

Hamilton goes empirical: estimation of inclusive fitness from life-history data

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Hamilton's theory of kin selection is one of the most important advances in evolutionary biology since Darwin. Central to the kin-selection theory is the concept of inclusive fitness. However, despite the importance of inclusive fitness in evolutionary theory, empirical estimation of inclusive fitness has remained an elusive task. Using the concept of individual fitness, I present a method for estimating inclusive fitness and its components for diploid organisms with age-structured life histories. The method presented here: (i) allows empirical estimation of inclusive fitness from life-history data; (ii) simultaneously considers all components of fitness, including timing and magnitude of reproduction; (iii) is consistent with Hamilton's definition of inclusive fitness; and (iv) adequately addresses shortcomings of existing methods of estimating inclusive fitness. I also demonstrate the application of this new method for testing Hamilton's rule.

Keywords: altruism; Hamilton's rule; inclusive fitness; individual fitness; kin selection; matrix population models

1. INTRODUCTION

Hamilton's kin-selection theory (Hamilton 1964) has been hailed as one of the most important advances in evolutionary biology since Darwin (Trivers 2000; Alonso & Schuck-Paim 2002). As the only acceptable evolutionary explanation of altruistic behaviour, kin-selection theory provides a framework for understanding a variety of perplexing biological phenomena, including eusociality, cooperative breeding and reproductive skew (Grafen 1984, 1991; Griffin & West 2002).

Central to the theory of kin selection is the concept of inclusive fitness, which is considered by many as a fundamental concept in evolutionary theory. Despite the elegance and explanatory power of the kin-selection theory, empirical estimation of inclusive fitness has remained an elusive task (Grafen 1982, 1984; Creel 1990; Lucas *et al.* 1996). Most studies that have empirically estimated inclusive fitness have either considered fitness only at a certain age or focused on some measures of reproductive output, such as lifetime reproductive success (LRS), while ignoring other components of fitness (Brown 1975; Grafen 1991; Creel & Waser 1994). However, LRS may not adequately quantify fitness because it considers only the amount of reproduction and ignores timing of reproduction, which can substantially influence fitness (Cole 1954; Lewontin 1965; McGraw & Caswell 1996; Käär & Jokela 1998; Oli *et al.* 2002). As an example, consider two genotypes in a population that produce the same number of offspring in their lifetimes but one begins reproduction as a yearling and produces all offspring within 4 years while the other begins reproduction when 5 years old and reproduces until 10 years of age. Clearly, offspring of the early-maturing genotype will begin reproduction before the late-maturing genotype attains sexual maturity, and the pattern is repeated over generations, resulting in a rapid infusion of the population by the early-maturing genotype. The early-maturing genotype will therefore have a greater fitness than the late-maturing genotype even though LRS is equal.

A fitness measure that considers all components of fitness is the matrix population model-based individual fitness, $\lambda^{(k)}$ (McGraw & Caswell 1996). The $\lambda^{(k)}$ has been shown to quantify fitness adequately, and has recently received substantial applications (Käär & Jokela 1998; Caswell 2001; Oli *et al.* 2002). Using the concept of individual fitness, I present a method for estimating direct, indirect and inclusive fitness for diploid organisms with age-structured life histories. Using example calculations, I demonstrate how this method can be used to test Hamilton's rule (Hamilton 1964).

2. THE MODEL

I begin by making a distinction between 'direct reproduction' and 'indirect reproduction' ('reproduction' is used to indicate the process of 'gene duplication'). I define direct reproduction as the production of offspring by an individual itself such that it contributes to that individual's 'direct fitness' (the component of total fitness gained through direct reproduction (Griffin & West 2002)). However, an individual may gain fitness indirectly, through reproduction of other individuals with whom it shares some of its genes, and this should also be considered in estimating total individual fitness (Hamilton 1971). Thus, I define indirect reproduction as the reproduction of all non-descendant relatives with whom an individual shares some of its genes. Indirect reproduction contributes to 'indirect fitness' (the component of total fitness gained through the reproduction of non-descendant relatives (Griffin & West 2002)). Finally, the total reproduction of an individual is the sum of the direct and indirect reproductions.

I consider a sexually reproducing organism with an age-structured life history that reproduces at discrete time intervals. I assume that reproduction begins at age α and terminates at age ω , and that post-reproductive individuals may survive until age $\beta \geq \omega$. Individuals may begin and end their reproductive careers at different ages, and they

may also have different lifespans; consequently, α , ω and β may vary between individuals. An individual k of age class i produces m_i offspring, each of which carries some of the genes of individual k . Thus, the direct reproductive rate of individual k of age class i is estimated as: $F_i^{(k)} = m_i^{(k)}g$, where g is the genetic contribution of each parent to each offspring ($g = 0.5$ if parents are unrelated, but $g > 0.5$ if they are). Note that $F_i^{(k)} = 0$ for $\alpha > i > \omega$; $F_i^{(k)}$ may be zero for $\alpha < i < \omega$ only if reproduction fails. During its lifetime, an individual survives each time-step with an age-specific survival probability $P_i = 1$. Age-specific survival probability is set to 1 because an individual survives with certainty until age β . Without loss of information, age classes beyond ω may be ignored because an individual does not reproduce beyond this age and, thus, makes no contribution to its direct fitness. Using the estimates of age-specific direct reproductive rates $F_i^{(k)}$ and age-specific survival probability of 1, a 'population projection matrix' can be constructed for individual k (McGraw & Caswell 1996):

$$A_{\text{direct}}^{(k)} = \begin{bmatrix} 0 & 0 & \dots & F_{\alpha}^{(k)} & F_{\alpha+1}^{(k)} & \dots & F_{\omega-1}^{(k)} & F_{\omega}^{(k)} \\ 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 \end{bmatrix} \quad (2.1)$$

In general, $A_{\text{direct}}^{(k)}$ is an ω by ω matrix with

$$a_{ij}^{(k)} = \begin{cases} F_i^{(k)} & \text{for } i = 1 \text{ and } \alpha \leq j \leq \omega \\ 1 & \text{for } i = j + 1 \text{ and } 1 \leq j \leq \omega - 1 \\ 0 & \text{elsewhere.} \end{cases}$$

The characteristic equation for a life cycle of the type represented in equation (2.1) is obtained by setting the determinant of the matrix $A_{\text{direct}}^{(k)} - \lambda I$ to zero, where I is the identity matrix and λ is the eigenvalue (Oli & Zinner 2001a,b). The general characteristic equation can be written as (McGraw & Caswell 1996; Oli & Zinner 2001a,b):

$$1 = \sum_{i=1}^{\omega} \frac{F_i^{(k)}}{(\lambda_{\text{direct}}^{(k)})^i} \quad (2.2)$$

The direct fitness of individual k , $\lambda_{\text{direct}}^{(k)}$, is then estimated as the largest real root of equation (2.2) or as the dominant eigenvalue of the matrix $A_{\text{direct}}^{(k)}$. If an individual dies without reproducing at least once, $F_i^{(k)} = 0$ for all i ; consequently, $\lambda_{\text{direct}}^{(k)} = 0$, as it should, regardless of how long the individual lives.

Individual k may gain indirect fitness if one or more other individuals who share some of their genes with individual k reproduce. Fitness gained by an individual through the reproduction of non-descendant relatives is its indirect fitness. Indirect fitness of individual k is determined by its indirect reproductive rates, which in turn depend on the coefficient of relatedness (Hamilton 1964, 1971), the number of non-descendant relatives and their direct reproductive rates, and the age of individual k . Specifically, the indirect reproductive rate of individual

k in age class i , $\theta_i^{(k)}$, is the sum of the relatedness-weighted direct reproductive rates of all non-descendant relatives of all ages when individual k is in age class i :

$$\theta_i^{(k)} = \sum_{l=1}^n r_{kl} F_l^{(l)}, \quad (2.3)$$

where r_{kl} is the coefficient of relatedness between individual k and individual l as defined by Hamilton (1964, 1971), n is the total number of non-descendant relatives ('neighbours') who share some of their genes with individual k and $F_l^{(l)}$ is the direct reproductive rate of individual l when individual k is in age class i . $F_l^{(l)}$ is estimated as: $F_l^{(l)} = m_l^{(l)}g$, where $m_l^{(l)}$ is the number of offspring produced by individual l when individual k is in age class i , and g is the genetic contribution of individual l to each of its offspring. Note that $\theta_i^{(k)}$ is independent of the ages of non-descendant relatives, and that the subscript i in $F_l^{(l)}$ and $m_l^{(l)}$ refers to the age class of individual k , not that of individual l . Note also that individual l will not contribute to $\theta_i^{(k)}$ if it is unrelated to individual k (because $r_{kl} = 0$) or if it fails to reproduce when individual k is in age class i (because $F_l^{(l)} = 0$).

Using the estimates of age-specific rates of indirect reproduction, $\theta_i^{(k)}$, and an age-specific survival rate of 1 until its death, one can construct the population projection matrix for individual k based only on the rate of indirect reproduction:

$$A_{\text{indirect}}^{(k)} = \begin{bmatrix} \theta_1^{(k)} & \theta_2^{(k)} & \dots & \theta_{\alpha}^{(k)} & \theta_{\alpha+1}^{(k)} & \dots & \theta_{\omega}^{(k)} & \theta_{\omega+1}^{(k)} & \dots & \theta_{\beta-1}^{(k)} & \theta_{\beta}^{(k)} \\ 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 \end{bmatrix} \quad (2.4)$$

In general, $A_{\text{indirect}}^{(k)}$ is a β by β matrix with

$$a_{ij}^{(k)} = \begin{cases} \theta_i^{(k)} & \text{for } i = 1 \text{ and } j \leq \beta \\ 1 & \text{for } i = j + 1 \text{ and } 1 \leq j \leq \beta - 1 \\ 0 & \text{elsewhere.} \end{cases}$$

Note that an individual may have non-zero $\theta_i^{(k)}$ for any $i \leq \beta$ if other individuals contribute to its indirect reproductive rate (whereas $F_i^{(k)}$ may be non-zero only for $\alpha \leq i \leq \omega$). The characteristic equation for a life cycle of the type represented in equation (2.4) is obtained by setting the determinant of the matrix $A_{\text{indirect}}^{(k)} - \lambda I$ to zero. The general characteristic equation may be written as:

$$1 = \sum_{i=1}^{\beta} \frac{\theta_i^{(k)}}{(\lambda_{\text{indirect}}^{(k)})^i} \quad (2.5)$$

The indirect fitness of individual k , $\lambda_{\text{indirect}}^{(k)}$, is then estimated as the largest real root of equation (2.5) or as the dominant eigenvalue of the matrix $A_{\text{indirect}}^{(k)}$.

The total reproductive rate of individual k of age class i is the sum of the direct reproductive rate and the indirect reproductive rate. Thus, the population projection matrix for individual k that includes both direct and indirect reproductive rates is:

$$A_{\text{total}}^{(k)} = \begin{bmatrix} \psi_1^{(k)} & \psi_2^{(k)} & \dots & \psi_\alpha^{(k)} & \psi_{\alpha+1}^{(k)} & \dots & \psi_\omega^{(k)} & \psi_{\omega+1}^{(k)} & \dots & \psi_{\beta-1}^{(k)} & \psi_\beta^{(k)} \\ 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 1 & \dots & 0 & 0 \\ \vdots & & \ddots & & & \ddots & & & \ddots & & \vdots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \dots & 1 & 0 \end{bmatrix}, \tag{2.6}$$

where $\psi_i^{(k)} = F_i^{(k)} + \theta_i^{(k)}$ for $\alpha \leq i \leq \omega$, and $\psi_i^{(k)} = \theta_i^{(k)}$ for $\alpha > i > \omega$. In general, $A_{\text{total}}^{(k)}$ is a β by β matrix with

$$a_{ij}^{(k)} = \begin{cases} \theta_i^{(k)} & \text{for } i = 1 \text{ and } \alpha > j > \omega \\ (\theta_i^{(k)} + F_i^{(k)}) & \text{for } i = 1 \text{ and } \alpha \leq j \leq \omega \\ 1 & \text{for } i = j + 1 \text{ and } 1 \leq j \leq \beta - 1 \\ 0 & \text{elsewhere.} \end{cases}$$

The general characteristic equation of the matrix $A_{\text{total}}^{(k)}$ is

$$1 = \sum_{i=1}^{\beta} \frac{\psi_i^{(k)}}{(\lambda_{\text{total}}^{(k)})^i}. \tag{2.7}$$

The total fitness of individual k , $\lambda_{\text{total}}^{(k)}$, is estimated as the largest real root of equation (2.7) or as the dominant eigenvalue of the matrix $A_{\text{total}}^{(k)}$. Statistical properties of $\lambda_{\text{direct}}^{(k)}$ are discussed by McGraw & Caswell (1996) and also apply to $\lambda_{\text{indirect}}^{(k)}$ and $\lambda_{\text{total}}^{(k)}$.

3. INCLUSIVE FITNESS

The concept of inclusive fitness has been the subject of much misunderstanding (Grafen 1982, 1984, 1991), and this must be clarified before inclusive fitness can be estimated. Grafen (1984) discussed several erroneous definitions of inclusive fitness, and similarly incorrect definitions continue to appear in the literature. Recently, Griffin & West (2002) defined inclusive fitness as ‘the effect of one individual’s actions on everybody’s numbers of offspring weighted by the relatedness’ (p. 20). This and many other definitions of inclusive fitness have focused on the magnitude of reproduction (Wilson 1975; Grafen 1991), which is an important component of fitness but, by itself, not fitness (McGraw & Caswell 1996). Ricklefs & Miller (2001) defined inclusive fitness as ‘the fitness of an individual plus the fitness of its relatives, weighted according to the coefficient of relatedness’ (p. 706). If one agrees with this definition, then an appropriate measure of inclusive fitness is $\lambda_{\text{total}}^{(k)}$; this definition, however, is not consistent with Hamilton’s description of inclusive fitness.

Hamilton (1964) described inclusive fitness as the ‘personal fitness which an individual actually expresses in its

production of adult offspring... *stripped* of all components which can be considered as 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... *augmented* by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitness of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to neighbours whom he affects.’ (p. 8). Much confusion exists regarding the quantities that are to be augmented or removed. A second source of confusion has been the quantification of fitness itself. Hamilton (1964) mentioned ‘offspring production’ in his original description of inclusive fitness; consequently, many authors have defined inclusive fitness only in terms of reproductive success (Creel 1990; Cockburn 1991; Griffin & West 2002). However, Hamilton’s (1971) subsequent statement that ‘If an altruistic act by A greatly increases the fitness of B , A ’s inclusive fitness may be increased in spite of decrease in A ’s individual fitness’ (p. 196) clearly implies that inclusive fitness incorporates all components of fitness, not just the amount of reproduction.

Estimation of inclusive fitness is meaningful only in the context of a behaviour (or a set of related behaviours, e.g. helping in cooperative breeding systems) of an individual (‘donor’) directed towards one or more conspecific individuals (‘recipients’) such that the fitnesses of both the donor and the recipients are affected by the donor’s action (Hamilton 1964). If the fitness of an individual is unaffected by the actions of other conspecific individuals and if an individual’s actions do not affect the fitness of other conspecific individuals, inclusive fitness of that individual is equal to its total fitness because there is nothing to be ‘stripped’ or ‘augmented’. However, if behavioural interactions among individuals influence each other’s fitnesses, one must consider the quantities that Hamilton suggested should be augmented and removed. In this context, the inclusive fitness of individual k , $\lambda_{\text{inclusive}}^{(k)}$ is:

$$\lambda_{\text{inclusive}}^{(k)} = \lambda_{\text{total}}^{(k)} - (\lambda_{\text{direct}}^{(k)} - \lambda_{\text{no behaviour}}^{(k)}) + \sum_{l=1}^n r_{kl} (\lambda_{\text{direct}}^{(l)} - \lambda_{\text{no behaviour}}^{(l)}), \tag{3.1}$$

where $\lambda_{\text{direct}}^{(k)}$ is the direct fitness of individual k , $\lambda_{\text{no behaviour}}^{(k)}$ is the expected direct fitness of individual k in the absence of behaviours directed towards it by other conspecific individuals, r_{kl} is the coefficient of relatedness between individual k and individual l , $\lambda_{\text{direct}}^{(l)}$ is the direct fitness of individual l , $\lambda_{\text{no behaviour}}^{(l)}$ is the expected direct fitness of individual l in the absence of behaviours directed towards it by individual k , and n is the total number of conspecific individuals (‘neighbours’) that are a part of the social environment of individual k .

The term $(\lambda_{\text{direct}}^{(k)} - \lambda_{\text{no behaviour}}^{(k)})$ quantifies the effect of the social environment of individual k on its direct fitness, which Hamilton (1964) suggested should be removed from the estimation of inclusive fitness. Note that this term is zero if individual k does not receive any actions, beneficial or harmful, from its neighbours; it is negative if such actions are harmful, and positive if neighbours’ actions are beneficial. The term $[r_{kl} (\lambda_{\text{direct}}^{(l)} - \lambda_{\text{no behaviour}}^{(l)})]$ quantifies the effect of individual k on the direct fitness of each of its neighbours, weighted by the coefficient of

relatedness between individual k and each of its neighbours; this is the quantity that Hamilton (1964) suggested should be augmented when estimating inclusive fitness. The sum in equation (3.1) can be positive, negative or zero, depending upon the nature of the social interactions between individual k and its neighbours. Note also that the inclusive fitness of an individual may be greater than its total fitness if its actions substantially improve the direct fitnesses of its close relatives ('altruistic' behaviours). If an individual's actions reduce the direct fitnesses of its neighbours ('selfish' or 'spiteful' behaviours), then its inclusive fitness may be less than its total fitness. If an individual does not receive any actions from, or direct its actions towards, its neighbours, then the inclusive fitness of that individual is equal to its total fitness, as it should be. Finally, I point out that neighbours who do not form a part of an individual's immediate social environment (and those with limited opportunity of social interactions with that individual) should not be considered in estimating inclusive fitness.

4. TESTING HAMILTON'S RULE

The evolutionary explanation of altruistic behaviour has been the most important application of the inclusive-fitness concept in evolutionary biology. Typically, it is assumed that an individual k performs an altruistic act towards its non-descendant relatives that reduces its own direct fitness, but increases the direct fitnesses of the relatives. Hamilton (1964) showed that genes responsible for the altruistic act should spread in the population if $rb - c > 0$, where c is the cost to the donor (i.e. the individual performing the altruistic act), b is the benefit to the recipients and r is the coefficient of relatedness, as discussed in § 3. This condition for the evolution of an altruistic behaviour is called 'Hamilton's rule', and has been the foundation of the evolutionary explanation of altruistic behaviour. But how does one test Hamilton's rule? What currency does one use to calculate costs and benefits? Clearly, the currency under consideration must be fitness, rather than its components.

Consider a species of cooperatively breeding bird, such as the superb blue wren (*Malurus cyaneus*) discussed by Grafen (1984). A young female may stay in her parents' nest and help raise her siblings, or disperse and try to raise her own offspring. Assume that, on average, a nest without a helper fledges 1.5 chicks per year, and that one with a helper fledges 2.8 offspring per year. Assume further that: (i) the mother had previously reproduced once without a helper as a yearling; (ii) the mother will reproduce without helpers until age $\omega = 5$; (iii) if the young female chooses to raise her own young, she would do so without helpers; (iv) the young female reproduces without helpers every year until age $\omega = 5$; and (v) there are no other non-descendant relatives.

Without the helper, the mother's population projection matrix would be (assuming $g = 0.5$):

$$A_{\text{direct}}^{(\text{mother})} = \begin{bmatrix} 0.75 & 0.75 & 0.75 & 0.75 & 0.75 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}.$$

The direct fitness, $\lambda_{\text{direct}}^{(\text{mother})}$, of the mother without her daughter's help, estimated as described in § 2, would be 1.697. If the daughter stays to help, the mother would fledge 2.8 offspring in the second breeding season. In that case, the second entry in the first row of the matrix would be 1.4, and the resulting $\lambda_{\text{direct}}^{(\text{mother})}$ would be 1.880. Thus, the benefit to the recipient of the young female's helping behaviour is $1.880 - 1.697 = 0.183$ in fitness currency.

If the young female chose to disperse and initiate nesting in the first year, her fitness would be 1.697. However, if she chose to help her parents instead, she would not reproduce during the first breeding season, and her direct reproductive rate that year would be zero. Her direct individual fitness would then be 1.396. So, the cost to the donor is $1.697 - 1.396 = 0.301$ in fitness currency. Should the helping behaviour evolve? One can apply Hamilton's rule. If the young female shares both of her parents with the siblings she is helping to raise, then $r = 1$ (Grafen 1984), and $rb - c = 1 \times 0.183 - 0.301 = -0.118 < 0$, and the helping behaviour should not evolve.

Assume now that, on average, a primiparous female would fledge only 0.5 chicks, owing perhaps to the lack of experience, if she chose to disperse and nest instead of helping raise her siblings. In this case, the cost to the donor is 0.087 in fitness currency. Applying Hamilton's rule, one finds that $rb - c = 1 \times 0.183 - 0.087 = 0.096 > 0$, and helping behaviour should evolve. However, helping behaviour should be less likely to evolve if the young female does not share both of her parents with the siblings she is helping to raise.

Under the assumptions listed above, costs and benefits are in inclusive-fitness currency because I have performed both 'augmentation' and 'stripping' as suggested by Hamilton (1964). For simplicity, I have considered costs and benefits in terms of direct fitness (by assuming no other non-descendant relatives), but these calculations can be easily extended to include indirect fitness. Moreover, the assumptions listed above are not required when data are available to replace them.

5. DISCUSSION

Nearly four decades have elapsed since Hamilton persuasively articulated the theory of kin selection (Hamilton 1964). The theory of kin selection has been successful in explaining a variety of perplexing biological phenomena, and the concept of inclusive fitness has become a fundamental concept in evolutionary theory (Griffin & West 2002). It is generally believed that natural selection acts on inclusive fitness (Creel 1990; Grafen 1991), and empirical tests of the kin-selection theory require estimation of inclusive fitness. However, no reasonable method was available until now for the empirical estimation of inclusive fitness from field data. Methods for estimating inclusive fitness were discussed by Grafen (1982, 1984), but these were based on the number of offspring at some point in time and thus only consider one component of fitness. Creel (1990) re-examined Hamilton's description of the inclusive fitness and suggested a method for estimating it. Under certain conditions, Creel's approach yields negative fitness (Lucas *et al.* 1996), clearly a biological impossibility. Additional difficulties with Creel's (1990) approach are discussed by Lucas *et al.* (1996) and Queller (1996). One of the very

few empirical estimates of inclusive fitness was reported by Creel & Waser (1994), but their approach considers fitness at a given age, and thus ignores possible trade-offs among components of fitness (Stearns 1992).

The method presented here adequately quantifies inclusive fitness, and also addresses the problems inherent in existing methods of inclusive-fitness estimation. First, this method allows empirical estimation of direct, indirect and inclusive fitnesses from life-history data. Second, estimates of inclusive fitness obtained from this approach are always non-negative, and an individual that realizes reproduction will always have a positive inclusive fitness. Third, the method presented here explicitly considers all components of fitness, whereas most existing methods ignore one or more of them. Fourth, my method is applicable to a wide spectrum of behavioural interactions, ranging from altruistic to spiteful, that may influence the fitness of an individual. Fifth, this approach allows statistical comparisons of inclusive fitness and its components across genotypes (e.g. 'helpers' and 'dispersers'). For example, one can estimate the inclusive fitness of each of the helpers and dispersers, and then apply randomization or standard statistical tests to compare the mean fitnesses of the two genotypes. This approach provides a framework for rigorous statistical tests of Hamilton's rule. Finally, my approach to estimating inclusive fitness is consistent with the original definition of inclusive fitness (Hamilton 1964), with appropriate 'augmentation' and 'stripping', and thus captures all essential elements of Hamilton's description of inclusive fitness.

While acknowledging the difficulties inherent in estimating inclusive fitness, I suggest that it is possible to estimate this important quantity accurately. The method outlined in this paper provides a framework within which direct, indirect and inclusive fitnesses can be empirically estimated. Data required to estimate direct, indirect and inclusive fitnesses include lifetime reproductive and survival histories of individual k and its non-descendant relatives, and the coefficients of relatedness between them. Many long-term studies of individually marked animals (Clutton-Brock *et al.* 1982; Wolfenden & Fitzpatrick 1984; Dhondt 1989; Grant & Grant 1992; Hoogland 1995; Armitage & Schwartz 2000) provide data adequate for estimating inclusive fitness and its components.

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