An inclusive fitness model for the evolutionary advantage of sibmating

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Summary

We construct an inclusive fitness model of the relative selective advantage of sibmating and outbreeding behaviour, under the assumption that inbred offspring pay a fitness penalty. We are particularly interested in the question of whether such inbreeding depression is enough to generate a stable phenotypic polymorphism, with both kinds of breeding observed. The model predicts that, under diploidy, such a polymorphism is never found, but under haplodiploidy, it exists for a narrow range of parameter values. The inclusive fitness argument is technically interesting because care must be taken with reproductive values. We also present a corrected version of a one-locus genetic model for sibmating and find that the inclusive fitness and genetic models give identical results when selection is weak.

Keywords: sibmating; inbreeding depression; haplodiploid; inclusive fitness; one-locus genetic

Introduction

Animal populations, especially insects, often exhibit a certain level of sibmating. The principal evolutionary advantage of this behaviour must be the increased number of copies of her genes that a female will pass to her offspring and this is perhaps principally balanced by the disadvantage of producing less viable offspring (inbreeding depression). It seems reasonable to conjecture that if the fitness penalty s attached to inbred offspring is small, then sibmating should be observed, whereas if this penalty is large, the population should outbreed. But intermediate levels of sibmating are often observed and so an obvious question is whether a simple genetic model which incorporates the above two factors can predict a stable polymorphism of outbreeding and sibmating behaviour for some range of values of inbreeding depression. Another question comes from the observation that sibmating is particularly common in haplodiploid organisms, in which the cost of inbreeding is paid only by the female offspring. Are the conditions for the relative evolutionary advantages of sibmating and outbreeding qualitatively different in diploid and haplodiploid populations?

Building on the work of Feldman and Christiansen (1984), Getz et al. (1992) examined these questions using a one-locus genetic model to analyse the invasion dynamics of sibmating and outbreeding genes in diploid and haplodiploid populations. In their model they assumed the existence of two alleles A and a at a mating behaviour locus such that each of the female genotypes AA, Aa and aa sibmate at frequency $\alpha_1 \leq \alpha_2 \leq \alpha_3$ respectively (i.e. the AA genotypes have a propensity to outbreed and the aa genotypes to sibmate with respect to the population mean). Their diploid and haplodiploid model, which develops dynamic equations for the frequencies of the different mating combinations, is incorrectly formulated: it does not account for the fact that, although the overall sibmating frequency of aa females is α_3, the frequency of

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those mating with aa males may be larger than α_3, while those mating with AA males may be smaller than α_3 (and similarly for the other mating frequencies). Also, they omitted a normalization step pertaining to male mating frequencies.

We have three objectives here. The first is to provide the correct equations for the one-locus genetic model and obtain sample numerical results and the second is to construct an inclusive fitness model (Hamilton, 1964) for the same problem. We restrict ourselves to the case in which there is no mating cost for a male who sibmates in terms of lost opportunities for outbreeding (the case $\mu = 0$ of Getz *et al.* (1992)). The advantage of the inclusive fitness approach is that it provides analytical stability conditions which allow us to construct a simple map of the evolutionary forces in $\alpha - s$ phase space (Fig. 1). Our third objective is to compare the results of the two models and thereby support a general mathematical result that under the assumptions of weak selection and semi-dominant gene action, the one-locus genetic model and the inclusive fitness model should obtain identical conditions for the evolutionary advantage of sibmating behaviour. We explain this result more fully below.

Results

Our models assume an infinite population with non-overlapping generations. We assume that females mate only once, with a sib with some probability α and at random among all the males in the population with probability $1 - \alpha$. In the outbreeding phase, all males compete equally, regardless of the level of sibmating (the case $\mu = 0$ of Getz *et al.* (1992)). Inbred offspring (offspring of sibmated parents) survive to breed with relative probability $1 - s$ relative to outbred offspring. Under diploidy this applies to both sexes and under haplodiploidy, only to female offspring.

The inclusive fitness analysis is presented in Appendix 1 and the results are displayed

(a) Diploid   (b) Haplodiploid
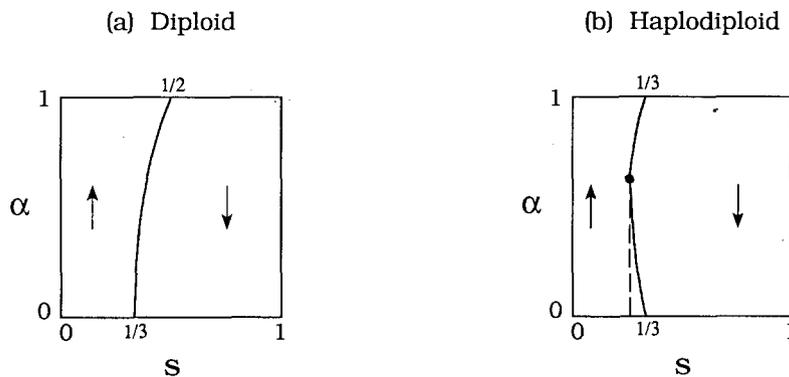
Figure 1. Inclusive fitness results under (a) diploidy and (b) haplodiploidy. In regions with an 'up' arrow $W_s(\alpha) > W_o(\alpha)$ and selection will act to increase α; in regions with a 'down' arrow, $W_s(\alpha) < W_o(\alpha)$ and selection will act to decrease α. The boundary curves are described by the equations (1) diploid, $2\alpha s^2 + 1 - 3s = 0$ and (2) haplodiploid, $\alpha^2 s(1 - 3s^2) + \alpha s(7s - 3) + 1 - 3s = 0$. Only under haplodiploidy do we find intermediate $(0 < \alpha < 1)$ values of sibmating which are stable; these correspond to the points on the lower arm of the boundary curve. The transitional value $s \simeq 0.30$ mentioned in the text for the haplodiploid case is the point at which the boundary curve is vertical and is the value of s which makes the discriminant D of the boundary equation vanish: $D = s^2(7s - 3)^2 - 4s(1 - 3s^2)(1 - 3s) = 0$. It is shown in (b) by a vertical broken line.

graphically in Fig. 1. The model assumes a population-wide level of sibmating α and calculates the inclusive fitnesses $W_s(\alpha)$ and $W_o(\alpha)$ of sibmating and outbreeding behaviour.

In the one-locus genetic model, females sibmate with genotype-dependent frequencies α_i as described above. The mating type recursion equations are presented in Appendix 2 and sample numerical results appear below. They are qualitatively similar to the results of Getz *et al.* (1992).

There is a general result (Taylor, 1989) which gives conditions under which the inclusive fitness analysis can predict the results of the one-locus genetic model. Suppose we have two alleles at a single locus, a normal allele coding for a sibmating probability of α and a mutant allele coding for $\alpha + \delta$ (in the homozygous state). Under the assumption of weak selection ($\delta \approx 0$) and semi-dominance (the heterozygote has sibmating probability $\alpha + (\delta/2)$), the normal allele will resist invasion (i.e. the mutant allele will decrease in frequency) when

$$W_s(\alpha) < W_o(\alpha) \qquad \text{in the case } \delta > 0$$

$$W_s(\alpha) > W_o(\alpha) \qquad \text{in the case } \delta < 0$$

These are the conditions for the α-allele to be stable to invasion by 'local' semi-dominant mutants.

According to this general result, Fig. 1 can be given a genetic interpretation. Under diploidy, a sibmating allele ($\alpha = 1$) is stable to invasion when $s < 1/2$ and an outbreeding allele ($\alpha = 0$) is stable when $s > 1/3$. Thus, in the region $1/3 < s < 1/2$, both pure states are stable. Under haplodiploidy, a sibmating allele ($\alpha = 1$) is stable when $s < 1/3$ and an outbreeding allele ($\alpha = 0$) is stable when $s > 1/3$. When s is between 0.30 (approximately) and $1/3$ there is another stable allele given by the α-value on the lower branch of the boundary curve (Fig. 1b). Thus, in this case, there are two possible stable alleles: one is pure and the other represents a phenotypic polymorphism.

We have verified this genetic interpretation of Fig. 1 with our one-locus model. For example we summarize below the results for the invasion of a rare semi-dominant sibmating allele.

Diploid

Inclusive fitness: for $\alpha = 0$ sibmating invades for $s < 1/3$. Genetic: for $\alpha_1 = 0$, $\alpha_2 = 0.01$, $\alpha_3 = 0.02$ sibmating gene invades for $s \leq 0.333$ but not for $s \geq 0.334$.

Inclusive fitness: for $\alpha = 0.5$ sibmating invades for $s < 0.382$. Genetic: for $\alpha_1 = 0.49$, $\alpha_2 = 0.50$, $\alpha_3 = 0.51$ sibmating gene invades for $s \leq 0.381$ but not $s \geq 0.382$.

Inclusive fitness: for $\alpha = 1$ sibmating invades for $s < 0.5$. Genetic: for $\alpha_1 = 0.998$, $\alpha_2 = 0.999$, $\alpha_3 = 1$ sibmating gene invades for $s \leq 0.499$ but not $s \geq 0.5$. (Note that for $\alpha_1 = 0.98$, $\alpha_2 = 0.99$ and $\alpha_3 = 1$, sibmating gene invades for $s \leq 0.494$ but not $s \geq 0.495$.)

Haplodiploid

Inclusive fitness: for $\alpha = 0$ sibmating invades for $s < 1/3$. Genetic: for $\alpha_1 = 0$, $\alpha_2 = 0.01$, $\alpha_3 = 0.02$, sibmating gene invades for $s \leq 0.333$ but not $s \geq 0.334$.

Inclusive fitness: for $\alpha = 0.5$ sibmating invades for $s < 0.309$. Genetic: for $\alpha_1 = 0.495$, $\alpha_2 = 0.500$, $\alpha_3 = 0.505$ sibmating gene invades for $s \leq 0.308$ but not $s \geq 0.309$.

Inclusive fitness: for $\alpha = 1$ sibmating invades for $s < 1/3$. Genetic: for $\alpha_1 = 0.998$, $\alpha_2 = 0.999$, $\alpha_3 = 1$ sibmating gene invades for $s \leq 0.333$ but not $s \geq 0.344$. (Note that for $\alpha_1 = 0.98$, $\alpha_2 = 0.99$ and $\alpha_3 = 1$, sibmating gene does not invade for $s \geq 0.33$.)

Effect of strength of selection and dominance

In the two cases $\alpha = 1$ above, the parenthetical remark indicates an effect of strength of selection on invasion dynamics. Further such results are presented in Table 1. For invasion of sibmating

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Table 1. The effect of strength of selection and dominance on invasion dynamics

Genetic system:	Diploid		Haplodiploid	
Invasion of selection strength	Sibmating $s <$	Open-mating $s >$	Sibmating $s <$	Open-mating $s >$
$\delta \approx 0$	0.333	0.5	0.333	0.333
$\delta = 0.25$	0.343	0.454	0.334	0.313
$\delta = 0.5$	0.355	0.425	0.334	0.300
$\delta = 0.75$	0.368	0.403	0.335	0.291
$\delta = 1.0$	0.395	0.386	0.338	0.282
$\delta = 1.0$	0.400	0.333	0.414	0.250

the mating parameters are $\alpha_1 = 0$, $\alpha_2 = \delta/2$ and $\alpha_3 = \delta$, while for the invasion of outbreeding the mating parameters are $\alpha_1 = 1 - \delta$, $\alpha_2 = 1 - \delta/2$, and $\alpha_3 = 1$. These results indicate that increasing the strength of selection increases the range of the parameter s for which a sibmating/ outbreeding polymorphism might exist. The results also imply that such polymorphisms are more likely in haplodiploid than diploid systems. When selection is weak, dominance has negligible effect; for the case $\delta \approx 0$, the conditions for the invasion of dominant or recessive alleles are identical to those of the first row of Table 1. However, dominance has some effect when coupled with strong selection, as illustrated by the last two rows of the table. In the last row ($\delta \approx 1^*$), the mating parameters are $\alpha_1 = 0$, $\alpha_2 = 0$ and $\alpha_3 = 1$.

Discussion

In all the cases we have checked, when selection is weak and gene action is additive, the inclusive fitness model provides exactly the same results as the one-locus model. This result is expected and has been discussed and demonstrated in greater or less generality by a number of authors (Hamilton, 1964, 1975; Charnov, 1977; Charlesworth, 1980; Seger, 1981; Grafen, 1985; Taylor, 1989). In spite of our theoretical expectation that the two models will coincide, one still has a feeling of awe (and a sigh of relief!) when an analytical formula gives exactly the same results as the numerical calculations of an 18 × 18 matrix.

An important difference between the two genetic systems is that, under diploidy, offspring of both sexes bear the cost of sibmating, whereas under haplodiploidy, this cost is borne only by the females. We might expect that this would make sibmating behaviour rather more common in haplodiploid populations (and this is observed in nature), but our results (Fig.1) offer no mathematical evidence for this. A general discussion of other factors which might account for the observed difference in sibmating levels in the two genetic systems is found in Getz *et al.* (1992).

From a gene invasion dynamics point of view, our results show no qualitative difference between the two genetic systems: when the inbreeding cost s is low, high values of α are stable and when the inbreeding cost is high, low values of α are stable. For intermediate inbreeding costs, we do find a qualitative difference – under diploidy, there is an intermediate range of s where both fixation states are stable, but under haplodiploidy there is an intermediate range of s where a stable polymorphism can exist. Thus, a mating strategy polymorphism is more likely to exist in haplodiploid than diploid systems.

We have restricted attention to the case in which there is no male penalty for sibmating in terms of reduced representation in the outbreeding pool (the case $\mu = 0$ of Getz *et al.* (1992)).

The imposition of a male penalty complicates the model in a number of ways, one of which is that fitness of sibmating behaviour is now dependent upon the sex ratio so that this must also be calculated. (For example, the more female-biased is the sex ratio, the more significant will be the sibmating penalty on the male offspring.) In addition, the ESS sex ratio will in turn depend on the level of sibmating, so that we in fact have a two-parameter ESS problem.

The inclusive fitness model constructed in Appendix 1 is interesting for two reasons. One of these is that it provides an analytic version of a mathematically complicated genetic model, which otherwise can provide only numerical results. The other is that the argument for haplodiploidy is technically interesting because care is required with reproductive values. It turns out that, in this case, the reproductive value of a male offspring depends on whether or not his parents were sibs, because the inbreeding depression suffered by his sisters affects the sex ratio among *his* sibs and this affects his expected number of matings with sisters. This problem does not arise under diploidy because inbreeding depression affects male and female offspring equally.

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Appendix 1: the inclusive fitness model

A female has a choice of two mating strategies, sibmating and outbreeding. In each case, her inclusive fitness W is calculated as her total expected number of offspring attaining breeding age, each offspring weighted by its relatedness to her and by its reproductive value:

$$W = n_f R_f v_f + n_m R_m v_m \tag{A1}$$

where n_i, R_i and v_i are the number (reaching breeding age), relatedness and reproductive value of her sex i offspring.

I begin with some general notation.

α The probability of inbreeding. Assumed uniform in the population.

t The sex ratio. Assumed to be independent of the mating strategy.

s The inbreeding penalty. Offspring of sibmated pairs breed with relative probability $1 - s$. Except that haplodiploid males do not incur this penalty.

F The mean inbreeding coefficient among breeding females.

G The mean coefficient of consanguinity (probability random alleles are IBD) between breeding sibs (Crow and Kimura, 1970, p. 68).

r_i Relatedness of outbred mother to sex i offspring.

$r_î$ Relatedness of sibmated mother to sex i offspring.

The coefficients F and G are determined by one-generation recursions and the same argument works for both genetic systems. If we use primes to denote next-generation values, then the F-equation is

$$F' = \frac{\alpha(1 - s)}{1 - \alpha s} G \tag{A3}$$

using the fact that, with relative probabilities $1 - \alpha$ and $\alpha(1 - s)$, a breeding female has outbred parents ($F' = 0$) and sibmated parents ($F' = G$). A similar argument, looking at the parents of a random sibmating female, yields the G-equation

$$G' = \frac{(1 - \alpha)}{1 - \alpha s} \frac{1 + F}{4} + \frac{\alpha(1 - s)}{1 - \alpha s} \frac{1 + F + 2G}{4} \tag{A4}$$

The solution to Equations A3 and A4 is

$$F = \frac{\alpha(1 - s)}{4 - 3\alpha - \alpha s}$$

$$G = \frac{1 - \alpha s}{4 - 3\alpha - \alpha s} \tag{A5}$$

for both genetic systems. In terms of these, the relatedness coefficients are (Michod and Hamilton, 1980)

$$\text{Diploid:} \qquad r_i = \frac{1}{2} \qquad r_î = \frac{1 + F + 2G}{2(1 + F)} \qquad (i = \text{m,f}) \tag{A6}$$

$$\text{Haplodiploid:} \quad r_f = \frac{1}{2} \qquad r_m = r_m̂ = 1 \qquad r_f̂ = \frac{1 + F + 2G}{2(1 + F)}$$

Diploidy

If we normalize so that each female expects one offspring, then, using Equation A1, a sibmated female has fitness

$$W_s = (1 - t)(1 - s)r_f̂ v_f + (t)(1 - s)r_m̂ v_m = 2(1 - s)r_î$$

and an outbred female has fitness

$$W_o = (1 - t)r_f v_f + (t)r_m v_m = 2r_i \qquad (A7)$$

where I have taken $v_m = 1/t$ $v_f = 1/(1 - t)$ since the reproductive value v_i of a sex i offspring at breeding age is proportional to its breeding success which is inversely proportional to the frequency of sex i. Using Equations A5, A6 and A7, the condition for sibmating to be at an advantage becomes:

$$W_s > W_o: \qquad 2\alpha s^2 + 1 - 3s > 0 \qquad (A8)$$

Haplodiploidy

What makes this system more complicated is that the reproductive value of a male depends on whether his parents were sibmated (v_{ms}) or outbred (v_{mo}). The reason for this is that the two types of male have different sex ratios among their mature sibs. It is shown below that the relative reproductive values are

$$v_f = \frac{1}{1 - t}$$

$$v_{ms} = \frac{1}{2t}\left[(1 - \alpha) + \frac{\alpha(1 - s)^2}{1 - \alpha s}\right] \qquad (A9)$$

$$v_{mo} = \frac{1}{2t}\left[(1 - \alpha) + \frac{\alpha(1 - s)}{1 - \alpha s}\right]$$

A sibmated female has fitness

$$W_s = (1 - t)(1 - s)\ r_f v_f + (t)r_m v_{ms}$$

and an outbred female has fitness

$$W_o = (1 - t)r_f v_f + (t)r_m v_{mo}$$

Using Equations A5, A6 and A9, the condition for sibmating to be at an advantage becomes:

$$W_s > W_o: \qquad \alpha^2 s(1 - 3s^2) + \alpha s(7s - 3) + 1 - 3s > 0 \qquad (A10)$$

I now calculate the reproductive values for the haplodiploid case, defined as the relative genetic contribution of the individual to the future gene pool. There are general matrix methods for doing this (Taylor, 1990), but in the present case there is also an elementary approach which is based on the fact that males make genetic contributions only through female offspring and, thus, we can use 'numbers of breeding daughters' as a currency to measure relative reproductive value. Indeed, with the assumption of a constant population size, the reproductive value of a male will then be $(w_o + w_s)v_f$ where w_o and w_s are his expected numbers of breeding daughters through outbreeding and sibmating, respectively. To calculate these, I count the numbers of breeding offspring of a breeding female. She can expect

$$m = \frac{t}{1 - t}\frac{1}{1 - \alpha s}$$

sons, but her number f of breeding daughters depends on whether she sibmates or not.

Sibmates: $$f_s = \frac{1 - s}{1 - \alpha s}$$

Outbreeds: $$f_o = \frac{1}{1 - \alpha s}$$

These counts have been normalized by the condition that the mean number of breeding daughters of a breeding female must be unity:

$$\alpha f_s + (1 - \alpha)f_o = 1$$

Using this, I note that the breeding sex ratio will be $1/m$. It follows that each male can expect $(1 - \alpha)/m$ outbreedings, which gives him

$$w_o = (1 - \alpha)f_o/m$$

daughters through outbreeding. To calculate w_s, his number of daughters through sibmating, we need to know about his parents. If they were sibmated, he has $\alpha f_s/m$ sibmating sisters and if they were outbred he has $\alpha f_o/m$ sibmating sisters and in both cases these sisters get f_s breeding daughters each, so his number of breeding daughters is

sibmated parents: $w_s = \alpha f_s^2/m$

outbred parents: $w_s = \alpha f_o f_s/m$

Then the reproductive values are:

sibmated parents: $v_{ms} = w_o + w_s = \dfrac{1}{m}\left[(1 - \alpha)f_o + \alpha f_s^2\right]v_f$

(A11)

outbred parents: $v_{mo} = w_o + w_s = \dfrac{1}{m}\left[(1 - \alpha)f_o + \alpha f_o f_s\right]v_f$

If, as above, we normalize by setting the reproductive value of a female to be $v_f = 1/(1 - t)$, then we get Equation (A9) above.

Appendix 2: the revised genetic model

Let x_{ij} and y_{ij} denote the frequency respectively of sibmating and outbreeding combinations of female genotype-i × male genotype-j, such that

$$\sum_{ij} x_{ij} + y_{ij} = 1 \tag{A12}$$

where a sum over genotypes will always be understood to be over all three genotypes, except in the case of male haplodiploidy when there are only two. Let p^f_{ijk} and p^m_{ijl}, respectively denote the proportions of females of genotype k and males of genotype l among the progeny of these mating combinations $i \times j$. The values of these progeny proportions are determined by a random assortment of alleles assumption.

If each female genotype produces an equal number of progeny (before the viability effects of inbreeding) then the relative (before normalization) proportion of sexually mature females and males, respectively of type k and l from panmictic matings of type ij is $p^f_{ijk}y_{ij}$ and $p^m_{ijl}y_{ij}$ while the sexually mature progeny proportions arising from sibmatings are reduced by a factor $1 - s^f$ for females and $1 - s^m$ for males to obtain $p^f_{ijk}(1 - s^f)x_{ij}$ and $p^m_{ijl}(1 - s^m)x_{ij}$, respectively. For diploidy, $s^f = s^m = s$ and for haplodiploidy, $s^f = s$ and $s^m = 0$.

To construct the next-generation proportions of mating types we take account of the probability α_k that a type k female offspring will sibmate, calculate the genotype of the male she will mate with and sum over all parental crosses $i \times j$. For sibmating, a female from an $i \times j$

mating will mate with an l-male with probability p_{ijl}^m and so the new proportion of $k \times l$ sibmatings is

$$x_{kl}' = K^f \sum_{ij} \alpha_k \left[p_{ijk}^f (1 - s^f) x_{ij} + p_{ijk}^f y_{ij} \right] p_{ijl}^m \tag{A13}$$

where K^f is a normalizing constant determined below.

To find the new outbreeding proportions, we note that the proportion of type l males in the outbreeding pool (equal representation from all mature males) is

$$q_1 = K^m \sum_{ij} p_{ijk}^m (1 - s^m) x_{ij} + p_{ijk}^m y_{ij} \tag{A14}$$

where K^m is a normalizing constant determined so that the q_1 have sum 1. Then the new proportion of $k \times l$ outbreedings is

$$y_{kl}' = K^f \sum_{ij} (1 - \alpha_k) \left[p_{ijk}^f (1 - s^f) x_{ij} + p_{ijk}^f y_{ij} \right] q_1 \tag{A15}$$

where K^f is determined by the condition $\sum_{kl} x_{kl}' + y_{kl}' = 1$.