not saying that the resulting analyses are necessarily easy, but by ignoring the class-structured version, NTW attack a straw man.

### 'Superior approach' or black box?

The previous analysis shows that NTW's article is actually a collection of old points about the potential limitations of inclusive fitness theory, which is based on severe misrepresentations of the latter. But is the 'simpler and superior approach' they advocate useful? Turning to Theorem 1 in their Appendix A, which NTW claim is their main result, it is striking that NTW have nothing new to propose. Their Theorem 1, which simply embodies the old idea of mutation-selection balance, adds nothing to the large body of theoretical work in evolutionary game theory and adaptive dynamics. In fact, it was already a starting point of previous works (Rousset & Billiard, 2000; Taylor *et al.*, 2007). Eqn (10) in the appendix of NTW is just equation (3.2) of Taylor *et al.* (2007), for example. To be precise, Taylor *et al.* (2007) derived their result for the Moran process, and NTW for a broader class of stochastic processes. But this is an obvious generalization from previous works, which was no more helpful for the purpose of these studies than it is currently. Significantly, Taylor *et al.* do not claim this as a new result, and rightly trace it back to Price (1970). Hence, Theorem 1 of NTW is not new; nor is it useful as it stands, because in general it provides a condition for evolution that can often only be evaluated numerically, thereby providing no useful biological insight, and potentially paving the way for misinterpretations.

Second, NTW describe their Theorem 1 as 'a general mutation-selection analysis, which does not assume a particular process or dynamics' when in fact the derivation of their Theorem 1 relies on the assumptions that reproduction is clonal and that population size is constant. In its current form, Theorem 1 does not take into account important aspects of ecological realism (e.g. demographic fluctuations and species interactions). In contrast, the class-structured version of inclusive fitness provides analytical results to take into account various forms of demographic or epidemiological fluctuations (Ronce *et al.*, 2000; Rousset & Ronce, 2004; Lehmann *et al.*, 2006; Alizon & Taylor, 2008; Wild *et al.*, 2009). These results are not always simple, but they have allowed inclusive fitness theoreticians to tackle biological problems for which NTW seem only to have a numerical or simulation approach to offer. Alternative results have also been derived using different techniques to shed light

on the evolution of helping in undersaturated habitats (van Baalen & Rand, 1998; Lion & Gandon, 2010) or on the evolution of host–parasite interactions (Lion & Boots, 2010). Such approaches provide helpful interpretations in terms of inclusive fitness. Thus, even when using other methodological approaches, experience shows that understanding the links between one's results and existing theory, such as the conceptual framework of inclusive fitness theory, is both a way to move forward and a safeguard against rediscovering special cases of known results (e.g. Nowak, 2006), as previously emphasized by Lehmann *et al.* (2007).

Of course, NTW's Theorem 1 could readily be extended beyond these assumptions (see e.g. Day & Gandon (2007) for an epidemiological application in unstructured populations), but the resulting approach would not necessarily be 'simpler' or 'superior,' despite what NTW argue. In particular, whether one needs to fully account for the effects of mutation will depend on the biological question of interest, and the usefulness of the approach advocated by NTW, when applicable, can only be demonstrated based on the new theoretical or biological insight it provides. Instead of presenting such a demonstration, NTW seem satisfied with pointing the way to numerical calculations that rely on a straightforward extension of Price's equation and have long been known to be feasible (Price, 1970; Rousset & Billiard, 2000; Taylor *et al.*, 2007), although not necessarily satisfying.

From a data analytic point of view, NTW argue that inclusive fitness is hard to evaluate from empirical data and claim in their Appendix A7 that their result (15) is a 'common sense' solution to this problem. It is true that it is often difficult to estimate all fitness effects of a trait, whether an inclusive fitness perspective is taken or not. Again, we note this is neither a new point (e.g. Grafen, 1984; Oli, 2003; Komdeur *et al.*, 2006) nor a specific problem of inclusive fitness theory. But NTW's alternative is simply inapplicable in real populations where for instance traits are not always expressed by all bearers of an allele, in which case an inclusive fitness formulation can be more applicable (Grafen, 1984). For example, with helpers at the nest (Grafen, 1984; Komdeur *et al.*, 2006), relatedness can serve as a statistical predictor of the probability that beneficiaries bear a deviant helping allele which they are not in a position to express. More fundamentally, the usefulness of an inclusive fitness framework does not rest on the ease of estimating all components of inclusive fitness, no more than the usefulness of a gravitational theory rests on separately measuring the different forces that may affect the motion of planets. Rather, theories are tested by checking key assumptions and deductions from such assumptions. Tests of deductions from inclusive fitness theory are often comparative, examining a range of ecological conditions and behavioural outcomes across populations and species (Frank, 1998; West, 2009).

NTW also argue that inclusive fitness theory is being forced to 'use quantities that no empirical biologist could measure or call 'relatedness.' Theoretical works sometimes do use rather abstract relatedness concepts, in particular to address the consequences of 'stepping stone' dispersal (e.g. Taylor *et al.*, 2007), but even in this case, as under simpler assumptions (Queller & Goodnight, 1989), one can analyse the mathematical models in terms of relatedness coefficients that are easy to estimate from genetic markers (e.g. Lehmann & Rousset, 2010, section 5) and that have indeed been estimated in hundreds of studies of spatial population structure. Thus, NTW's criticisms of data analytic aspects are either spurious or point to difficulties inherent to the subject, for which they provide no solution.

It is striking to see that the theorem they develop in their Appendix A (assertedly a general theorem and their main result) has no clear bearing on the model for the evolution of eusociality developed in Appendix C. Crucially, none of the seven numbered conclusions NTW draw from their model refers to a specific claim from inclusive fitness theory. For example, their claims that queen and workers are not engaged in a 'standard cooperative dilemma' and that 'there is no pay-off matrix' are irrelevant to the validity of inclusive fitness arguments. Their claim that 'relatedness does not drive the evolution of eusociality' only rests on the fact that in their model, 'the relatedness parameters would be the same for all species' and that 'whether or not eusociality evolves depends on the demographic parameters of the queen.' But the diversity of population structures out of which eusociality did *not* evolve is much larger, and equally important to consider in any argument about this evolution. Because they do not vary relatedness, NTW cannot show that it is not a driver of eusociality and their model only confirms that for fixed nonzero relatedness, selection depends on both  $b$  and  $c$  (Abbot *et al.*, in press).

We fail to see how NTW's results will help us solve open biological questions. Importantly, NTW do not provide any new mathematical tools to tackle the interplay between ecology and evolution, and their eusociality model is simply a numerical black box, which is therefore open to misinterpretations. We think the replacement of an analytical framework by a numerical model is a step backward, because it paves the way for the kind of verbal arguments against which both inclusive fitness and evolutionary game theoreticians have long fought a hard battle.

### The rhetoric of social evolution

We think the publication of this article in a high-profile journal, along with the large media coverage it received, is an illustration of some serious shortcomings in current scientific practice. Arguably, the impact of NTW's paper reflects to a large extent the rhetorical ability of the

authors, rather than the scientific value and novelty of the paper.

The format of the paper itself is an obstacle to scientific communication. The article has two parts: a short illustrated essay for the general reader and a 43-page online mathematical Appendix. Readers who are not mathematically inclined or simply short on time may be tempted to simply trust the authors and gauge the scientific value of the paper based on the 'weight' of the supplementary material or on the prestige of the authors. But as we have just shown, there is no significant mathematical novelty in this work. This latter point is best illustrated by the fact that their asserted main result is only the starting point of a recent paper by Taylor *et al.* (2007), although NTW do not cite this paper in regard to it.

Stylistically, the paper often departs from the neutrality of scientific prose, using a variety of rhetorical tricks typically found in the discourses of politicians or the writings of polemicists, rather than in academic articles. When they ask falsely evident rhetorical questions,<sup>1</sup> liken inclusive fitness theory to geocentrism, or claim without justification that their approach is 'common sense' (their Appendix, p. 20), NTW are a long way away from what is generally expected of scientific discourse.

In particular, it is troubling to see the authors turn to the argument of geocentrism and its unfalsifiable epicycles to discredit inclusive fitness (their Appendix). The allusion to 'Darwinian epicycles' is indeed a typical rhetorical trick used to attack evolutionary biology.<sup>2</sup> Rhetoric aside, NTW are confused about epicycles in a way that is revealing about the utility of inclusive fitness theory. Epicycles are not specific to geocentrism: they were needed in Copernicus' heliocentric theory as well, because it still rested on circular orbits, and it was not until Kepler's theory of elliptic orbits that epicycles were laid to rest. As Poincaré (1905) emphasized, geocentrism and heliocentrism are logically equivalent ways of accounting for celestial motion. The value of heliocentrism is that it makes sense through one factor (Earth's rotation) of phenomena that appear as coincidences in the geocentric perspective. Hamilton's rule (whether in the inclusive or neighbour-modulated perspectives) has the same value, in revealing common features of individual fitness across a range of biological scenarios.

<sup>1</sup>E.g. 'if we have a theory that works for all cases (standard natural selection theory) and a theory that works only for a small subset of cases (inclusive fitness theory), and if for this subset the two theories lead to identical conditions, then why not stay with the general theory?', in the main text.

<sup>2</sup>See for instance Discovery Institute fellow C. Hunter's interview at [http://www.evolutionnews.org/2009/06/darwins\\_failed\\_predictions\\_an021311.html](http://www.evolutionnews.org/2009/06/darwins_failed_predictions_an021311.html) and his website <http://www.darwinspredictions.com>.

## The fragility of scientific publishing

We think the wide impact of an article that rests on such fragile foundations calls into question the efficiency of the editorial process in the most famous scientific journals. Nature's extravagant editorial characterization of the paper as 'the first mathematical analysis of inclusive fitness theory' recklessly tramples on nearly 50 years of accumulated knowledge. It is often said that science is self-correcting, but this can be so only if authors are engaged by the validity of what they are writing, if reviewers are engaged in the same way, and if science, rather than only media buzz, impact, and citations, matters to editors. These conditions are not necessarily fulfilled. Part of the problem lies in the increasingly specialized nature of science, and the increasing number of techniques that scientists have to handle. Students of ant societies, for example, may have to spend substantial effort in the field, yet they also have to care about possible artefacts of molecular markers, to understand the limits of various statistical methods, to understand some of the mathematical theory of evolution and to navigate through an increasingly large literature. Faced with such burden, both readers and journal editors have growing incentives to abandon critical thinking for more social considerations such as the prestige of the authors. Sometimes, the prospect of a 'hot' controversy seems to be enough to lure the editorial board into accepting a manuscript. Despite their claims of novelty and the media frenzy, NTW's article is actually a collection of worn-out arguments and thus represents a conceptual and technical step backward. Importantly, it does not provide any new theoretical tools or concepts to address the many exciting biological questions for future research on social evolution and structured populations.

## Acknowledgments

We thank Minus van Baalen, Sylvain Gandon, Vincent Jansen, Laurent Keller, Laurent Lehmann, Allen Moore, David Queller and Stuart West for helpful comments on a previous version of the manuscript.

## References

- Abbot, P., Abe, J., Alcock, J., Alizon, S., Alpedrinha, J.A.C., Andersson, M., *et al.* (137 co-authors) in press. Inclusive fitness theory and eusociality. *Nature* **471**, doi: 10.1038/nature09832.
- Ajar, É. 2003. Analysis of disruptive selection in subdivided populations. *BMC Evol. Biol.* **3**: 22.
- Alizon, S. & Taylor, P. 2008. Empty sites can promote altruistic behavior. *Evolution* **62**: 1335–1344.
- van Baalen, M. & Rand, D.A. 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* **193**: 631–648.
- Boomsma, J.J. & Grafen, A. 1991. Colony-level sex ratio selection in the social Hymenoptera. *J. Evol. Biol.* **3**: 383–407.

- Crozier, R.H. 2008. Advanced eusociality, kin selection and male haploidy. *Aust. J. Entomol.* **47**: 2–8.
- Crozier, R.H. & Pamilo, P. 1996. *Evolution of Social Insect Colonies*. Oxford University Press, Oxford.
- Dawkins, R. 1979. Twelve misunderstandings of kin selection. *Z. Tierpsychol.* **51**: 184–200.
- Dawkins, R. 1989. *The Selfish Gene*, 2nd edn. Oxford University Press, Oxford.
- Day, T. & Gandon, S. 2007. Applying population-genetic models in theoretical evolutionary epidemiology. *Ecol. Lett.* **10**: 876–888.
- Day, T. & Taylor, P.D. 1998. Unifying genetic and game theoretic models of kin selection for continuous traits. *J. Theor. Biol.* **194**: 391–407.
- Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.* **103**: 99–111.
- Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *J. Math. Biol.* **34**: 485–510.
- Foster, K.R., Wenseleers, T. & Ratnieks, F.L.W. 2006. Kin selection is the key to altruism. *Trends Ecol. Evol.* **21**: 57–60.
- Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton.
- Gardner, A., West, S.A., & Wild, G. in press. The genetical theory of kin selection. *J. Evol. Biol.*, doi: 10.1111/j.1420-9101.2011.02236.x.
- Geritz, S.A.H., Kisdi, É., Meszéna, G. & Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**: 35–57.
- Grafen, A. 1982. How not to measure inclusive fitness. *Nature* **298**: 425–426.
- Grafen, A. 1984. Natural selection, kin selection and group selection. In: *Behavioural Ecology. An Evolutionary Approach* (J.R. Krebs & N.B. Davies, eds), pp. 62–84. Blackwell, London.
- Grafen, A. 1985. A geometric view of relatedness. *Oxford Surv. Evol. Biol.* **2**: 28–89.
- Hamilton, W.D. 1964. The genetical evolution of social behavior I. *J. Theor. Biol.* **7**: 1–16.
- Hamilton, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**: 1218–1220.
- Hamilton, W.D. 1972. Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.* **3**: 193–232.
- Hamilton, W.D. 1975. Innate social aptitudes in man, an approach from evolutionary genetics. In: *Biosocial Anthropology* (R. Fox, ed.), pp. 133–157. Malaby Press, London.
- Hamilton, W.D. 1979. Wingless and fighting males in fig wasps and other insects. In: *Sexual Selection and Reproductive Competition in Insects* (M. Blum & N. Blum, eds), pp. 167–220. Academic Press, New York.
- Hardy, I.C.W. (ed.) 2002. *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, Cambridge.
- Komdeur, J., Richardson, D. & Burke, T. 2006. Fitness consequences of cooperative breeding in the Seychelles warbler. *Acta Zoologica Sinica* **52**: S257–S261.
- Krebs, J.R. & Davies, N.B. 1993. *An Introduction to Behavioural Ecology*. Blackwell, Oxford.
- Ladret, V. & Lessard, S. 2007. Fixation probability for a beneficial allele and a mutant strategy in a linear game under weak selection in a finite island model. *Theor. Popul. Biol.* **72**: 409–425.
- Lehmann, L. & Keller, L. 2006. The evolution of cooperation and altruism a general framework and a classification of models. *J. Evol. Biol.* **19**: 1365–1376.
- Lehmann, L. & Rousset, F. 2010. How life history and demography promote or inhibit the evolution of helping behaviours. *Philos. Trans. R. Soc. (Lond.) B* **365**: 2599–2617.
- Lehmann, L., Perrin, N. & Rousset, F. 2006. Population demography and the evolution of helping behaviors. *Evolution* **60**: 1137–1151.
- Lehmann, L., Keller, L., West, S. & Roze, D. 2007. Group selection and kin selection: two concepts but one process. *Proc. Natl. Acad. Sci. USA* **104**: 6736–6739.
- Lehmann, L., Feldman, M.W. & Rousset, F. 2009. On the evolution of harming and recognition in finite panmictic and infinite structured populations. *Evolution* **63**: 2896–2913.
- Lion, S. & van Baalen, M. 2008. Self-structuring in spatial evolutionary ecology. *Ecol. Lett.* **11**: 277–295.
- Lion, S. & Boots, M. 2010. Are parasites prudent in space? *Ecol. Lett.* **13**: 1245–1255.
- Lion, S. & Gandon, S. 2010. Life history, habitat saturation and the evolution of fecundity and survival altruism. *Evolution* **64**: 1594–1606.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science* **314**: 1560–1563.
- Nowak, M.A., Tarnita, C.E. & Wilson, E.O. 2010. The evolution of eusociality. *Nature* **466**: 1057–1062.
- Ohtsuki, H. 2010. Evolutionary games in Wright's island model: kin selection meets evolutionary game theory. *Evolution* **64**: 3344–3353.
- Okasha, S. 2010. Altruism researchers must cooperate. *Nature* **467**: 653–655.
- Oli, M.K. 2003. Hamilton goes empirical: estimation of inclusive fitness from life-history data. *Proc. R. Soc. (Lond.) B* **270**: 307–311.
- Poincaré, H. 1905. *La Valeur de la Science*. Flammarion, Paris.
- Price, G. 1970. Selection and covariance. *Nature* **227**: 520–521.
- Queller, D.C. & Goodnight, K.F. 1989. Estimating relatedness using genetic markers. *Evolution* **43**: 258–275.
- Queller, D.C. & Strassmann, J.E. 1998. Kin selection and social insects. *BioScience* **48**: 165–175.
- Ronce, O., Gandon, S. & Rousset, F. 2000. Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* **58**: 143–159.
- Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton University Press, Princeton, NJ.
- Rousset, F. & Billiard, S. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* **13**: 814–825.
- Rousset, F. & Ronce, O. 2004. Inclusive fitness for traits affecting metapopulation demography. *Theor. Popul. Biol.* **65**: 127–141.
- Roze, D. 2009. Diploidy, population structure, and the evolution of recombination. *Am. Nat.* **174**: S79–S94.
- Roze, D. & Rousset, F. 2003. Diffusion approximations for selection and drift in subdivided populations: a straightforward method and examples involving dominance, selfing and local extinctions. *Genetics* **165**: 2153–2166.
- Roze, D. & Rousset, F. 2004. The robustness of Hamilton's rule with inbreeding and dominance: kin selection and fixation probabilities under partial sib mating. *Am. Nat.* **164**: 214–231.
- Taylor, P.D. 1990. Allele-frequency change in a class-structured population. *Am. Nat.* **135**: 95–106.
- Taylor, P.D. 1992. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.* **6**: 352–356.

- Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.
- Taylor, P.D., Day, T. & Wild, G. 2007. From inclusive fitness to fixation probability in homogeneous structured populations. *J. Theor. Biol.* **249**: 101–110.
- West, S. 2009. *Sex Allocation*. Princeton University Press, Princeton, NJ.
- Wild, G. & Traulsen, A. 2007. The different limits of weak selection and the evolutionary dynamics of finite populations. *J. Theor. Biol.* **247**: 382–390.
- Wild, G., Gardner, A. & West, S.A. 2009. Adaptation and the evolution of parasite virulence in a connected world. *Nature* **459**: 983–986.
- Wilson, E.O. 1975. *Sociobiology*. Harvard University Press, Cambridge, MA.

*Received 17 January 2011; revised 31 January 2011; accepted 1 February 2011*