

# THE THEORY OF INCLUSIVE FITNESS

David C. Queller

Department of Biology, Washington University in St. Louis

EMAIL: QUELLER@WUSTL.EDU

A review of

SOCIAL EVOLUTION AND INCLUSIVE FITNESS THEORY: AN INTRODUCTION.

*By James A. R. Marshall. Princeton: Princeton University Press. \$39.95. xvii + 195 p. Index. ISBN: 9780691161563. 2015.*

This is a *pre-copyedit* version of:

Queller, D.C. The theory of inclusive fitness. Book review of "*Social Evolution and Inclusive Fitness Theory: An Introduction*" by J.A.R. Marshall. ***Quarterly Review of Biology*** 91:343-347.

W. D. Hamilton was responsible for two major innovations in the early 1960's (Hamilton, 1964). First, he invented, formalized, and made a strong case for the importance of kin selection, the idea that genetic alleles will be selected in part via their effects on others who share the allele. His other main contribution was the idea of inclusive fitness, a general and intuitive way of analyzing this kind of selection. Though Hamilton's ideas have been hugely influential, there has been no book focused on the topic of inclusive fitness theory. That gap has now been filled by James Marshall's "Social Evolution and Inclusive Fitness Theory".

There are various ways to approach inclusive fitness. Marshall's main theoretical approach appeals to me because it is one that I initiated earlier in my career (Queller, 1992), using the Price equation. Marshall's Chapter 3 provides a nice introduction to this equation, well worth reading in its own right because of the ever-expanding utility of the Price equation in evolutionary research. Simplifying a little, it shows that the selective change in the population average of some entity  $G$  can be written as  $Cov(G,W)$ , where  $W$  is fitness. It is often useful to let  $G$  be the breeding value for a trait, for example an altruistic trait. Then, we can write individual fitness  $W$  as a function of whatever causal parameters are relevant to the particular case. For a simple altruistic behavior, those parameters could be the individual's own breeding value  $G$  and its partner's breeding value  $G'$ . This fitness function can be substituted for  $W$  and, when the function is a linear one describable by multiple regression, it is easy to show that average  $G$  increases when

$$\beta_{WG \cdot G'} + \beta_{G'G} \beta_{WG \cdot G'} > 0 \quad \text{or} \quad -c + rb > 0 \quad [1]$$

This is Hamilton's rule, with relatedness popping out as a genetic regression coefficient and the costs and benefits being partial regression coefficients describing how fitness is affected by one's own genes and by partner genes. The right hand side of each equation is called the inclusive fitness effect of the behavior and it determines whether the behavior increases or not.

Beyond this core result there is of course still much to say and Marshall says it. How do you incorporate phenotypes? When is relatedness due to pedigrees alone and when might it be due to other factors? What if populations are viscous? What if there is class structure in the population? What if behaviors are expressed conditional on the behaviors of others, for example tit-for-tat? What is the relationship to multi-level selection? What about when the fitness function is non-linear or non-additive? This has long been an issue in kin selection theory and Marshall shows several ways that it can be dealt with.

Other theoretical approaches to inclusive fitness are not generally thoroughly treated here. This is probably a good decision with respect to explication; reviewing all of the approaches taken would soon become cumbersome. But readers wanting to dig deeper should be aware that these other methods exist. For example, though Marshall makes it clear that his approach is very similar to quantitative genetics, there is no discussion of the "indirect genetic effects" approach that is explicitly quantitative genetic (Moore et al., 1997). Useful results

form that approach include a demonstration that Fisher's fundamental theorem of natural selection has to be modified: it is *inclusive* fitness that increases at the rate of the additive genetic variance in fitness (Bijma, 2010). There is brief treatment of the clever Taylor-Frank maximization method, which is very handy for frequency dependent cases, provided selection is weak. Here one writes an equation for fitness in terms of the behavior of one's own behavior and the behavior of others, differentiates fitness to find when the behavior is expected to increase, and application of the chain rule causes relatedness to pop out (Taylor and Frank, 1996).

Finally there are traditional population-genetic models. These are in some sense the gold standard in evolutionary biology but, curiously, in kin selection and associated areas, they have been more valuable in checking insights from inclusive fitness rather than generating new insights on their own. I think this may be because they provide too much detail. You crank through a model and get a reliable result but, unless you already had Hamilton's rule in mind, it may not be apparent that the results can be assembled into such a simple and general form. Sometimes population-genetic analyses seem to contradict Hamilton's rule in some way. This is generally when they are using different definitions. First, benefits and costs may be defined in some manner convenient for the model but in ways that differ from partial regression benefits and costs of equation 1. Second, it is often assumed that relatedness must be from kinship but Hamilton's coefficient is more general than that. For example, an unconditional altruistic suicide allele cannot be favored even if it is helping clone-mates ( $r = 1$  at most loci) because the recipients do not include those with the suicide gene. Therefore the  $r < 0$  at relevant suicide locus (less than zero because the recipients have less than a random chance of carrying the suicide gene). Inclusive fitness handles the example well provided we use relatedness at the appropriate locus.

Both kin selection and inclusive fitness have recently been attacked in a high-profile but flawed paper in Nature by Nowak, Tarnita and Wilson on the evolution of eusociality (Nowak et al., 2010). It is inevitable that Marshall's book will be read partly in this light and this is a shame because over-focusing on these arguments might obscure his point that kin selection and inclusive fitness have been among the more important contributions to evolutionary biology since the forging of the modern synthesis. On the other hand, Marshall does offer a timely and sturdy defense, particularly of inclusive fitness theory, that many readers would find valuable. It starts from first principles and builds a more extended analysis than was possible in the many critiques of the Nowak et al. paper. That said, it is not written as a direct response and its tone is not overly combative.

One of the claims of Nowak et al., following up on previous work by Wilson (Wilson, 2008), is that the grandest accomplishment of kin selection theory – its explanation of the eusocial insects – is incorrect. Wilson's alternative is not really clear to me, with confusing explanations shifting between group selection and some sort of maternal control (workers are described as extrasomatic extensions of their queen). As Marshall shows, group selection is not really an alternative explanation

to kin selection. It is just an alternative way of parsing selection that depends just as heavily on relatedness among group members (in the form of between-group genetic variance). Maternal control, on the other hand, is a true alternative hypothesis to pure worker altruism (although one that can still be understood through inclusive fitness – of the queen). In this hypothesis, queens manipulate some offspring into being effectively sterile. It is even possible that such suppressed offspring might sometimes behaviorally shift, without any genetic evolution, into brood care duties. But even if this were true at the origin of eusociality, and this is very far from being demonstrated, kin selection must be responsible for most of the subsequent molding of worker traits, that is, for the immense variety of social adaptations that make social insects so special. Kin selection is not just about giving up reproduction; it is about how any trait affecting kin evolves. It is irrelevant only if worker genes have zero power over worker phenotypes. The relative power of queens and workers is an important area for research, but the default has to be genes within a worker body usually have more power over worker phenotypes than genes outside it. It beggars the imagination to think that queens could exert absolute power over worker bodies for millions of years across the myriad of social insect lineages.

The other main claim of Nowak *et al.* is that inclusive fitness is a theoretical method that is inferior to population genetics, and that there is nothing to gain from using it. In one sense this is an easy claim to refute because we have already gained so much. Marshall's book is primarily about theory but the last chapter contains a brief but excellent summary of some of the evidence (Andrew Bourke's *Principles of Social Evolution* Bourke (Bourke, 2011) gives a complimentary account; instead of lots of theory and some evidence, it provides some theory and lots of evidence). Marshall concludes that "inclusive fitness theory is among the most extensively tested and verified theories in the biological sciences". I'm not sure it is as well tested as cell theory, Mendelian genetics, and the theory of common descent, but one can't quibble with the gist of the claim.

The larger question of whether inclusive fitness is inferior to population genetics is somewhat harder to refute because modeling methods are a partly a matter of taste and of what one wants out of a model. Some modelers prefer lots of detail to make the model as realistic as possible, but taking that to extremes would give us a model that was as detailed as the natural world, and just about as hard to understand. Others prefer simplicity, but if you make a model too simple it will sometimes leave out something important and be wrong.

Much of the dispute hinges on fitness and non-additive interactions. In Hamilton's original model, costs and benefits added neatly together and I think everyone agrees that Hamilton's rule emerges nicely under those conditions. If they are not additive, equation [1] is still correct but one could argue that, in averaging over non-additive effects, it does not capture causality as well as it might. Non-additivity also causes frequency dependence; as allele frequency changes during the course of selection, so do the selection regression coefficients that describe how the

genes or phenotypes affect fitness. This also true for any frequency-dependent selection arising from dominance and epistasis in non-social models. This means that specifying selection coefficients in one generation gets you to the next generation, but not farther, because the genetic environment has changed in a way that will alter the selection coefficients. We therefore get a snapshot of selection but not necessarily a long-term prediction.

In this respect, and others, the covariance approach to inclusive fitness resembles quantitative genetics, which is not surprising given how both depend on variances, covariances, and regressions. If you are happy with quantitative genetics then you should be happy with inclusive fitness. Both represent approaches that highlight high-level generalities (selection gradients, heritabilities, relatedness) that can provide insight even when the underlying genetic details are unknown. Is it possible to do population-genetic models that have greater genetic detail? Yes, of course, and these can be useful. But they are often harder for theoreticians to construct, harder for non-theoreticians to interpret and understand, and impossible for empiricists to apply.

As an example, take the latest salvo from the Nowak group (Olejarz et al., 2015). This model shows that relatedness can have effects seemingly contrary to inclusive fitness expectations, specifically that worker sterility can sometimes evolve more easily with doubly mated queens (lower relatedness) than with singly mated queens (higher relatedness). First, let me say this is an interesting result. However, what I want to know is whether this is interesting biologically or instead more of somewhat contrived mathematical curiosity. With my one or two readings of the paper before the deadline for this review, I am leaning towards the mathematical curiosity view. It would have been nice if the authors, who I suspect understand their model pretty well, had given us more guidance.

First, the paper does not model the origin of workers even though that is what is primarily discussed in the introduction and discussion. Instead, the model assumes that workers have already fully given up production of daughters and asks whether they should also give up production of sons. This is an interesting question but is not the same as the origin of eusociality. Second, the paper depends heavily on the kinds of non-additivity discussed above: their  $r_z$  curve describes how colony efficiency changes non-linearly with the fraction of non-reproductive workers. Third, it appears to depend on genes of large effect, large in the sense that the worker genotype absolutely determines whether it is reproductive or sterile rather than some difference in probability. As a result, the different Mendelian ratios you get out of single mating versus double mating fall on very different segments of the non-linear  $r_z$  colony productivity curve. So what I would like to know, though I think I know the answer, is whether the strange effects of the model disappear if it instead considered genes causing a *small* difference in the probability of being non-reproductive. Then we could have the biological discussion of what kinds of genes might be more plausible. The traditional Darwinian/Fisherian answer would be that small-effect genes are more important, but there is room for debate.

My explanation above may account for why the model would differ somewhat from at least the simple inclusive-fitness expectation, but how does it generate the apparently radically different result of sometimes yielding greater worker altruism under the lower relatedness of double mating? In the examples the paper gives, this appears to depend on a particular form of the  $r_z$  curve – colony efficiency has to peak and then decline as the fraction of non-reproductive offspring increases. Setting aside the issue of how plausible this is, it can cause singly mated colonies, which will have a broader range of worker numbers, to more often fall in the colony-harming portion of the  $r_z$  curve. Here sterility is not altruistic but spiteful, harming both the worker's reproduction and that of its kin. Inclusive fitness theory would also predict that spite is more favorable (or less unfavorable) with low relatedness, so how much of the apparent difference between the approaches is real? The authors do not seem interested in exploring that.

Progress is likely to be made by integrating insights from inclusive fitness and population genetics and there are examples of researchers who effectively do this. For example, Hisashi Ohtsuki was the first author on a paper from the Nowak lab showing a new result for cooperation in networks (Ohtsuki et al., 2006) that was later shown by others to be interpretable in terms of inclusive fitness (Lehmann et al., 2007). Instead of seeing that as a problem, Ohtsuki saw it as an opportunity and went on to make a number of nice contributions to inclusive fitness theory e.g. (Ohtsuki, 2010).

In the opposite direction, consider Hanna Kokko, a co-author of one of the strong critiques of the Nowak paper (Abbot et al., 2011). Together with Lutz Fromhage, she later constructed a model in the Nowak style to show how haplodiploidy and single mating can interact in a way favorable to the evolution of worker behavior (Fromhage and Kokko, 2011). This works not because of high relatedness *per se*. Instead it works for reasons parallel to the male model just discussed. Haplodiploidy and single-mating create some colonies with very high fractions of workers, which yields extra returns under accelerating productivity curves. We still need the debate over small versus large effects and on the shape of productivity curves but the point is that those who like inclusive fitness can still create value with other kinds of models.

I have focused, perhaps too much, on the recent controversy because that is what many readers will think of today in the context of inclusive fitness. If you are interested in the controversy, you should read Marshall's book. But more broadly, given the proven success of inclusive fitness theory, read this book if you are interested in social evolution and want a deeper understanding of Hamilton's rule and its nuances. When the current controversy has faded, Marshall's book will still stand as an important summary of this valuable way of thinking.

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