



## Kin selection under blending inheritance

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### ABSTRACT

Why did Darwin fail to develop his insights on kin selection into a proper theory of social adaptation? One suggestion has been that his inadequate understanding of heredity kept the problem out of focus. Here, I determine whether it is possible to develop a quantitative theory of kin selection upon the assumption of blending inheritance. I find that, whilst Hamilton's rule of kin selection can be readily derived under the assumption of blending inheritance, this mechanism complicates the computation of relatedness coefficients, and can even cause them to fluctuate over generations. Nevertheless, I show that the ultimate criterion for selection to favour any social trait – i.e. a time-average of Hamilton's rule – remains the same as under particulate inheritance. By eliminating the gene from the theory of kin selection, I clarify the role that it plays in the theory of social adaptation.

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### 1. Introduction

Darwinism is a theory of the process and purpose of biological adaptation. Natural selection leads to the accumulation of those traits whose heritable components are associated with greater individual reproductive success and so, Darwin (1859) argued, individual organisms will appear increasingly well adapted to maximize their personal reproductive success. This argument has been mathematically formalized by Grafen (2002). Although working in ignorance of the mechanism of heredity – indeed, assuming this to involve a type of blending of the characters of an individual's parents – Darwin provided a convincing materialistic account of the origin of design in the living world, a phenomenon that had previously been attributed to the work of deities (Paley, 1802).

The only major revision to the theory of Darwinian adaptation has been to accommodate social interactions between relatives. Darwin (1859, Chapter 7) noted the “special difficulty” posed to his theory by sterile workers among the social insects: how can natural selection give rise to their adaptations, if they have no descendants? His solution was to point out that natural selection can operate both directly, upon the individual's own reproductive success, and also indirectly, upon the reproductive success of her relatives, who may carry a heritable tendency for her characteristics in latent form (Darwin, 1859, Chapter 7; see also Ratnieks

et al., 2011). This theory of “kin selection” (Maynard Smith, 1964) was developed by Hamilton (1963, 1964, 1970, 1996), who showed that natural selection should lead individuals to appear designed as if to maximize the sum of their direct and indirect fitness, i.e. their “inclusive fitness” (see also Grafen, 2006a). This allows for altruistic adaptations, that lower the personal fitness of the individual, whilst providing a benefit to her relatives.

It is unclear why Darwin failed to develop his initial insights on kin selection into a proper theory of social adaptation. Hamilton (1972) suggested that Darwin's inadequate understanding of heredity had kept the problem out of focus. Moreover, some have claimed that it was simply not possible to formulate a theory of kin selection prior to the discovery of classical genetics (e.g. Borrello, 2010, p. 8; Cunningham, 2010, p. 31). Is the logic of kin selection crucially founded upon particulate inheritance, so that elucidation of the true function of Darwinian adaptation was contingent upon the discovery of Mendelian genetics (Mendel, 1866) and its reconciliation with Darwinism (Yule, 1902; Fisher, 1918, 1930)? In support of this idea is the fact that Hamilton (1963, 1964) approached the problem of altruism by taking a “gene's eye” view, recognizing that the ultimate beneficiary of natural selection is not the individual but the gene, which is stably inherited over generations.

In opposition to this idea is the fact the canonical derivation of Hamilton's rule of kin selection (Hamilton, 1970; Frank, 1998) makes use of Price's (1970) equation, which can be applied to any system of inheritance (Price, 1972, 1995; Frank, 1995; Gardner, 2008; Jäger, 2008; Helenterä and Uller, 2010). Since Hamilton's rule emerges as a simple partition of Price's equation it should, in principle, also apply to any system of inheritance. However, the

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implications of non-particulate inheritance for the theory of kin selection remain obscure. How different would the theory of social adaptation have appeared, had it been founded upon a different mechanism of inheritance?

In this article, I develop the theory of kin selection under the assumption of blending inheritance. My main aim is to assess what aspects of the modern theory of social adaptation could have been developed in the ignorance of classical genetics. To this end, I review some basic results for the “paint-pot” theory of blending inheritance (Fisher, 1930; Hardin, 1959), and I derive Hamilton’s rule of kin selection in this context. I then examine the consequences of blending for relatedness coefficients of genealogical kin, revealing that these may differ from their Mendelian equivalents. Indeed, they may even fluctuate over time. However, I show that a time average of the evolutionary response to kin selection under blending coincides exactly with that derived under Mendelian considerations. By eliminating the gene from the theory of kin selection, I clarify its role in the theory of social adaptation.

## 2. Models and analysis

### 2.1. Blending inheritance under neutrality

Here I provide a basic treatment of blending inheritance – specifically, the paint-pot model of blending (Fisher, 1930; Hardin, 1959) – in a neutral population context. This analysis recovers results presented by Fisher (1930), although here the input of mutational variance is made mathematically more explicit.

I assume an infinite population with discrete, non-overlapping generations. An individual’s phenotypic value can be written as  $p=h+e$ , where  $h$  is her heritable “breeding” value and  $e$  is an uncorrelated, unbiased environmental effect (i.e.  $\text{cov}(e,h)=E(e)=0$ ). Hence, the population-average phenotype is equal to the population-average breeding value (i.e.  $E(p)=E(h)$ ). An individual’s breeding value is the average of those of her mother and father ( $x$  and  $y$ , respectively), plus an uncorrelated, unbiased mutational effect ( $m$ , such that  $\text{cov}(m,x)=\text{cov}(m,y)=E(m)=0$ ). That is,  $h=(x+y)/2+m$ . Note that the population-average breeding value does not change over generations:

$$E(h) = E\left(\frac{x+y}{2} + m\right) = \frac{1}{2}(E(x)+E(y))+E(m) = E(h'), \quad (1)$$

where  $E(h')=E(x)=E(y)$  is the population-average breeding value for the previous generation (that is, the prime indicates a step back, rather than a step forward, in time). This simple result refutes the “swamping” argument of Jenkin (1867); there is no tendency for blending to favour wildtype over variant trait values (see also Davis, 1871; Bulmer, 2004).

However, the population variance in breeding value may change, as shown by the fact that:

$$\begin{aligned} \text{var}(h) &= \text{var}\left(\frac{x+y}{2} + m\right) = \frac{1}{4}(\text{var}(x)+\text{var}(y)+2\text{cov}(x,y))+\text{var}(m) \\ &= \frac{1+f}{2}\text{var}(h')+\text{var}(m), \end{aligned} \quad (2)$$

where  $f=\text{cov}(x,y)/\text{var}(x)$  is the coefficient of inbreeding.

Assuming no mutational input ( $\text{var}(m)=0$ ), the heritable variance in every phenotypic character is expected to decline geometrically, with its value in each generation being a fraction  $(1+f)/2$  of its value in the previous generation (Fisher, 1930). In the absence of inbreeding ( $f=0$ ), this represents a halving of heritable variance. Heritability can only be maintained in the limit of full inbreeding ( $f=1$ ). This erosion of heritable variation is the main difficulty that blending inheritance posed for Darwin’s theory of natural selection (Fisher, 1930).

However, fresh mutational input can maintain heritability. For example, if there is a constant supply of variance  $\text{var}(m)$  in every generation, then dynamical Eq. (2) can be solved for equilibrium ( $\text{var}(h)=\text{var}(h')$ ) to obtain:

$$\text{var}(h) = \frac{2\text{var}(m)}{1-f}, \quad (3)$$

e.g. in the absence of inbreeding ( $f=0$ ), the equilibrium heritable variance is twice that of the mutational input added to the population in every generation. Note that this scenario is exactly equivalent to the “infinitesimal model” of Fisher (1918), if the mutational input is regarded as being analogous to the variation created by recombination. More generally, if the mutational input varies from generation to generation, the analogy with the infinitesimal model breaks down, and the heritable variance will fluctuate over time.

### 2.2. Kin selection under blending inheritance

The canonical derivation of Hamilton’s rule is based upon Price’s equation (Hamilton, 1970; Price 1970, 1972; Queller, 1992; Frank, 1998; Gardner et al., 2011). This expresses the change in the average heritable component of any character between generations, that is ascribed to the action of natural selection, by

$$\Delta_S E(h) = \text{cov}(v,h), \quad (4)$$

i.e. the change is equal to the covariance between an individual’s breeding value  $h$  and her relative fitness  $v$  (i.e. number of offspring, relative to the population average of this quantity; Price, 1970, 1972). Eq. (4) explicitly neglects the impact of non-selective evolutionary factors on change in heritable traits (e.g. biased mutation). For simplicity, I also neglect class structure, such that reproductive value coincides exactly with offspring number (Fisher, 1930; Grafen, 2006b).

Assuming nonzero heritable variance, the covariance in Eq. (4) can be expressed as a product of the heritable variance  $\text{var}(h)$  and a coefficient  $\beta(v,h)\equiv\text{cov}(v,h)/\text{var}(h)$ . This coefficient happens to be equal to the slope of the straight line fitted, by the method of least-squares, to the set of population data  $(v,h)$ , i.e. it is a least-squares linear regression coefficient (Price, 1970; Frank, 1998; Gardner et al., 2011). This yields

$$\Delta_S E(h) = \beta(v,h)\text{var}(h), \quad (5)$$

which captures Darwin’s (1859) basic requirements for a response to natural selection: heritable variation ( $\text{var}(h) > 0$ ) for a character that is correlated with relative fitness ( $\beta(v,h) \neq 0$ ).

Correlations between an individual’s heritable character and her fitness can occur for two reasons. First, the character may be expressed in the phenotype of the focal individual, and mediate her reproductive success (direct fitness effect). Secondly, the character may be carried by the individual’s social partners, expressed in their phenotypes, and mediate her reproductive success through their social interactions with her (indirect fitness effect; Fisher, 1930; Hamilton, 1964, 1970). For simplicity, assume that individuals are paired with a single social partner, whose breeding value for the character of interest may be denoted  $H$ . Then, the regression of relative fitness against breeding value can be partitioned, without loss of generality, into these direct and indirect fitness effects:

$$\Delta_S E(h) = [\beta(v,h|H) + \beta(v,H|h)\beta(H,h)]\text{var}(h), \quad (6)$$

where  $\beta(v,h|H)\equiv -c$  is the partial regression of the individual’s relative fitness against her own breeding value (i.e. holding fixed the effect of her social partner’s breeding value),  $\beta(v,H|h)\equiv b$  is the partial regression of the individual’s relative fitness against her social partner’s breeding value (i.e. holding fixed the effect of

her own breeding value), and  $\beta(H,h) \equiv r$  is the kin selection coefficient of relatedness, which describes the statistical association between the breeding values of social partners (Hamilton, 1970; Queller, 1992; Frank, 1998; Gardner et al., 2011).

Thus, assuming heritable variation upon which natural selection can act ( $\text{var}(h) > 0$ ), the condition for a selective increase in the average heritable component of any character of interest is given by Hamilton's rule:  $-c + br > 0$  (Hamilton, 1963, 1964, 1970). Although I have assumed only a single social partner, for ease of exposition, this derivation of Hamilton's rule can be readily extended to multiple social partners interacting in multiple roles (Grafen, 2006a). Importantly, the present derivation has made no assumption of particulate inheritance, and hence applies equally to a blending scheme. Thus, kin selection operates – in outline – in the same way, irrespective of whether inheritance is particulate or blending. In the next section, I examine whether the details of the evolutionary response to kin selection differ between inheritance schemes, by examining the consequences of blending inheritance for the kin selection coefficient of relatedness.

### 2.3. The correlation between relatives on the supposition of blending inheritance

I now consider the consequences of blending inheritance for the kin selection coefficient of relatedness. A standard simplifying assumption often made by kin selection analyses is that selection is vanishingly weak, so that – to first order in the selection coefficient – Hamilton's rule can be expressed in terms of relatedness coefficients that are calculated in a neutral population (Bulmer, 1994). I make this weak selection assumption for the remainder of the analysis. I also continue to assume discrete, non-overlapping generations, with mating and social interaction occurring only between individuals belonging to the same generation, and avoidance of inbreeding ( $f=0$ ). Finally, I assume that the only cause of relatedness between social partners is coancestry.

As under particulate inheritance, the coefficient of relatedness under blending inheritance is given by

$$r \equiv \frac{\text{cov}(H,h)}{\text{var}(h)} \quad (7)$$

Thus, the relatedness to self is found by substituting  $H=h$ , to obtain  $r_{\text{SELF}} = \text{cov}(h,h)/\text{var}(h) = 1$ . Similarly, the relatedness to a full sibling is found by writing  $h=(x+y)/2+m$  and  $H=(x+y)/2+M$ , where  $M$  is the sibling's mutational effect. Continuing with the assumption that mutation is random and unbiased, this gives  $r_{\text{SIB}} = \text{cov}((x+y)/2, (x+y)/2)/\text{var}(h) = (1/2) \times (\text{var}(h')/\text{var}(h))$ . More generally, under the assumption of blending inheritance, the kin selection coefficient of relatedness  $r$  is equal to the product of two quantities,  $\rho \times V$  (see Appendix for details). The first factor  $\rho$  is the traditional genealogical relationship of two individuals, i.e.  $\rho=1$  for self,  $\rho=1/2$  for a full sibling,  $\rho=1/4$  for a half sibling and  $\rho=1/8$  for a cousin. The second factor  $V$  is computed by dividing the heritable variance of the most-recent common ancestor's generation by that of the present generation.

Thus, the coefficient of relatedness depends upon the dynamics of heritable variance between generations. If there is no input of novel mutation, then the heritable variation halves in every generation (i.e.  $\text{var}(h) = \text{var}(h')/2 = \text{var}(h'')/4$ , etc.). This means that relatedness to self is  $r_{\text{SELF}} = 1$ , relatedness to full siblings is  $r_{\text{SIB}} = (1/2) \times (\text{var}(h')/\text{var}(h)) = 1$ , relatedness to half siblings is  $r_{\text{HALFSIB}} = (1/4) \times (\text{var}(h')/\text{var}(h)) = 1/2$ , and relatedness to cousins is  $r_{\text{COUSIN}} = (1/8) \times (\text{var}(h'')/\text{var}(h)) = 1/2$ , where  $\text{var}(h'')$  is the heritable variance two generations prior to the focal generation. Certain of these coefficients differ from those obtained under Mendelian inheritance:  $r_{\text{SELF}} = 1$ ,  $r_{\text{SIB}} = 1/2$ ,  $r_{\text{HALFSIB}} = 1/4$ , and  $r_{\text{COUSIN}} = 1/8$ . The reason for this discrepancy is illustrated by considering the

relatedness to full siblings. Under Mendelian inheritance, the genetic complements of full siblings reflect independent, partial samples of genes drawn from the same two parents, hence they will tend to differ genetically. In contrast, under blending, full siblings share exactly the same inheritance and hence, in the absence of *de novo* mutation, they are identical in their heritable characteristics.

However, under blending, natural selection can only have a sustained impact upon evolution if mutational variance is nonzero. In the simplest scenario, a constant supply of mutational variance is added in every generation, such that the heritable variation is maintained at some constant level (i.e.  $\text{var}(h) = \text{var}(h') = \text{var}(h'') = 2 \text{var}(m)$ ). In this scenario,  $V=1$  for all coefficients of relatedness, and hence  $r=\rho$  for all degrees of relationship, i.e. coefficients of relatedness under blending coincide exactly with those obtained under Mendelian inheritance.

More generally, the input of mutational variance might vary between generations – indeed, this was Darwin's (1859, Chapter 4) view – and hence the heritable variation will display more complicated dynamics through time. Thus, the response to kin selection quantified in Eq. (6) can be re-written as

$$\Delta_S E(h) = -c \text{var}(h) + b \rho \text{var}(h^*), \quad (8)$$

where  $h^*$  denotes a breeding value in the generation occupied by the most recent common ancestor of socially interacting relatives (I assume, for simplicity, that individuals are paired according to their relationship, i.e. siblings, cousins, etc.). This response to selection is expected to fluctuate across generations (owing to fluctuations in  $\text{var}(h)$  and  $\text{var}(h')$ ). However, since selection is weak, of most interest is the average response to selection occurring over a large number of generations. Taking a time average (denoted  $E_T(\cdot)$ ) of the response to natural selection over a large number of generations, assumed to be longer than the cycle period of the heritable variance dynamics, I obtain

$$E_T(\Delta_S E(h)) = -c E_T(\text{var}(h)) + b \rho E_T(\text{var}(h^*)) \\ = [-c + b \rho] E_T(\text{var}(h)), \quad (9)$$

where from Eq. (3),  $E_T(\text{var}(h)) = 2 \times E_T(\text{var}(m))$ . Hence, the condition for natural selection to favour an increase in the average value of any character of interest is  $-c + b \rho > 0$ , where  $\rho$  is the coefficient of genealogical relationship, which coincides exactly with the result obtained under the assumption of Mendelian inheritance (Hamilton, 1963, 1964).

### 3. Discussion

I have developed a theory of kin selection under the assumption of blending inheritance. Specifically, I have: recovered and elaborated upon Fisher's (1930) results for the evolution of the average and variance in heritable trait value in neutral populations, under the assumption of blending; used Price's (1972) equation to derive Hamilton's (1963, 1964, 1970) rule of kin selection, without reference to particulate inheritance; examined the impact of blending upon the kin selection coefficient of relatedness, showing that this may differ from its Mendelian counterpart, and may even fluctuate over generations; and shown that a time average of Hamilton's rule yields the same selection criterion for traits, irrespective of whether inheritance is Mendelian or blending.

This analysis reveals that the theory of kin selection could, in principle, have been developed in ignorance of the particulate nature of inheritance. This refutes the suggestion that Darwin could not have known about kin selection – on the basis that this requires an understanding of classical genetics – which has recently been used to argue for the historical primacy of group

selectionism (Borrello, 2010, p. 8) and even against materialism in evolutionary biology (Cunningham, 2010, p. 31)! Moreover, I have shown that the key predictions of kin selection are actually unaffected by this biological detail: an individual is still expected to behave as if she values her own life as being equal to those of two siblings, or eight cousins.

However, the analysis of kin selection is more tortuous under the assumption of blending, so it is likely that Darwin's ignorance of the mechanism of heredity did present a real barrier to his development of a proper theory of social adaptation (cf. Hamilton, 1972). Importantly, kin selection can only operate when there is both heritability of traits and relatedness between social partners, and the high rate of spontaneous mutation that is necessary to maintain heritability under the assumption of blending inheritance also erodes relatedness. Darwin assumed that heritable variation is introduced into natural populations in infrequent bursts, associated with environmental disturbance ("a change in the conditions of life, by specially acting on the reproductive system, causes or increases its variability"; Darwin, 1859, Chapter 4). Accordingly, in the majority of generations there would be negligible response to any form of selection, and in those rare burst generations in which the response to selection would be strongest, the correlation between relatives would be greatly eroded. Under this scheme, an understanding of how kin selection mediates the design criterion for organismal adaptation is achieved only by careful tracking of the dynamics of heritability and relatedness over multiple generations, which was certainly beyond Darwin's mathematical ability.

In contrast, particulate inheritance ensures a relatively high and relatively constant degree of heritability, even under very low rates of mutation that have minimal impact upon relatedness. Hence, it allows sustained selection, with a fixed valuation of one's relatives, over multiple generations of evolutionary change. Accordingly, an analysis of genetic change across a single generation is often representative of the change that occurs over multiple generations, such that a quantitative theory of kin selection is very amenable to simple analysis. Furthermore, Hamilton's (1963, 1964, 1972) elucidation of the theory of kin selection was spurred by taking a "gene's-eye view" of the evolution of altruism. This does appear to have focused his thinking and, clearly, such an approach is only possible under the assumption of particulate inheritance.

The term "blending inheritance" has been used to refer to a number of distinct ideas about heredity. For example, Bulmer (2003) has distinguished the idea of physical fusion of hereditary particles from that of phenotypic blending of parental characters, both of which have been described as blending inheritance. Darwin's hypothesis of pangenesis involved only partial fusion, with a hybridization of patent gemmules and segregation of latent gemmules, in order to account for reversions to ancestral phenotypes (Bulmer, 2003). The present analysis has focused upon the simpler "paint-pot" model of blending inheritance, developed by Fisher (1930) and named by Hardin (1959). More generally, whilst mechanistic details impact upon the computation of relatedness coefficients and their dynamics over multiple generations, the action of kin selection can be expressed in purely phenomenological terms using Price's (1970, 1972) equation, with Hamilton's (1963, 1964) rule  $rb - c > 0$  emerging irrespective of mode of inheritance.

I have shown that the ultimate selection criterion for social characters – and hence the rationale for the design of organisms – remains the same irrespective of whether inheritance is particulate or blending. This leaves open several issues regarding the power of natural selection to drive phenotypic change under each inheritance scheme. Much attention has been given to the idea that the response to natural selection is vastly reduced under

blending inheritance, owing to the rapid loss of heritable variation. This problem is resolved by invoking a high rate of mutation. The present analysis has assumed that mutation is unbiased, so that its sole contribution to evolutionary change is to fuel the response to selection. However, any mutational bias would introduce a further, non-selective component to evolutionary change. Since this could feasibly be of similar magnitude to the action of natural selection, the extent to which phenotypic evolution is driven by a Darwinian rationale (i.e. the "externalism" of Pigliucci and Müller, 2010) appears much reduced under the assumption of blending inheritance.

Finally, eliminating the gene from the present analysis has clarified its role in the standard theory of kin selection. In particular, the gene is neither a unit of selection nor a unit of adaptation in the standard theory, but merely provides a material basis for the inheritance of organismal characters. As a component of natural selection, kin selection is driven by the differential reproductive success of individual organisms (Darwin, 1859; Fisher, 1930; Price, 1970). Hence, the individual is the unit of selection. Moreover, as a consequence of the action of natural selection (including kin selection), the individual organism appears adapted to maximize her inclusive fitness (Hamilton, 1963, 1964, 1970, 1996; Grafen, 2006a). Hence, the individual is the unit of adaptation. The idea that the gene can be considered an adaptive agent in its own right is the altogether separate notion of the "selfish gene" (Hamilton, 1972; Dawkins, 1976, 1978, 1982; Gardner and Welch, 2011).

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## Appendix

Here I derive the kin selection coefficient of relatedness in terms of the coefficient of genealogical relationship and the ratio of heritable variance in ancestral and present generations, as given in the main text.

The relatedness between an individual and her social partner is defined as

$$r \equiv \frac{\text{cov}_I(h_j, h_i)}{\text{cov}_I(h_i, h_i)}, \quad (\text{A1})$$

where  $i \in I$  is the index of an individual chosen at random from the population,  $h_i$  is this individual's breeding value,  $j$  is the index of her social partner, and  $h_j$  is the breeding value of her social partner. Note that an individual's breeding value can be expressed as a function of the breeding values of her ancestors in some past generation and all the mutational effects that have accrued within her more recent ancestry:

$$h_k = \sum_{l=1}^{2^n} \frac{x_{(k,l,n)}}{2^n} + \sum_{t=0}^{n-1} \sum_{l=1}^{2^t} \frac{m_{(k,l,t)}}{2^t}, \quad (\text{A2})$$

where  $x_{(k,l,n)}$  is the breeding value of the  $k$ th individual's  $l$ th ancestor in the  $n$ th generation prior to the focal one, and  $m_{(k,l,t)}$  is the mutational effect occurring in the  $k$ th individual's  $l$ th ancestor in the  $t$ th generation prior to the focal one. For example, setting  $n=1$  yields the individual's breeding value in terms of those of her

two parents and her own mutational effect:

$$h_k = \frac{X_{(k,1,1)} + X_{(k,2,1)}}{2} + m_{(k,1,0)} \quad (\text{A3})$$

The numerator of the RHS of Eq. (A1) is given by

$$\text{cov}_I(h_j, h_i) = \text{cov}_I \left( \sum_{l=1}^{2^n} \frac{x_{(j,l,n)}}{2^n} + \sum_{t=0}^{n-1} \sum_{l=1}^{2^t} \frac{m_{(j,l,t)}}{2^t}, \sum_{l=1}^{2^n} \frac{x_{(i,l,n)}}{2^n} + \sum_{t=0}^{n-1} \sum_{l=1}^{2^t} \frac{m_{(i,l,t)}}{2^t} \right) \quad (\text{A4})$$

Let  $n = \mu$ , where  $\mu$  is the most recent generation in which the two individuals  $i$  and  $j$  share at least one common ancestor, and denote the number of their common ancestors in this generation by  $v$ . The two individuals may either derive from a single common ancestor in this generation (in which case  $v=1$ ) or else from a single mated pair (in which case  $v=2$ ). Because they share no common ancestors in any of the generations  $t < \mu$ , all mutational effects are uncorrelated with any other variable, so Eq. (A4) can be simplified to

$$\begin{aligned} \text{cov}_I(h_j, h_i) &= \text{cov}_I \left( \sum_{l=1}^{2^\mu} \frac{x_{(j,l,\mu)}}{2^\mu}, \sum_{l=1}^{2^\mu} \frac{x_{(i,l,\mu)}}{2^\mu} \right) \\ &= \frac{1}{2^{2\mu}} \text{cov}_I \left( \sum_{l=1}^{2^\mu} x_{(j,l,\mu)}, \sum_{l=1}^{2^\mu} x_{(i,l,\mu)} \right) = \frac{v}{2^{2\mu}} \text{var}(h^{(\mu)}), \end{aligned} \quad (\text{A5})$$

where  $\text{var}(h^{(\mu)})$  is the heritable variance in generation  $\mu$ . Noting that the denominator of the RHS of Eq. (A1) is equal to  $\text{var}(h^{(0)})$ , i.e. the heritable variation in the present generation, the kin selection coefficient of relatedness can be written in the form

$$r = \rho V, \quad (\text{A6})$$

where  $\rho = v/2^{2\mu}$  is the genealogical relationship between two individuals (for example,  $\rho=1$  for self,  $\rho=1/2$  for full siblings,  $\rho=1/4$  for half siblings, and so on) and  $V = \text{var}(h^{(\mu)})/\text{var}(h^{(0)})$  is the ratio of heritable variance in the most recent generation in which the two individuals share common ancestors and that of the present generation.

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