partly explained by analytical difficulties. The polymer cannot be specifically radioactively labelled, except in cells made permeable to NAD. Analysis of poly(ADP-ribose) formation has therefore depended on awkward procedures involving degradation of the polymer to phosphoribosyl-AMP (by cleavage of the phosphate–phosphate bonds with snake venom phosphodiesterase) and quantification of the latter compound, or on access to antibodies recognizing poly(ADP-ribose). Effective monoclonal antibodies are not, however, available. Fortunately, a series of nicotinamide analogues (for example, 3-aminobenzamide) act as specific inhibitors of poly(ADP-ribose) polymerase, and several important studies on the role of poly(ADP-ribose) rely heavily on the use of such compounds.

A particularly interesting finding[11] is that treatment of mammalian cells with these inhibitors in the presence of bromodeoxyuridine causes a substantial increase in sister chromatid exchange. The recombination observed is largely due to the occurrence of bromodeoxyuridine in DNA (which is necessary in order to visualize chromatid exchanges), because the incorporation of this hydrolytically labile residue leads to an increased background of spontaneously occurring DNA chain scissions[12]. These strand interruptions would facilitate recombination events as long as they remain open, but they could also serve to induce poly(ADP-ribose) formation and thereby trigger their own repair. Indeed, the extent to which the detour repair pathway has been activated may be of general importance in assessments of the relative sensitivities of mammalian cells under different conditions to DNA-damaging agents. □

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How not to measure inclusive fitness

from Alan Grafen

THE introduction of the concept of inclusive fitness by Hamilton[1] in 1964 led to a revolution in thinking about the evolution of social behaviour, by making clear how selection can act on a gene through its effects on its bearer's relatives. This led to a better understanding of the evolution of insect societies, and by 1977 it had been stated as the 'central theorem' of behavioural biology[2] that 'animals maximize their inclusive fitness'. Detailed studies of populations of individually marked animals are now being performed, and it is essential that when the data collected are used to calculate inclusive fitness the correct measure is employed.

Several recent studies[3,4] give cause for considerable concern that erroneous measures that look like, but are in fact different from, inclusive fitness are becoming prevalent. This problem can also be seen by surveying fourteen recently published books[5-18], including the most used animal behaviour textbooks. All use the term inclusive fitness, but of the ten that do define it, none does so correctly. In a loosely argued discussion, the misdefinition may not lead to serious error. For modellers and for field workers with data, on the other hand, the precise definition matters a great deal.

One erroneous measure, which can be called 'simple weighted sum' (SWS), may be defined by borrowing Barash's erroneous definition of inclusive fitness[9]:

> "the sum of individual fitness (reproductive success) and the reproductive success of an individual's relatives, with each relative devalued in proportion as it is more distantly related"

As we never know about all of an animal's relatives, SWS itself has never been measured. Versions of SWS where only certain relatives are included have been used by Bygott *et al.*[3] and McGregor *et al.*[4]. Hamilton[1] described inclusive fitness as

> "the animal's production of adult offspring . . . stripped of all components . . . due to the individual's social environment, leaving the fitness he would express if not exposed to any of the harms or benefits of that environment, . . . and augmented by certain fractions of the quantities of the harm and benefit the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship . . ."

Two major differences emerge. First, SWS counts all the animal's own offspring while inclusive fitness counts the number the animal would have had in the absence of help and hindrance from other animals. Second, SWS counts all relatives' offspring. Inclusive fitness counts only those that owe their existence to the animal's help, and counts negatively those relatives' offspring that would have existed but for the hindrance of the animal.

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The contribution to SWS from an animal's own offspring may be greater or smaller than that contribution to inclusive fitness. The contribution from relatives' offspring must be positive to SWS, but may be positive or negative to inclusive fitness.

In many cases it will be extremely difficult to assess how many offspring an animal would have had but for the intervention of another animal, yet this must be done to measure inclusive fitness. There is, however, a simpler way to include kinship effects in a measure of reproductive success — simply count the number of the animal's offspring. Such a measure inevitably predicts the course of evolution for, if animals bearing an allele have more offspring than non-bearers, then the allele will spread. It is perhaps not commonly appreciated that this measure also includes kinship effects.

If I have an allele for helping sibs, then my sibs gain through my help. But since they are more likely to share my alleles than is the population as a whole, they will help me and so their contribution is included in my number of offspring. Even in a case where I help but am not helped in return (suppose in a clutch of young birds, the first hatching helps the second break out of its shell but the second cannot return this kind of help), kinship effects are still included when we average over all bearers of the helping allele, including first and second hatchlings.

If number of offspring is a measure of reproductive success that encompasses kinship effects, why did Hamilton invent inclusive fitness and why is the central theorem phrased in terms of it? The importance of Hamilton's measure is that, in calculating whether a hypothetical behavioural trait will spread, it is equivalent to the number of offspring measure but is often very much simpler to use and much more revealing. In particular it leads immediately to Hamilton's rule $(B/C>1/r)$, where B is the benefit to the recipient, C is the cost to the actor (both measured in number of offspring), and r is the coefficient of relatedness, which expresses clearly the role of relatedness. The two measures are equivalent in that they always make the same prediction about the direction of selection of an allele, although they will not usually be numerically equal. It is this equivalence that Hamilton[1] proved in 1964 to justify inclusive fitness.

Maynard Smith[19] provides a well worked out example to illustrate the computational and conceptual advantages of inclusive fitness in modelling. He considers a diploid population with two alleles A and a at one locus. AA and Aa genotypes are

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altruistic at cost C to the donor and benefit B to the recipient. Two separate cases are considered: in the first, the recipients are all half-sibs while in the second they are all double first cousins. What is the condition for A to spread?

The inclusive fitness method gives the answer directly, through Hamilton's rule. In both cases $r = 1/4$, and so in both cases A will spread if $B/C>4$.

The standard population genetics method, counting the expected number of offspring of animals with each genotype, leads to one set of three equations for each case, and the equations are different in the two cases. The condition for A to spread can be derived from either set of equations, and turns out to be independent of the frequency of A (though all three equations involve this variable), and in fact to be $B/C>4$. The important points are that in this method each different kind of relative has to be dealt with differently, obscuring the single important parameter r, and that considerable mathematical skill is needed to derive correctly the set of equations and to deduce correctly from them. These disadvantages are overcome by Hamilton's rule at the cost of making some simplifying assumptions that are likely to be true enough for data analysis and rough modelling[20,21].

There are thus two valid measures of reproductive success. Number of offspring will usually be more suitable in field studies where the mean numbers can easily be compared between groups of interest. Inclusive fitness will usually be more suitable for modelling, when the hypothetical trait in question is defined in terms of differences in numbers of offspring. Inclusive fitness can be used in field studies when we have a particular decision in mind that animals can make, when the logic of this decision guides us into calculating entirely in terms of differences in numbers of offspring, and where by experiment or natural variation we can measure those differences. For an example of this see Emlen's discussion[22] of helping at the nest in birds.

The errors that SWS can lead to as a measure of reproductive success can be documented in two recent cases where a restricted version of SWS has been calculated from field data. Bygott *et al.*[3] were assessing the evolutionary advantage a male lion gains through belonging to a large group of males — larger groups keep control of a pride of females longer and may also control more prides. Bygott *et al.* presented two different measures of reproductive success as a function of male group size. The first was number of offspring in a lifetime, and was higher in groups of three and more than in groups of one or two. The second was calculated as: sum of (a) the animal's offspring and (b) 0.22 times the total number of his fellow group members' offspring (0.22 is an estimate of the average coefficient of relatedness between two males in a group). Not surprisingly this restricted version of SWS shows a dramatic increase as group size increases. The authors used this result to argue that the advantage of larger groups was so great that relaxing their assumption of equal matings by males in a group would not bring the advantage into doubt, even for the least successful members of a large group.

McGregor *et al.*[4] studied the evolutionary significance of repertory size in the song of male great tits. They showed that number of offspring increased with repertory size and then went on to calculate a restricted version of SWS, adding to number of offspring the following relatives appropriately devalued: grandoffspring, great-grandoffspring, nieces, nephews, great-nieces and great-nephews. Using this measure, the population mean repertory size was close to the size that maximized reproductive success. McGregor *et al.* concluded that there were indirect effects at work that favoured birds with small repertory size, compensating them for their small number of offspring; and that repertory size is maintained near its optimum by natural selection. Since these conclusions contradict the finding that a valid measure of reproductive success, number of offspring, increases with repertory size, they cannot be correct. We can attribute the error to use of SWS.

Two theoretical points can be used to show up the flaws in SWS. First, in a simple and standard populations genetics model, SWS cannot be calculated because it is infinitely large. In a diploid panmictic lifetime-monogamous infinite population with no selection, and with discrete generations, consider only those animals in my generation that are related to me through a common ancestor no more than n generations ago. The contribution of those animals to my SWS is $1 + (n/2)$. As we count more and more distant relatives this becomes indefinitely large, as all components of SWS are positive.

Second, even when SWS is restricted to animals whose reproduction can be influenced by an individual, it gives erroneous results. Consider an infinite panmictic monogamous diploid species with discrete generations and sibships of size s. Let there be a rare dominant allele A that causes its bearers to decrease its own number of offspring by c while increasing its sibs' number of offspring by a total of b distributed equally, and suppose these costs and benefits combine additively. The condition for A to spread initially is

$$\tfrac{1}{2}\, b-c> 0$$

This follows from both the inclusive fitness method and the full population genetics model. I have computed the condition for A to spread using the following restricted version of SWS: the sum of (a) the individual's offspring plus (b) 0.5 times the total number of offspring of the other sibs in the individual's sibship. That condition is

$$((s+2)/(s+3))b-c> 0$$

This condition is different from that above and gives an erroneous measure that is systematically too favourable to altruistic alleles.

Using the same example we can calculate the condition for A to spread according to the other common misdefinition of inclusive fitness, given, for example, by Wilson[14]; it is the sum of (a) the individual's own number of offspring and (b) the effects of the individual on its relatives' number of offspring weighted by the degrees of relatedness. This measure gives the condition for A to spread as

$$b-c> 0$$

This measure is also systematically too favourable to the altruistic allele.

Of the ten books that were mentioned earlier as misdefining inclusive fitness, five[9-13] define it as SWS, as have (astonishingly) Maynard Smith[23] and (regrettably) myself[24]. The remaining five books[14-18] follow Wilson[14] in giving the definition discussed in the previous paragraph.

In conclusion, not all measures of reproductive success are equal. SWS and restrictions of it are erroneous. Two correct and convenient measures are inclusive fitness and number of offspring. Unfortunately, many modern texts that extol the virtues of inclusive fitness either fail to define it or define it wrongly. Analysers of expensive or extensive data should make very sure that they are using a valid measure of reproductive success. ☐

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