☐ Multilevel and kin selection in a connected world

Arising from: G. Wild, A. Gardner & S. A. West *Nature* **459,** 983–986 (2009)

Wild *et al.*[1] argue that the evolution of reduced virulence can be understood from the perspective of inclusive fitness, obviating the need to evoke group selection as a contributing causal factor. Although they acknowledge the mathematical equivalence of the inclusive fitness and multilevel selection approaches, they conclude that reduced virulence can be viewed entirely as an individual-level adaptation by the parasite[1]. Here we show that their model is a well-known special case of the more general theory of multilevel selection, and that the cause of reduced virulence resides in the opposition of two processes: within-group and among-group selection. This distinction is important in light of the current controversy among evolutionary biologists in which some continue to affirm that natural selection centres only and always at the level of the individual organism or gene, despite mathematical demonstrations that evolutionary dynamics must be described by selection at various levels in the hierarchy of biological organization.

In the original group selection debate, reduced virulence was advanced as evidence for a trait that is selectively disadvantageous within groups but nevertheless evolves in the total population. The model by Wild *et al.*[1] affirms the need for group selection in this sense. We can illustrate this point and the equivalence between multi-level (group) and kin (inclusive fitness) selection approaches[1] using the standard Price[2] method to partition selection in their model into the sum of within ($\Delta W_{(k,l)_{\text{within}}}$) and among ($\Delta W_{(k,l)_{\text{among}}}$) group selection components.

$$\Delta W_{(k,l)_{\text{within}}} = [\delta(v_{(k,l-1)} - v_{(k,l)}) - \delta\beta'(z)(1-d_p)k(v_{(k,l)} - v_{(k-1,l+1)})]$$
$$(1 - r_{(k,l)})$$
$$+ \delta\beta'(z)\left[(1-d_p)k\ v_{(k-1,l+1)} + d_p\sum_{(i,j)} v_{(i,j)}(i+1)p_{(i+1,j-1)}\right]$$
$$- \delta v_{(k,l-1)}$$

$$\Delta W_{(k,l)_{\text{among}}} = [\delta(v_{(k,l-1)} - v_{(k,l)}) - \delta\beta'(z)(1-d_p))k(v_{(k,l)} - v_{(k-1,l+1)})]$$
$$r_{(k,l)}(l)$$

In which $\beta(z)$ is parasite transmissibility, z is parasite virulence, d_p is the rate at which parasite offspring 'disperse' to new, randomly chosen patches, i is the number of uninfected hosts, j is the number of infected hosts, class (k, l) is a patch with k uninfected hosts and l infected hosts, $r_{(k,l)}$ is the relatedness between two different parasites on the same class-(k, l) patch, $v_{(k, l)}$ is the reproductive value of a class-(k, l) parasite, and prime denotes differentiation.

Notably, the first component is individual selection under the multilevel perspective, which favours increased virulence, as others have shown[3]. It is the second group-selection component that favours reduced virulence. Thus, the reduction in optimal virulence does not seem to be the simple "individual-level adaptation" that the authors claim[1]. We believe that their privileging the inclusive-fitness perspective over the equivalent multilevel selection perspective is a research preference and not a scientific result. By their logic, models of meiotic drive might similarly be used to define individual-level adaptation out of existence. The Price formulation convinced Hamilton[4] that kin selection was group selection; indeed, the evolutionary response to group selection requires relatedness and that to kin selection requires an among-group selection differential[5].

We believe that the statement by Wild *et al.*[1] that "in clear contrast to recent claims[4–7], analysis of equation (1) shows that the effect of parasite dispersal on virulence can be explained entirely using inclusive fitness theory" is misleading. The work that they cite is clear about the equivalence between views, and none makes such a contrary claim. For example, Hölldobler and Wilson[6] state that "mathematical gene-selectionist (inclusive fitness) models can be translated into multilevel selection models and vice versa… One can travel back and forth between these theories with the point of entry chosen according to the problem being addressed." These are different views on the same mechanism, not different mechanisms, a view shared by Hamilton[4].

Perhaps a more balanced presentation of the Wild *et al.*[1] model would credit both inclusive-fitness theory and multilevel selection theory as insightful frameworks, and would encourage the literacy to translate between them. We think that inclusive-fitness theory is useful for identifying the net direction of selection and providing testable hypotheses about evolutionary equilibria. Multilevel selection theory is also a valid perspective, which provides insight into evolutionary dynamics, in which estimates of the strength of selection and quantitative genetic parameters are readily coupled to predict selection response. For example, when seeking to maximize individual traits like 'egg laying' or 'survival' in hens, breeders find that selecting the most productive coops works better than selecting the most productive individuals[7], because it allows variation in social effects to contribute to the response. Indeed, the heritability of survival is 1.5- to 6-fold higher when indirect effects are considered[8], demonstrating both the effectiveness and the economic utility of the multilevel selection approach.

There are limitations to both theories that are not acknowledged by Wild *et al.*[1]. The behaviour of populations with explicit spatial structure cannot be modelled using an 'average local site' without loss of information about a system's dynamical behaviour. Inhomogeneities among regions may only manifest after many generations, so that a cheater mechanism, although initially 'fit' or successful, may in the long-term self-destruct[9,10]. Despite the equivalence of inclusive fitness and group selection as steady state, same-generation theories, neither captures such effects[9–11].

We acknowledge the different uses of inclusive fitness and multilevel selection theory, and think that it is time to put the anachronistic debate between single-level and multilevel selection behind us.

Michael J. Wade[1], **David S. Wilson**[2], **Charles Goodnight**[3], **Doug Taylor**[4], **Yaneer Bar-Yam**[5], **Marcus A. M. de Aguiar**[5], **Blake Stacey**[5], **Justin Werfel**[5], **Guy A. Hoelzer**[6], **Edmund D. Brodie III**[4], **Peter Fields**[4], **Felix Breden**[7], **Timothy A. Linksvayer**[8], **Jeffrey A. Fletcher**[9], **Peter J. Richerson**[10], **James D. Bever**[1], **J. David Van Dyken**[1] & **Peter Zee**[1]

[1]Department of Biology, Indiana University, Bloomington, Indiana 47405, USA.
e-mail: mjwade@indiana.edu
[2]State University of New York at Binghamton, Departments of Biology and Anthropology, Binghamton, New York 13902, USA.
[3]University of Vermont, Department of Biology, Burlington, Vermont 05405, USA.
[4]University of Virginia, Department of Biology, Charlottesville, Virginia 22904, USA.
[5]New England Complex Systems Institute, 24 Mount Auburn Street, Cambridge, Massachusetts 02138, USA.
[6]University of Nevada Reno, Department of Biology, Reno, Nevada 89557, USA.
[7]Simon Fraser University, Department of Biological Sciences, Burnaby, British Columbia V5A 1S6, Canada.
[8]University of Copenhagen, Centre for Social Evolution, Department of Biology, Universitetparken 15, Copenhagen DK-2100, Denmark.
[9]Portland State University, Systems Science Graduate Program, Portland, Oregon 97207, USA.

[10]University of California Davis, Department of Environmental Science and Policy, Davis, California 95616, USA.

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