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Inside-out, or Outside-in, multi-level selection "vs." inclusive fitness debate permlink

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Posted on: February 21, 2010 5:43 AM, by Razib Khan

An interesting exchange in *Nature* on ways to conceptualize the evolution of virulence. First, Adaptation and the evolution of parasite virulence in a connected world:

> Adaptation is conventionally regarded as occurring at the level of the individual organism, where it functions to maximize the individual's inclusive fitness...However, it has recently been argued that empirical studies on the evolution of parasite virulence in spatial populations show otherwise...**In particular, it has been claimed that the evolution of lower virulence in response to limited parasite dispersal**...provides proof of Wynne-Edwards's...idea of adaptation at the group level. Although previous theoretical work has shown that limited dispersal can favour lower virulence, it has not clarified why, with five different suggestions having been given...Here we show that the effect of dispersal on parasite virulence can be understood entirely within the framework of inclusive fitness theory. Limited parasite dispersal favours lower parasite growth rates and, hence, reduced virulence because it (1) decreases the direct benefit of producing offspring (dispersers are worth more than non-dispersers, because they can go to patches with no or fewer parasites), and (2) increases the competition for hosts experienced by both the focal individual ('self-shading') and their relatives ('kin shading'). **This demonstrates that reduced virulence can be understood as an individual-level adaptation by the parasite to maximize its inclusive fitness**, and clarifies the links with virulence theory more generally....

Ebola is very virulent. Swine flu is less virulent than ebola. The common cold is less virulent than swine flu. You get the picture. If a pathogen is very virulent it needs to be very transmissible to be evolutionarily successful (replicate itself); otherwise, it will kill its host before it is transmitted and so kill the golden goose. By contrast, if a pathogen is not very virulent, it can be relatively chilled out in terms of transmission since the host isn't going to die anytime soon. Models of virulence aren't of purely academic interest, since they are critical components of an evolutionary understanding of epidemics, and their potential future trajectories.

In any case, the "multi-level" point here is obviously that one can easily imagine conceptually that a fast replicator strain within a host can kill the golden goose. So even though that strain is successful *within* the host, it will decrease group level fitness. By contrast, those hosts which do not produce fast replicator strains within their population of pathogens will persist and the pathogens will have a better chance of being transmitted. The group level logic here is rather evident, but the authors of the above paper think that one can eliminate the need for this sort of thinking within a traditional individual level inclusive fitness framework.

In any case, I'll skip the formal analysis and jump to their conclusion:

> ...Thus, irrespective of the relative strengths of within-group versus between-group selection, individuals are predicted to maximize their inclusive fitness. **In contrast, groups are only predicted to evolve traits that function to maximize their fitness in extreme situations where there is no conflict of interest between the members of the group**...Put another way, the presence of group selection does not invalidate the idea that the individual is an adaptive unit, and it does not validate the idea that the group is an adaptive unit

This is a standard individual selectionist dismissal of the multi-level selection viewpoint: group selection happens, but it is a rare dynamic which only crops up in marginal cases.

Recently this letter prompted a rely. Multilevel and kin selection in a connected world. In this response the authors basically argue that the equation at the heart of the first paper is just a restatement of the Price Equation. They say:

> Perhaps a more balanced presentation of the Wild et al...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...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.

Can't we all get along? The authors of the original letter aren't having any of it. They respond:

> The conclusion of Wade et al...**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 andmultilevel-selection approaches. Irrespective of the dynamical approach taken, parasite adaptation (the appearance of design due to the action of selection)...occurs at the level of the individual organism for the purpose of maximizing its inclusive fitness...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)...It is because inclusive fitness is a theory of adaptation that it has been so successful empirically, especially relative to multilevel-selection...
>
> We illustrate the misunderstanding of Wade et al...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 fitness...In our model there are several levels of selection, but only one level of adaptation-- the individual organism. Second, Wade et al...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...Indeed, the search for a multilevel principle of adaptation has often led to the wrong one--group adaptationism...Third, they suggest that models of meiotic drive could also be used to define individual-level adaptation out of existence...The inclusive-fitness approach assumes withinindividual selection is negligible...which is justified by the huge empirical success of the theorr... 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... 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 selection...However, although Hamilton...showed the dynamical equivalence ofmultilevel selection and inclusive fitness, he never claimed that selection maximized anything other than inclusive fitness.

I really need to read the supplementals for the first letter to comment in any detail, but I will say that I feel that the authors of that letter come on a bit too strongly in their rebuttal to the response to their letter. Though the distinction between selection and adaptation is an important one.

The tone of the discussion here shows how formalization doesn't get rid of all semantic tussling. It seems that the critics of the original letter were more concerned with the interpretation of their formal analysis, not the analysis itself.

Here's the equation at the heart of the letter which started this:

$$\begin{aligned}\Delta W_{(k,\,l)} = &-\delta v_{(k,\,l)} \\ &+ \delta\beta'(z)\left[(1-d_{\mathrm{p}})k v_{(k-1,\,l+1)} + d_{\mathrm{p}}\sum\nolimits_{(i,\,j)} v_{(i,\,j)}(i+1)p_{(i+1,\,j-1)}\right] \\ &- \delta\beta'(z)(1-d_{\mathrm{p}})k(v_{(k,\,l)} - v_{(k-1,\,l+1)}) \qquad (1)\end{aligned}$$

p(i, j) = the equilibrium frequency

i & j = local number

$$-\delta\beta'(z)(1-d_p)k(v_{(k,\,l)}-v_{(k-1,\,l+1)})r_{(k,\,l)}(l-1)$$
$$+\delta(v_{(k,\,l-1)}-v_{(k,\,l)})r_{(k,\,l)}(l-1)$$

of uninfected and infected hosts respectively

β(z) = parasite transmissibility

δ = scalar value, increase in virulence phenotype

ΔW(k, l) = change in inclusive fitness in patch with k uninfected and l infected hosts

v(k, l)) = reproductive value of parasite in patch with k uninfected and l infected hosts

d_p = dispersal rate, as a proportion

r = relatedness between parasites in class k & l

z = virulence

Citations:

Nature 459, 983-986 (18 June 2009) | doi:10.1038/nature08071

Nature 463, E8-E9 (18 February 2010) | doi:10.1038/nature08809

Nature 463, E9-E10 (18 February 2010) | doi:10.1038/nature08810

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1

Google yields "•virulent - Of a disease or disease-causing agent, highly infectious, malignant, or deadly."

That's a wonderfully confusing definition. It seems your source uses "virulent" to mean deadly, lethal. Mind you, both of those are a syllable shorter and more widely understood, so no respectable biologist would dream of using them, I suppose?

Posted by: bioIgnoramus | February 21, 2010 10:01 AM

2

The "New Germ Theory" article in which Ewald & Cochran are interviewed on the subject of evolved virulence is here.

Posted by: TGGP | February 21, 2010 11:06 AM

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