



COMMENTARIES

How to measure inclusive fitness, revisited

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(Received 14 September 1994; initial acceptance 31 October 1994;
final acceptance 13 March 1995; MS. number: AS-1136)

An individual's inclusive fitness is derived by augmenting its traditional Darwinian fitness by certain components, and stripping it of others (Hamilton 1964). The component to be added is the sum of all effects of the individual on his neighbours, weighted by the coefficient of genetic relationship (r) between them. In the original derivation of inclusive fitness, the component to be subtracted was verbally defined as 'all components which can be considered as due to the individual's social environment' (Hamilton 1964). It is not widely appreciated that this verbal definition of the component to be subtracted does not agree with its algebraic definition. Creel (1990a) used Hamilton's algebraic definition of inclusive fitness to show that the component to be subtracted, e^0 , is actually equal to the average effect of one individual on others' fitness (dT^0 , in Hamilton's 1964 formulation). Thus, the calculation of e^0 requires that we know the fraction of individuals in the population that provide help and the mean amount of help provided per helper. e^0 is simply the product of these two numbers (see below). Subtracting e^0 resolves what has become known as the 'double accounting' problem (Grafen 1984; Brown 1987).

The verbal definition of e^0 is important, because it is primarily the verbal definition of inclusive fitness that has been put to empirical use (Grafen 1982, 1984). The flaw in the original verbal definition of e^0 can be seen by applying it to the case of a breeder in an obligately cooperative species (Creel 1990a). In a group with a single breeding pair, the breeder's inclusive fitness (using the old

verbal definition) is equal to its Darwinian fitness stripped of the effects of helpers. This is equivalent to the reproductive success of a breeder in an unaided pair. But in obligately cooperative species, unaided pairs cannot rear young (e.g. dwarf mongooses, *Helogale parvula*: Creel 1990a; African wild dogs, *Lycaon pictus*: Malcolm & Marten 1982). Under the original verbal definition of e^0 , the inclusive fitness of breeders in groups of any size would therefore be zero. Bringing the verbal definition of e^0 into line with its original algebraic definition resolves the bizarre problem of zero inclusive fitness for breeders. But as we discuss here, it raises two new and conceptually thorny issues.

(1) Calculation of e^0 is not always irrelevant when using Hamilton's rule. Creel (1990a) suggested that Hamilton's rule (that help is favoured when $rb > c$, where b is the effect of a helper on breeder reproductive success, r is the genetic relatedness between helper and breeder, and c is the cost of helping to the helper) is unaffected by the definition of e^0 , because e^0 is stripped from the inclusive fitness of both breeders and helpers. Thus ' e^0 drops out of an inequality comparing inclusive fitness for alternative strategies' (Creel 1990a). The implication is that the correct definition of e^0 is not relevant to a correct calculation of Hamilton's rule. However, this statement does not hold if inclusive fitness effects are summed over more than a single reproductive season and if alternative decisions differ in their risk of mortality. This is true because e^0 is subtracted from each individual's fitness each time during its lifespan that direct or indirect fitness components are measured, that is, once every breeding season. We can illustrate why e^0 will not cancel out using a simple example.

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Assume that if an individual dispersed it would produce, on average, 0.5 offspring as a breeder in a new group the current year but would have zero probability of surviving another year. The inclusive fitness of this individual would be $0.5 - e^0$. Alternatively, assume that the individual could remain in its current group, and if it did so it would survive the current year as a helper, helping its sibling produce 0.5 more offspring than it otherwise would have produced. Also, assume that this helper then bred the next year, producing 1.0 offspring and dying thereafter. The lifetime inclusive fitness of this option is $(0.5 \times r - e^0) + (1.0 - e^0)$. In this case, the fitness components to be subtracted from dispersers' and non-dispersers' fitnesses will not cancel out. More generally, differences in mortality risks between alternatives will cause differences in expected longevity, which will in turn cause differences in the relative weighting of e^0 on lifetime inclusive fitness. We emphasize that since e^0 relates to the average ability of individuals to give (or equivalently to receive) help, it should be calculated on a per-breeding-season basis, as we use it here.

A number of recent analyses have shown that future effects are important components in the estimation of inclusive fitness (e.g. Brown 1987; Mumme et al. 1989; Creel 1990b; Lucas et al., in press). In addition, differences in mortality risks between alternative behaviour patterns (e.g. dispersal versus non-dispersal, or helping versus non-helping) are likely to be nearly ubiquitous (Brown 1987; Waser et al. 1994). Together, these data suggest that an accurate evaluation of e^0 is warranted.

(2) Helpers often will have negative inclusive fitness. Applying the definition of e^0 in a dynamic optimization analysis of dispersal decisions in cooperatively breeding dwarf mongooses, Lucas et al. (in press) found that subordinate helpers of many age-sex classes had negative inclusive fitness. To illustrate this, assume that helpers do not breed (and breeders do not help), so that a helper's fitness is entirely indirect (Brown 1987). Indirect fitness is the product of a helper's effect on breeder reproductive success (b) multiplied by its relatedness to the breeder (r). Inclusive fitness is obtained by stripping e^0 from this indirect fitness, where e^0 is the product of an average helper's effect on breeder reproductive success (b) multiplied by the proportion of individuals in the population that are helpers (p) (Creel 1990a).

Therefore the helper's inclusive fitness is $(r - p) \times b$. This will be negative whenever the coefficient of relationship is less than the proportion of individuals in the population that are non-breeding helpers.

From published demographic data (e.g. Stacey & Koenig 1990) it appears that negative inclusive fitness for helpers will be common, unless helpers often obtain hidden direct reproduction. For 12 cooperatively breeding species ranging from lions, *Panthera leo*, to splendid fairy wrens, *Malurus splendens*, mean helper-breeder relatedness falls between 0.23 and 0.47 (Macdonald 1980; Woolfenden & Fitzpatrick 1984; Austad & Rabenold 1985; Emlen & Wrege 1988; Mills 1990; Packer et al. 1991; Creel & Waser 1994; also see Stacey & Koenig 1990). If the dichotomy between helping and breeding were absolute, this range of r -values would yield negative fitness for helpers in groups larger than 2.6 (for $r=0.23$) to 3.8 (for $r=0.47$). Many cooperatively breeding mammals live in group sizes large enough to yield negative fitness for helpers (e.g. African wild dogs with mean adult pack size of 11: Fuller et al. 1992). Modal group size for most cooperatively breeding birds is less than four (two, in most cases: Stacey & Koenig 1990), but even for these species many helpers will have a negative fitness unless relatedness is high.

Of course, the calculation of inclusive fitness is affected by direct fitness effects. Direct production of offspring by helpers has recently been discovered in several species (e.g. dwarf mongooses: Keane et al. 1994; stripe-backed wrens: Rabenold et al. 1990). This direct reproduction will obviously increase the inclusive fitness of helpers, but at least in dwarf mongooses, the number of young produced by helpers is insufficient to give them positive inclusive fitness (Lucas et al., in press).

The role of the indirect component of inclusive fitness on the evolution of helping behaviour has been controversial. Some authors argue that indirect effects are relatively unimportant (Zahavi 1974; Ligon 1981; Walters et al. 1992); others suggest that indirect effects cannot be overlooked (Mumme et al. 1989; Emlen & Wrege 1991; Creel & Waser 1994). Although we have shown here that the inclusive fitness of helpers can actually be negative, we want to emphasize that this does not mean that indirect fitness effects will be unimportant in the evolution of helping behaviour in these species. For example, we show elsewhere that,

despite negative indirect fitness for subordinate dwarf mongooses, indirect effects can play a major role in the evolution of social behaviour in this species (Lucas et al., in press).

Non-breeders will likely suffer negative fitness, irrespective of their choice of behaviour, if the frequency of helpers in a population is large. Indeed, the inclusive fitness of non-helping non-breeders will always be negative whenever helping exists. In itself, this is not relevant to the choice of behaviour; instead, we need to know the payoff to helping relative to other alternatives available to a non-breeder. Generally, the inclusive fitness of non-helping subordinates will be more negative than that of helpers. We need not be concerned with where a fitness value falls relative to zero, only with where it falls relative to the fitness of alternative phenotypes.

Several problems may remain with the estimation of inclusive fitness. One of these deals with traits whose fitnesses are frequency-dependent. Hamilton's (1964) derivation of inclusive fitness did not apply to such traits, as he indicated explicitly. The payoffs to traits like 'helping' and 'breeding' are, in reality, almost certainly frequency-dependent, so that models of inclusive fitness like the one we discuss here are only approximations of reality.

D. C. Queller (personal communication) has raised a further question about the nature of e^0 . Creel's (1990b) approach, like prior discussions of how to measure inclusive fitness (e.g. Grafen 1982, 1984), assumed that the value of e^0 is the same for all behavioural genotypes. For example, in the above example comparing the inclusive fitnesses of hypothetical dispersers and non-dispersers, the same value of e^0 is used to estimate both genotypes' inclusive fitnesses. Queller (personal communication) suggested that the value of e^0 associated with two different genotypes should be different. This is an important issue that we cannot resolve.

A further problem that may not have been adequately appreciated arises when one estimates the fitness of conditional strategies (see Parker 1989). In the simple dispersal/non-dispersal example used above, the strategies modelled are not sensitive to the state (other than the age) of the potential dispersers: the genes whose spread is being modelled are genes that predispose their bearers to 'disperse' or 'stay' whatever their nutritional state, dominance, group size, related-

ness to other group members, and so on. The alternative genotypes that compete in the real world are likely to be more complicated, and might for example influence their bearers' tendencies to disperse conditional on some combination of, for example, dominance and relatedness. An approach that explicitly allows the modelling of such conditional traits is dynamic optimization; we have presented a model of dwarf mongoose dispersal that incorporates such conditionalities elsewhere (Lucas et al., in press).

Since its formulation 30 years ago, the idea of inclusive fitness has had enormous impact, but its empirical application remains limited. The process of measuring inclusive fitness completely and correctly has been an iterative one. Among his listing of 'misconceptions of kin selection', Dawkins (1979) discussed sources of confusion over the definition of r . Grafen (1982, 1984) pointed out several common mis-definitions of inclusive fitness as well as the 'double accounting' problem discussed here. Brown (1987) suggested that inclusive fitness might be usefully broken into direct and indirect, current and future components. The most difficult components of inclusive fitness to conceptualize and estimate are the future effects; Mumme et al. (1989) and Creel (1990b) discussed the ways in which 'future indirect' fitness components might arise. Emlen & Wrege (1994) and Creel et al. (1991) suggested partial solutions to the problem of estimating future fitness components, both direct and indirect. Lucas et al. (in press) show how dynamic optimization can be used to provide a complete, lifetime accounting. We believe that methods of estimating inclusive fitness are converging, as they must if tests of behavioural ecological hypotheses are to become quantitative.

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