

1 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 parasite¹. 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 multilevel (group) and kin (inclusive fitness) selection approaches¹ using the standard Price² 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.

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

$$\begin{aligned} \Delta W_{(k,l)(\text{among})} &= [\delta(v_{(k,l-1)} - v_{(k,l)}) - \delta\beta'(z)(1 - d_p)k(v_{(k,l)} - v_{(k-1,l+1)}) \\ &\quad r_{(k,l)}(l) \end{aligned}$$

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 shown³. 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 claim¹. 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 Hamilton⁴ 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 differential⁵.

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 Wilson⁶ 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 Hamilton⁴.

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 individuals⁷, 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 considered⁸, 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. Wade¹, David S. Wilson², Charles Goodnight³, Doug Taylor⁴, Yaneer Bar-Yam⁵, Marcus A. M. de Aguiar⁵, Blake Stacey⁵, Justin Werfel⁵, Guy A. Hoelzer⁶, Edmund D. Brodie III⁴, Peter Fields⁴, Felix Breden⁷, Timothy A. Linksvayer⁸, Jeffrey A. Fletcher⁹, Peter J. Richerson¹⁰, James D. Bever¹, J. David Van Dyken¹ & Peter Zee¹
¹Department of Biology, Indiana University, Bloomington, Indiana 47405, USA.

e-mail: mjwade@indiana.edu

²State University of New York at Binghamton, Departments of Biology and Anthropology, Binghamton, New York 13902, USA.

³University of Vermont, Department of Biology, Burlington, Vermont 05405, USA.

⁴University of Virginia, Department of Biology, Charlottesville, Virginia 22904, USA.

⁵New England Complex Systems Institute, 24 Mount Auburn Street, Cambridge, Massachusetts 02138, USA.

⁶University of Nevada Reno, Department of Biology, Reno, Nevada 89557, USA.

⁷Simon Fraser University, Department of Biological Sciences, Burnaby, British Columbia V5A 1S6, Canada.

⁸University of Copenhagen, Centre for Social Evolution, Department of Biology, Universitetsparken 15, Copenhagen DK-2100, Denmark.

⁹Portland State University, Systems Science Graduate Program, Portland, Oregon 97207, USA.

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

Received 13 August; accepted 21 December 2009.

1. Wild, G., Gardner, A. & West, S. A. Adaptation and the evolution of parasite virulence in a connected world. *Nature* **459**, 983–986 (2009).
2. Price, G. R. Selection and covariance. *Nature* **227**, 520–521 (1970).
3. Frank, S. A. Models of parasite virulence. *Q. Rev. Biol.* **71**, 37–78 (1996).
4. Hamilton, W. D. in *Biosocial Anthropology* (ed. Fox, R.) 133–155 (Malaby Press, 1975).
5. Bijma, P. & Wade, M. J. The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *J. Evol. Biol.* **21**, 1175–1188 (2008).
6. Hölldobler, B. & Wilson, E. O. *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies* 35 (Norton, 2009).
7. Muir, W. M. Group selection for adaptation to multiple-hen cages: selection program and direct responses. *Poult. Sci.* **75**, 447–458 (1996).
8. Ester, E. *Genetics of Survival in Cannibalistic Laying Hens*. PhD thesis, Wageningen Univ. (2009).
9. Werfel, J. & Bar-Yam, Y. The evolution of reproductive restraint through social communication. *Proc. Natl Acad. Sci. USA* **101**, 11019–11024 (2004).
10. Goodnight, C. et al. Evolution in spatial predator-prey models and the “prudent predator”: The inadequacy of steady-state organism fitness and the concept of individual and group selection. *Complexity* **13**, 23–44 (2008).
11. Durrett, R. & Levin, S. The importance of being discrete (and spatial). *Theor. Popul. Biol.* **46**, 363–394 (1994).

Competing financial interests: none


doi:10.1038/nature08809

Author Queries

Journal: **Nature**

Paper: **nature08809**

Title: **Multilevel and kin selection in a connected world**

Query Reference	Query
1	 <p>AUTHOR: When you receive the PDF proofs, please check that the display items are as follows (doi:10.1038/nature08809): Figs 0; Tables: None; Boxes: None. Please check all author affiliations are correct, and again please check the formatting of the equations.</p>

For Nature office use only:

Layout	<input type="checkbox"/>	Figures/Tables/Boxes	<input type="checkbox"/>	References	<input type="checkbox"/>
DOI	<input type="checkbox"/>	Error bars	<input type="checkbox"/>	Supp info (if applicable)	<input type="checkbox"/>
Title	<input type="checkbox"/>	Colour	<input type="checkbox"/>	Acknowledgements	<input type="checkbox"/>
Authors	<input type="checkbox"/>	Text	<input type="checkbox"/>	Author contribs (if applicable)	<input type="checkbox"/>
Addresses	<input type="checkbox"/>	Methods (if applicable)	<input type="checkbox"/>	COI	<input type="checkbox"/>
First para	<input type="checkbox"/>	Received/Accepted	<input type="checkbox"/>	Correspondence	<input type="checkbox"/>
Display items	<input type="checkbox"/>	AOP (if applicable)	<input type="checkbox"/>	Author corr	<input type="checkbox"/>