INCLUSIVE FITNESS IN EVOLUTIONARY MODELLING

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1   Introduction

The notion of Darwinian fitness allows us to understand how natural selection influences the evolution of organismal traits. For example, we might explain a plant's morphology, or a bird's behaviour in terms of the fitness advantages (reproductive or survival benefits) such morphology or behaviour confers.

The notion of **inclusive fitness** is used specifically to understand how selection will act on those traits that influence the fitness of several genetically-related individuals simultaneously. Inclusive fitness recognizes that an individual may have a "genetic share" in the fitness of its neighbours, and so it is a more general (more "inclusive") measure of evolutionary success.

The development of inclusive fitness is usually credited to the biologist W. D. Hamilton, who used the idea to explain the selective advantage of altruistic traits [12]. Before Hamilton's seminal work was published, the advantage of altruistic traits was difficult to explain using fitness alone. The fact that an individual would be willing to decrease its fitness by some amount (traditionally denoted, c) to increase the fitness of a neighbour by some other amount (traditionally denoted, b) seemed counterintuitive to many evolutionary biologists. Hamilton, showed, that the selective advantage of these "problematic" traits is clear provided the recipient of the altruistic act is genetically related to the actor, and provided one adopts an inclusive fitness perspective. In this case, the fitness of the actor is $1 - c$, and the fitness of the recipient is $1 + b$; if the actor and the recipient are related to one another by a factor r, then the actor's inclusive fitness is simply, $1 - c + (1 + b)r$. Relative to the situation in which the actor does nothing (i.e. the situation in which both actor and recipient fitness is 1), the inclusive-fitness change is

$$-c + br. \tag{1}$$

A selective advantage is obtained whenever this change is positive, or, in biological terms, whenever b is large enough and the actor and recipient are sufficiently close genetic relatives.

This report details the activities and outcomes of our 5-day half-workshop devoted to inclusive fitness and evolutionary biology—the first such meeting of its kind. Ours was a real "workshop" in that, rather than focus on talks, we spent most of our time in discussion clarifying and amplifying a number of issues around the nature and scope of inclusive fitness theory. The next section gives an overview of the current state of inclusive-fitness theory; it also outlines how the current state of the theory shaped our goals. Although our workshop did not focus on talks, there were a number of short ones that served to connect our ongoing discussion with the major themes and ideas of the speaker. Sections 3 and 4 provide highlights from the various talks given and, in some cases, the discussion that followed. Section 5 details the outcome of the workshop and the new research directions it has spawned.

2   Overview of the Field and Recent Developments

Since Hamilton's work on altruism [12] was published, the inclusive-fitness approach to evolutionary modelling has been generalized and modified to deal with a wide range of biological scenarios. Inclusive fitness can now be used to study class-structured populations (in other words, populations composed of different kinds or "classes" of individual, e.g. males/females, young/old) [29], or populations that experience stochastic demographic fluctuations [26]. The inclusive-fitness approach can also effectively complement the application of other modelling tools (e.g. optimal control theory [4]), making mathematical results more palatable to even the most math-averse evolutionary biologist.

The success of Hamilton's central idea has also been buoyed by the development of an alternative modelling approach known as the **direct-fitness** method [31]. In fact we decided to revert to Maynard Smith's original terminology and designate this the **neighbour-modulated fitness** approach. This approach can be thought of as a "sister" to the inclusive-fitness approach. While inclusive fitness places an actor at the centre of the analysis, neighbour-modulated fitness focuses attention on the recipient (Fig. 1). Although inclusive fitness and neighbour-modulated fitness are, in most cases equivalent [32], neighbour-modulated fitness corresponds more closely to the approaches used in other mathematical treatments of evolution (e.g. game theory, and population genetics). In fact, links between inclusive-fitness and other mathematical treatments are sometimes more easily established using neighbour-modulated fitness [28, 24]. Whatever their relative advantages or disadvantages may be, inclusive fitness and neighbour-modulated fitness have emerged as a the primary tools for modelling what evolutionary biologists call **kin selection**.

The recent literature has seen a number of papers that either focus on the limitations of kin-selection theory [33, 7], or marvel at the breadth of its scope [35]. Although conflicting opinions have long been a part of kin-selection's history, their continued prominence is, at least in part, due to simple misunderstanding (misunderstanding that exists even among the theory's practitioners). One overall goal ("Goal I") of the workshop, then, was to **clear up misconceptions** by investigating our own assumptions and by **investigating theoretical connections** between inclusive fitness and other approaches to modelling evolution.

Theoretical developments aside, kin-selection theory has played a major role in developing our understanding of many natural systems [15]. We were interested, therefore, in determining what **future contributions** kin selection theory might make to biology as a whole ("Goal II").

3   Highlights, Goal I – Misconceptions and Theoretical Connections

3.1   Confusion between kin selection and inclusive fitness

In some treatments the terms "kin selection" and "inclusive fitness" seem to be used interchangeably. In other cases authors make a strict distinction between these terms. As we have suggested above, they are not really parallel terms but refer to different levels of organization. Our discussions identified the confusion between the notions of kin selection and inclusive fitness as a major problem in the current literature.

We took kin selection to be a process—the process whereby the frequency of particular copies of a gene (alleles) is affected when the behaviour of a bearer of that allele affects the fitness of relatives (kin) who will carry that allele with some positive probability. Kin selection is very often at work in social behaviour, as an organisms neighbours tend often to be kin.

Inclusive fitness on the other hand is a method of keeping track of the frequency of an allele under the effects of selection. It is an accounting scheme cleverly designed to keep track of changing numbers of an allele over a generation of selection under precisely those circumstances in which kin selection operates, situations in which behaviour affects the fitness of kin. This accounting method has significant power both computationally and conceptually. Computationally, the focus of inclusive fitness at the individual rather than the genetic level, on whole organisms rather than on alleles, simplifies the calculations and in some cases can perform them when a more elemental population genetics approach would be intractable. Conceptually, the expressions provided by an inclusive fitness analysis can readily be interpreted in terms of fitness effects and relatedness between interactants and thereby it can tell us a story which enriches our understanding of the process and the different selective forces at work.
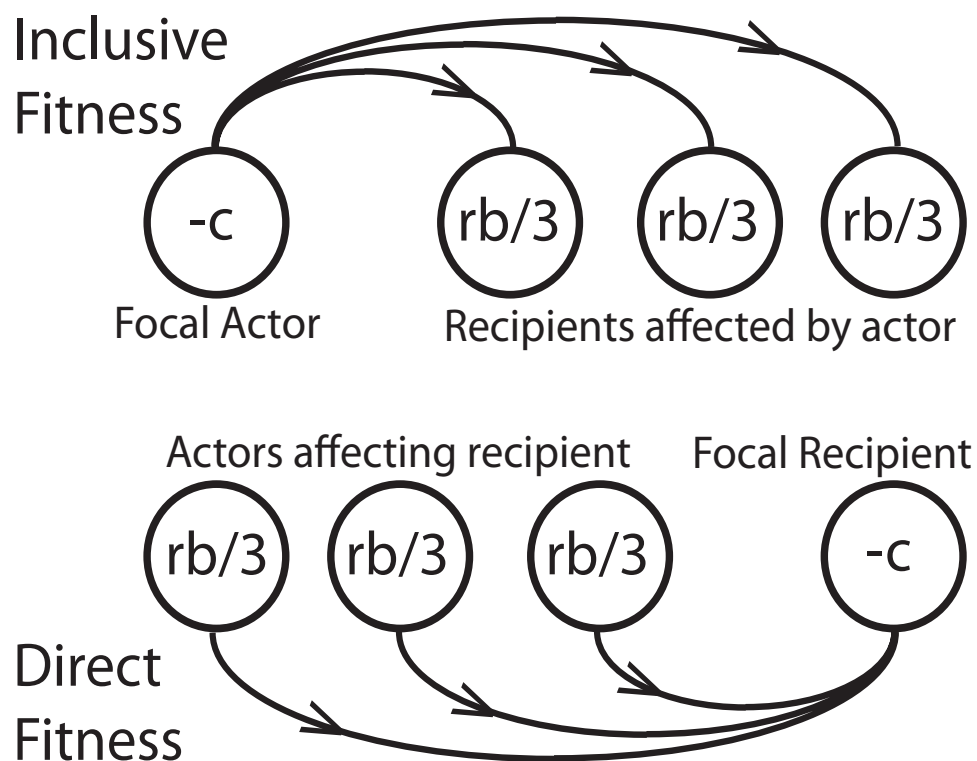
Figure 1: The inclusive-fitness approach (top) makes kin-selection based arguments by fixing attention on one actor, supposing that actor exhibits deviant behaviour and summing all the fitness consequences that deviant behaviour has for recipients related to the actor. As an example, suppose the actor's deviant behaviour causes it to decrease is own fitness by an amount c, but confers a benefit of $b/3$ to each of three recipients that are related to the actor by a factor of r. In this case the direction of allele frequency change is correctly predicted by $-c + 3 \times rb/3 = -c + rb$. In contrast, the neighbour-modulated fitness approach (bottom) makes a kin selection based argument by fixing attention on one recipient and supposing that its deviant genotype alters its behaviour and alters the behaviour of nearby actors at rate r. The same example above is now described as follows: the altered genotype of the recipient means that its fitness is reduced by c and that each of three actors are r times as deviant as the recipient, with each "unit of deviation" benefitting the recipient by an amount $b/3$. The allele-frequency change is again correctly predicted by $-c + rb$, but this result has been achieved by a different method of counting.

3.2 What (Who) are kin?

This is perhaps one of the most obscure questions in the field. From the beginning [12] "kin" were conceived either as relatives that bore standard labels (e.g. offspring, cousins, great uncles, etc.), or as neighbours in structured populations who, because of limited dispersal, were likely to share genes with the focal individual. In the former case, an individual's precise genetic relationship is known; in the latter case relatedness is entirely probabilistic in nature.

Although a considerable body of work has focused on the effect of kin selection on interactions in structured populations (interactions among "probabilistic relatives"), some researchers still to use the term "kin" in the narrow, "standard label" context only. For example, there has been much work on tag-based interactions, where tags (sometimes called "greenbeards") can be used to estimate the level of probabilistic relationship between interactants [9]. Here, individuals with similar tags are not considered "kin" per se, and so it is difficult for the average evolutionary biologist to determine whether kin selection is indeed at work.

Where do we draw the line between interactions that are kin-based and those that are not? In David Queller's presentation he raised the age-old distinction between "kin" and "kith" and suggested that this might be a useful distinction for our purposes. David put forward the idea that tag-based assortment be considered to be influenced by something he called **kith selection**. Discussion raised some doubt that a firm or useful line between kin and kith could be drawn.

3.3 Additivity and frequency dependence

Hamilton [12] did not require that the different fitness effects (i.e the costs and benefits) of an interaction be additive, but he did point out that relatedness could only be easily calculated – either through a pedigree or a recursive analysis – under an assumption of additivity of gene action both within and between individuals. When interactions have synergistic effects assumptions of additivity fail. While calculations can still be made in certain simple population structures, generalized relatedness measures (ones that depend on higher-order moments of the distribution of alleles) have to be used; these tend to be frequency dependent and difficult to calculate.

Andy Gardner and David Queller each presented a different perspective on dealing with synergy with the inclusive-fitness approach. Both perspectives were based on the well-known Price equation [22]. The Price equation expresses the change that occurs in the expected individual phenotype (a random variable, P) over the course of a single generation in terms of an individual's fitness (a random variable, W) and genetic make-up (a random variable, G). In the simplest of cases, the Price equation says,

$$\Delta \mathrm{E}(P) = \frac{\mathrm{Cov}(W, G)}{\mathrm{E}(W)}. \tag{2}$$

Gardner pointed out that, even with synergistic effects, the covariance in equation (2) can be decomposed using additional information about the phenotypes of its neighbour, say P', so that

$$\mathrm{E}(W)\Delta \mathrm{E}(P) = \beta \, \mathrm{Cov}(G, P) + \beta' \mathrm{Cov}(G, P'), \tag{3}$$

where β denotes the average effect of an individual's phenotype on its own fitness, and where β' denotes the average effect of a neighbour's phenotype on an individual's fitness. Note that β and β' are least-squares regression coefficients and may, in principle, depend on the frequency distribution of a particular allele ($\mathbf{p}$). The coefficients β and β' also analogues to the cost and benefit terms in equation (1), respectively. With this in mind, we might re-write equation (3) as

$$\mathrm{E}(W)\Delta \mathrm{E}(P) = \mathrm{Cov}(G, P)\left(-c(\mathbf{p}) + b(\mathbf{p})r\right). \tag{4}$$

By definition, $\mathrm{E}(W)$ is positive; we can assume (wlog) that $\mathrm{Cov}(G, P)$ is also positive. And so (4) tells us that the sign of the average change in phenotype is correctly predicted by a frequency-dependent version of line (1):

$$-c(\mathbf{p}) + b(\mathbf{p})r,$$

where $r = \mathrm{Cov}(G, P')/\mathrm{Cov}(G, P)$. In short, Gardner showed that the structure of Hamilton's expression (1) can be preserved in the face of synergistic interactions.

Using a different covariance decomposition, Queller showed

$$\Delta\mathrm{E}(P) \propto -c + br + d\tilde{r}, \tag{5}$$

where b and c are *exactly* the same as they were in equation (1), and $\tilde{r}$ is a coefficient of synergy. Equation (5) shows that synergistic effects can also be studied by adding frequency-dependent terms to Hamilton's classical frequency-independent expression (1).

While in certain cases the choice between (4) and (5) comes down to modeller's preference, in other cases the choice may have important practical consequences. In particular it was suggested that Queller's formulation (5) might be more amenable to experimental testing, or at least more convenient for purposes of experimental design. This suggestion is particularly interesting, but was not explored in depth during the workshop.

3.4 Relationship with evolutionary game dynamics

Interestingly, our half-workshop was twinned with another focused on Evolutionary Game Dynamics. There has been much confused debate over the past few years on the relationship between this active area of investigation and inclusive fitness, and we scheduled a number of common sessions in order to take advantage of this conjunction. Our view is that the opportunity to share ideas with those involved in evolutionary game dynamics was a valuable one, as was the chance to simply get to know one another better. It appears that new collaborations are already emerging from this time together.

On a more technical note, we should stress that both approaches – inclusive fitness and evolutionary game theory – address evolutionary change in behaviour, and although they are often equivalent [1, 5, 30] the approaches typically emphasize different model assumptions.

Wild presented some recent results [34] that take a kin-selection view of the branching-processes models sometimes used in evolutionary game dynamics [6]. Wild showed that, when the action of selection is weak, rare deviant strategies tend approximately to a quasi-stationary distribution in the population, and that relatedness coefficients used in kin-selection theory are simply expectations based on such distributions. He also suggested that expressions like those in (1) could be used in the same way the basic reproduction number is used in mathematical epidemiology—as a heuristic (but formally justifiable) substitute for less biologically transparent tools for testing the stability of dynamic systems.

Evolutionary game dynamics, of late, has paid much attention to evolution in lattice-structured populations, employing the moment-closure methods from statistical physics to make analytical progress [18, 19]. Lion presented results that use the moment closure methods, but he was able to interpret the results explicitly in terms of inclusive fitness. Although the main point of Lion's talk was to show how different assumptions about the way in which costs are incurred and benefits are accrued influence model predictions, the ease with which the kin-selection version of his analysis proceeded highlighted the fact that inclusive fitness can be used to streamline game-theoretic arguments.

3.5 Relationship with population genetics

Population genetics is the "gold standard" method against which other methods of modelling evolution are measured. Unfortunately when confronted with population structure, the calculations population-genetic methods require are often intractable. In such cases, inclusive fitness can provide a feasible way forward, but one must be willing to accept its technical assumptions.

Much the work carried out by Rousset and his colleagues over the past 10 years [23, 24, 25, 26] has focused on establishing a strong connection between results that are of interest to population geneticists (i.e. results related to the **fixation probability**, a type of probability of absorption), and results typically obtained through kin-selection means. Rousset detailed some of his work for us, and though it has been quite successful, challenges related to model populations with a particular structure ("isolation-by-distance" models) remain.

In his talk, Whitlock reviewed ideas of mutation rate, hard and soft selection, frequency-dependent selection, non-additivity, all familiar to us, but in quite a different context. He also pointed out that statistical methods for estimating the extent of population subdivision (and, by extension, relatedness [25]) in nature are

readily available. The availability of these measures suggests that opportunities to test kin-selection theory in the "real world" abound.

3.6 Confusion among proponents of group selection/multilevel selection

There have been claims made in the literature that selection favours adaptations that cannot be understood in inclusive-fitness terms [13, 27, 37, 38]; only selection at the level of the group, it is argued, is able to provide the necessary adaptive context. As demonstrated elsewhere though [35], claims like these tend to misunderstand the the scope of kin-selection theory and its technical limitations. There was no disagreement within our workshop on the connections between kin selection theory and the theory that explicitly considers the action of selection at multiple levels of biological organization, and we did not discuss the issue very much (we mention it in this report only because the issue was raised in our workshop proposal). Furthermore, (as discussed below) Alan Grafen's presentation illustrated that inclusive fitness is not just an accounting method, but also an answer to the problem of what organisms should appear designed to maximise.

3.7 A role for group theory

In one of our final talks, Taylor outlined some remarkable work that uses ideas from group theory to solve kin selection problems in an elegant manner. Briefly, Taylor used the symmetry found in certain graph theoretic descriptions of social interactions to impose an algebraic group structure on his model population that made potentially difficult calculations rather easy. Given the success enjoyed by "evolutionary graph theory" [16], the workshop participants wondered if we will now see "evolutionary group theory."

4 Highlights, Goal II – Future Applications of Kin Selection

4.1 Inclusive fitness as a maximand

The inclusive fitness of an actor can, in some cases, serve as an objective function whose value will increase under the action of selection. In these cases, an actor's behaviour can be understood as an adaptation "designed" for the purpose of maximizing this objective function. This result can sometimes be misunderstood; it does not say inclusive fitness must always be maximized. As Grafen's presentation pointed out, the result outlines the conditions under which inclusive fitness should to be maximized in nature.

The inclusive-fitness-as-a-maximand result provides formal, mathematical justification for the explanations routinely used by field biologists [10]. As our discussions indicated, inclusive fitness maximization is taken for granted across much of biology; it is the basis for a great deal of field work and for grants awarded for field work [14]; it is also arguably the reason why higher organisms appear to have a sense of purpose that guides their behaviour. Understanding the extent to which biologists are justified in using inclusive-fitness theory in the field, then, is of utmost importance and more work needs to be done. In particular, Grafen's result needs to be extended to address cases in which the rates at which inclusive fitness costs and benefits accrue change with changing allele frequency.

Our discussion also revealed that there is currently no maximization result based on neighbour-modulated fitness (NMF). Given the preference some theoreticians have for this approach, we asked whether an NMF-based maximization result could be developed (and we conjectured that this might well be the case). Some members of our workshop will investigate this issue further.

4.2 Kin selection in realistic ecological scenarios

With kin-selection theory one is often able to find simplifications that make even complicated models tractable. In his talk, Alizon showed how he used this advantage of kin-selection theory to investigate how competition among the various pathogen strains that infect a host ultimately influence evolution.

In contrast, to Alizon's work, van Baalen reported that he had experienced tremendous difficulty when attempting to use inclusive fitness to model the evolution of certain colonial species of insect. This difficulty led van Baalen to suggest that inclusive-fitness methodology (or even direct-fitness methodology), may not be the appropriate tool for dealing with some of the more ecologically complex systems (participants did,

however, offer suggestions to address van Baalen's concerns). Subsequent discussion revealed that several workshop participants were eager to establish a more general inclusive-fitness methodology—one which could handle even difficult sets of ecological assumptions.

4.3 Kin selection, autism and psychiatric disorders

In many instances, two neighbours have different "genetic interests" in their neighbourhoods. As a result their inclusive fitness interests are said to be **in conflict** and selection favours different conditional behaviours in each of the conflicting parties [8, 20, 21, 36]. When the "neighbours" in question are actually homologous genes, a phenomenon called **genomic imprinting** can result [11].

Úbeda's presentation addressed the conflict between (and genomic imprinting of) genes expressed in the mammalian brain—a genes thought to be involved in autism and psychiatric disorders like schizophrenia [2]. Specifically, Úbeda showed how kin-selection theory can inform clinical studies of these disorders. By combining inclusive fitness and life-history theory, he showed that sex-specific patterns of dispersal and sex-specific variation in mating success have the potential to influence patterns of genomic imprinting in genes disorder-related genes. His work demonstrated how human ecology might actually set the stage for the evolution of those patterns of imprinting now linked to autism and psychoses. The idea that kin-selection theory might act as a bridge connecting human ecology and psychiatry/medical genetics is an intriguing one that the members of the group will pursue.

4.4 A kin-selection perspective for sexual-selection theory

Alonzo's presentation focused on the possibility of new applications for kin-selection theory. In particular, she emphasised that whilst interactions between mates involves much potential for cooperation and conflict, the methods and insights of kin selection and inclusive fitness theory have rarely been applied to the field of sexual selection. A number of topics were raised where interactions between these areas could be useful, and several of of the participants are actively investigating these questions. Wild and West are examining how structured populations and relatedness between individuals could influence the strength of selection for conflict between mates. West, Wild and Gardner are using a combination of theoretical and empirical approaches to examine how promiscuity can reduce relatedness within families and hence reduce selection for cooperation, across a range of organisms from wasps to birds [3].

5 Outcome of the Meeting

Overall, the meeting served to focus our future research endeavours. Our attempts to eliminate sources of confusion within this key group of people identified points of disagreement that, in turn, put a spotlight on new questions to tackle. In particular,

- we will explore the utility of Queller's notion of "kith selection";

- we will determine whether there are indeed practical advantages to keeping frequency-dependent fitness changes separate from frequency independent ones, as was done in equation (5);

- we will investigate the extent to which algebraic group theory can be used to improve kin-selection methodology;

- we will investigate how reasonable it is to consider neighbour-modulated fitness (NMF) to be a maximand like inclusive fitness.

Points on which we could agree were equally valuable. Agreement established a common ground that will form the foundation for future meetings, at BIRS or elsewhere. Many participants found they had common interests, despite their (arguably) disparate backgrounds. Indeed, it appears that this meeting will help smaller groups of workshop participants achieve progress on issues related to the application of kin-selection theory to

- the evolution of complex ecological interactions;

- the interplay between human ecology and psychiatry/medical genetics;

- the evolution of cooperative and antagonistic interactions between the sexes.

In closing, we wish to thank BIRS for helping us bring together researchers from around the world to discuss inclusive-fitness theory. We certainly look forward to the future progress this meeting will have enabled.

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