

## Evolution of social behaviour

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**Nowak et al.<sup>1</sup> wish to explain why the version of kin selection theory that is summarised by the formula  $R > c/b$  ( $c$ =cost of performing ‘altruistic’ act,  $b$ =benefit derived by recipient of act,  $R$ =relatedness between the two) is of little utility for understanding the evolution of eusociality. But in trying to do so they omit much that is relevant and risk misrepresenting the issue to anyone who is not familiar with the literature. A fairer account would include the following facts.**

- (1) Darwin said much more than implied by Nowak et al. He did regard the sterile worker caste in ants as one might a “well-flavoured vegetable [that] is destroyed”<sup>2</sup> and whose variety can be regenerated by sowing seeds from the same stock - an analogy that embodies the essence of kin selection. However, he did not stop at that. He added “..natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters”<sup>2</sup>. This, an analogy to the roles of the germ line and soma, is a possibility also advocated by Nowak et al. Elsewhere he pointed out that those members of a tribe who “...were always ready to aid one another, and to sacrifice themselves for the common good”, would leave behind fewer children than other members of the tribe but the tribe itself “..would be victorious over most other tribes; and this would be natural selection”<sup>3</sup> – essentially the same hypothesis that was investigated by Haldane<sup>4</sup> and Wright<sup>5</sup>, namely that within-group selection against ‘altruists’ could be counterbalanced by between-group selection that favoured groups with altruists disproportionately. In short, Darwin did not confine himself to a single explanation for the evolution of social behaviour.
- (2) Fisher<sup>6</sup> too, and not only Haldane, pointed out that a trait that is detrimental to its bearer (e.g., warning colouration) can spread by natural selection if its expression favours the survival of others who share genes with the bearer by common descent.
- (3) Surprisingly, Nowak et al. ignore the abundant literature on social behaviour in microorganisms. Much of it relates directly to their central contention. For example, both clonal<sup>7</sup> and multi-clonal<sup>8</sup> groups of cellular slime mould amoebae exist in nature. Some amoebae within the group sporulate and the rest die; laboratory experiments<sup>9,10</sup> show that genetic heterogeneity can exert a significant non-linear effect on the relative sporulation efficiencies of different genotypes. Irrespective of the level of genetic relatedness within a group, social behaviour can be interpreted as the outcome of selection between different autonomously

generated phenotypes<sup>11</sup>. Experiments with bacterial social groups show similar non-linear effects<sup>12, 13</sup> and point to the importance of demography and group effects as mediators of social behaviour. In both cases indices of ‘altruism’ are insensitive to genetic relatedness.

- (4) Readers who do not go through the Supplementary Material that is provided online may not realise that it was G. E. Price<sup>14</sup> who provided a general quantitative treatment for the evolution of a trait by natural selection acting at the individual level. His formulation emphasised that selection acts on phenotypes and that it is useful to think of selection and transmission as separate components of change<sup>15</sup>. It accommodated kin selection as a special case and showed that Hamilton’s ‘relatedness’  $R$  was a special case too – of a coefficient of regression.

## References.

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