

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.

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

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.

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Wild, Gardner & West reply

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We previously showed how inclusive-fitness theory separates various components of selection on parasite virulence¹. Wade *et al.*² do not seem to dispute our results or make new predictions. Instead, they state that insufficient attention was given to multilevel-selection theory². However, we pointed out the links to multi-level selection¹, and we believe that a misunderstanding has arisen because they have fundamentally conflated selection and adaptation.

Wade *et al.*² show that our inclusive-fitness equation can be rearranged into multilevel-selection form. However, we had stated this in our paper¹ and noted that it has been appreciated for >30 years^{1,3}. Indeed, the recent claim that Price’s equation (the mathematical underpinning of our results¹ and those of Wade *et al.*²) cannot capture multilevel selection and leads to ‘classification errors’ was made in a previous publication⁴ by one of the same authors.

Our paper¹ was a response to claims that inclusive-fitness theory could not explain virulence evolution in structured populations. Wade *et al.*² suggest that we have been “misleading”. However, our point is easily demonstrated by examining previous work^{4–7,9} (by some of the same authors) that asserts the effect of parasite dispersal could not be explained by kin selection or inclusive-fitness theory, and the effect of parasite dispersal supports Wynne–Edwards’ idea that selection maximizes group fitness. These assertions have been used as the basis for claims about adaptation at the group level that we believe to be theoretically and empirically incorrect^{7–9}.

Wade *et al.*² also claim that our model is a special case of the more general theory of multilevel selection. We believe this to be misleading on two points. First, there has been no equivalent multilevel-selection analysis of virulence evolution. Second, although our model is (like all models) a special case, more general analyses could be developed with either inclusive-fitness or multilevel-selection.

The conclusion of Wade *et al.*² may occur because they did not distinguish selection (dynamics) from adaptation (design). There are several ways to model the dynamics of selection, all of which are correct, including inclusive-fitness and multilevel-selection approaches. Irrespective of the dynamical approach taken, parasite adaptation (the appearance of design due to the action of selection)¹⁰ occurs at the level of the individual organism for the purpose of maximizing its inclusive fitness^{11–13}. In contrast, social groups appear to be designed to maximize their fitness only when this coincides with the maximization of inclusive fitness (when within-group selection is negligible)¹⁴. It is because inclusive fitness is a theory of adaptation that it has been so successful empirically, especially relative to multilevel-selection^{3,15}.

We illustrate the misunderstanding of Wade *et al.*² with four examples. First, they suggest that reduction in optimal virulence is not a simple individual-level adaptation. We believe that this is incorrect because, irrespective of the strength of between-group selection,

individuals are adapted to maximize inclusive fitness¹¹. In our model there are several levels of selection, but only one level of adaptation—the individual organism. Second, Wade *et al.*² claim that privileging the inclusive-fitness perspective over the equivalent multilevel-selection perspective is a research preference and not a scientific result. We disagree, because although both approaches capture dynamics, only inclusive fitness doubles as a theory of adaptation^{12–14}. Indeed, the search for a multilevel principle of adaptation has often led to the wrong one—group adaptationism^{3,14}. Third, they suggest that models of meiotic drive could also be used to define individual-level adaptation out of existence². The inclusive-fitness approach assumes within-individual selection is negligible¹³, which is justified by the huge empirical success of the theory¹⁵. Likewise, the group-adaptation approach requires the assumption that within-group selection is negligible¹⁴, which may be valid for some cases, but in general is not justified. Indeed, Wade *et al.*² have highlighted that within-group selection is an important driver of virulence evolution in our model, rendering a group-adaptation interpretation impossible. Fourth, they state that Hamilton was convinced by the Price formulation that kin selection was group selection². However, although Hamilton¹¹ showed the dynamical equivalence of multilevel selection and inclusive fitness, he never claimed that selection maximized anything other than inclusive fitness.

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