

CORRESPONDENCE

Replies to 'The evolution of eusociality' by Nowak et al. (Nature 466, 1057–1062; 2010). [SEE COMMENT P.653](#)

Call for a return to rigour in models

Why are numerous reactions to the Nowak *et al.* paper so ferocious? And how is it possible that theorists even seem to disagree about mathematics? An important key to the heatedness of the debate is that many theory papers on the evolution of cooperation use the Price equation. This is regularly treated as if its generality makes it the $E = mc^2$ of population genetics. Those who use it, however, tend to forget that it is only general because it contains no modelling assumptions. And without these, one cannot derive theoretical predictions.

The Price equation inspires theoreticians to confuse identity with causality, and probability theory with statistics (M. van Veelen *J. Theor. Biol.* 237, 412–426; 2005). It is this theoretical blur that obfuscates whether or not claims are theoretical results that follow from actual model assumptions.

References to 'results' derived with the Price equation are a recurring element in discussions of inclusive fitness. As long as the Price equation is thought useful for finding theoretical predictions, these 'results' will collide with results from actual models, which is a recipe for hot-headed debates.

Nowak and colleagues' paper is exciting because it goes back to basics: it builds proper models. Rather than saying the paper is wrong, it would be more fruitful if critics also went back to basics: state model assumptions, derive predictions, test empirically. Such a return to rigour would help the field advance to the next level.

Matthijs van Veelen, Julián García, Maurice W. Sabelis, Martijn Egas *University of Amsterdam, the Netherlands, c.m.vanveelen@uva.nl*