

THEORETICAL ASPECTS OF BROTHER-SISTER MATING IN BIRDS AND MAMMALS

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Abstract

The incidence of close inbreeding in birds and mammals is low, but the evidence reviewed below suggests that it is not entirely avoided. In fact, birds and mammals may have evolved to tolerate a low rate of close inbreeding. Two possible advantages to close inbreeding that may offset the inbreeding depression are: the closer relatedness of the parents to inbred offspring, and a head start in reproduction. We focus on brother-sister mating and describe two population genetic models that predict the conditions for natural selection to favor a low rate, as opposed to the complete avoidance, of brother-sister mating. It is argued that these conditions may apply to humans. Moreover, the atypical minor marriages identified by Wolf that apparently contradict the Westermarck hypothesis can be accommodated by assuming that humans are by nature mildly incestuous.

Introduction

The propensity to inbreed (i.e., mate with kin) varies widely among biological taxa (Thornhill 1993). Close inbreeding occurs routinely in some plants and insects, but is unusual in birds and mammals. Of special interest for an understanding of humans are the African apes, where nuclear family incest (i.e., a mating between father and daughter, mother and son, or brother and sister), in particular, is seldom observed. In the chimpanzee, matings between adult males and their mothers are rare, but such cases are known (Goodall 1986: 466-467). Most (but not all) females refuse the sexual advances of males in their natal group old enough to be their fathers. The incidence of copulations between maternal sibs is low (Pusey 1980). However, matings between paternal half sibs may not be uncommon in the gorilla (Stewart & Harcourt 1986).

The claim is often made that innate behavioral mechanisms have evolved in birds and mammals to prevent close inbreeding. Incest may be actively avoided based on recognition of family members. Alternatively, because of a sex difference in dispersal, sons and daughters may not encounter their opposite-sex sibs or parents as adults. In the black-tailed prairie dog, for example, both mechanisms are said to be at work (Hoogland 1992). Daughters usually remain in their natal coterie territory, whereas the sons emigrate. A father

may also leave or be evicted before his daughter matures. A female is less likely to come into estrus when her father is still present. Estrous females avoid males that are familiar from continuous association in the natal coterie territory. In spite of the above, matings between father and daughter do occur. Moreover, and perhaps surprisingly, the incidence of close inbreeding, mostly between half sibs, did not differ from the number expected if matings were occurring at random in the study area.

Neither could the null hypothesis of random mating be rejected in a study of mate choice in the song sparrow (Keller & Arcese 1998). The incidence of nuclear family incest was 18 out of 479 (3.8 percent). Of these 18 matings, 10 were between full sibs raised in different nests, 6 were between full sibs raised in the same nest, and 2 were between mother and son. Note that, in a “real” population comprising a finite number of individuals (as opposed to an ideal infinite population), a low level of close inbreeding is expected when matings occur at random, and observations were consistent with this expectation.

A study on Darwin’s medium ground finch again yielded no evidence for avoidance of inbreeding (Gibbs & Grant 1989). However, when the effect of song on mate choice in the same population was later analyzed, it was found that a female in her second breeding year (but not her first) tended to mate with a male who sang a song differing from her father’s. Since song is culturally transmitted from father to son in this species, close kin other than the father can also be recognized and avoided. Darwin’s medium ground finch apparently has the means to avoid close inbreeding, but it is not clear that they do so on average (Grant & Grant 1996).

Behavioral mechanisms for the avoidance of close inbreeding have also been demonstrated in the Japanese macaque (Enomoto 1978), the African lion (Packer & Pusey 1993), and the acorn woodpecker (Koenig et al. 1998), to name a few other examples. Hence, the often-made claim that innate behavioral mechanisms have evolved to prevent close inbreeding may strictly apply to some avian and mammalian species. Nevertheless, the fact remains that low rates of close inbreeding, including nuclear family incest, are widely observed. It can be argued that no mechanism is foolproof and that close inbreeding occurs by mistake. But these observations are perhaps also consistent with the view, entertained in this paper, that some species of birds and mammals have evolved, either to mate with close kin at some low rate, or to mate indiscriminately with regard to relatedness.

It is widely recognized—in domesticated livestock, laboratory rodents, wild animals bred in captivity, and humans—that inbred individuals have lower fitness than outbred ones (Lacy et al. 1993). The decrease in fitness, normalized by the fitness of the outbred individual, is called the inbreeding depression and is estimated in practice by comparing survival to some arbitrary age. The more closely inbred an individual is, the more severe the inbreeding depression is likely to be. Inbreeding depression due to nuclear family incest, in particular, has been quantified for 38 species of mammals in captivity; the average is 33 percent, but the estimates vary widely among the species studied (Ralls et al. 1988). In humans the

corresponding estimate is 29 percent, although this estimate is inflated by the inclusion of morbidity (Adams & Neel 1967; see also Seemanová 1971).

Studies of wild populations of birds and mammals have yielded conflicting results. For example, inbreeding depression occurs in the song sparrow (Keller et al. 1994) and possibly the great tit (van Noordwijk & Scharloo 1981), but statistically significant effects of inbreeding on reproductive success are not seen in Darwin's medium ground finch (Gibbs & Grant 1989), the black-tailed prairie dog (Hoogland 1992), or the dwarf mongoose (Keane et al. 1996).

Inbreeding depression, given that it occurs, clearly selects against inbreeding, the more so the closer is the inbreeding. Therefore, other things being equal, behavioral mechanisms for the avoidance of close inbreeding are predicted to evolve in all species subject to inbreeding depression. However, other factors may favor inbreeding, and the evolutionary outcome will depend on the relative strengths of the countervailing forces.

For example, a parent is more closely related to an inbred as opposed to an outbred child—inbred blood is thicker than outbred blood. In other words, by mating with kin rather than non-kin, an individual can transmit more copies of its genes (identical by descent) to its offspring, possibly enough to compensate for the inbreeding depression. Thus, provided its mate does not forfeit further breeding opportunities as a result, it may be in that individual's genetic interests to inbreed. The argument can be phrased in terms of inclusive fitness (see below) (Smith 1979; Maynard Smith 1980; Waser et al. 1986; see also Nagylaki 1976).

Another factor that may offset the natural selection against inbreeding is reproductive compensation—if offspring lost due to inbreeding depression are replaced. Similarly, if ecological or economic conditions are such that kin can mate earlier than non-kin, then lifetime reproductive success may be comparable (or even greater) for the inbreeding pair. Keller and Arcese (1998) argue that song sparrows tolerate inbreeding to get a head start in reproduction. In modern human societies, age at marriage is lower when the spouses are cousins (and generally when related) than when they are unrelated. Perhaps because of this, or because of reproductive compensation, cousin marriages enjoy a higher fertility (live births) than non-consanguineous unions (Bittles 1994, this volume).

It is well known that brother-sister marriages were common in Roman Egypt (e.g., Scheidel 1995, 1997, this volume). The evidence comprises about 300 census returns preserved on papyri, from which pedigrees have been reconstructed. The female spouse is described as “my wife and sister of the same father and the same mother” (Hopkins 1980: 320). When on-going marriages in Roman Egypt are broken down by age, there is a relatively higher (though statistically non-significant) incidence of brother-sister and other close-kin marriages among the younger couples. Therefore, it is possible that sibs were marrying earlier than unrelated couples (Bagnall & Frier 1994). Moreover, one of the most fertile couples are full sibs, with eight surviving children.

In this paper, we focus on brother-sister mating. As already noted, sib mating rarely occurs in birds and mammals. This is also true of the human, where nuclear family incest, marital and non-marital, has been prohibited and usually avoided in almost all societies past and present that we know about (Murdock 1949). The exceptional case of Roman Egypt is likely a sociological phenomenon and not attributable to the presence of many individuals with an innate incestuous tendency. Thus, the relevant question would appear to be whether birds and mammals have evolved to avoid brother-sister mating entirely, or to tolerate a low rate of sib mating.

More specifically, our purpose in this paper is to weigh the relative merits of two genetically-determined behaviors, (a) complete avoidance of brother-sister mating, and (b) a low rate, α , of brother-sister mating. Two haploid genotypes, A_1 and A_2 , are assumed to produce these behaviors, where mate choice is exercised by the female. The use of haploid models to investigate the evolutionary dynamics of brother-sister mating is justified, since the relatedness of a parent to inbred and outbred offspring is in the ratio 3:2 (in agreement with diploid genetics). Our formulation also follows the standard practice of assuming an infinite population size, whence a suitably small value of α may be interpreted as the probability of the random occurrence of a brother-sister mating in a real finite population.

We describe two exact population genetic models motivated by the above discussion on the possible advantages to inbreeding, which we call the “extra mating” model and the “head start” model. For each model, we state the mathematical conditions that predict which behavior should evolve, and discuss the biological significance of these results. Briefly, the extra mating model predicts that, for a low rate of brother-sister mating to evolve, it is necessary that the inbreeding depression be less than one-third, and that some incestuous males be permitted to mate polygynously. The head start model suggests that two circumstances favor a low rate of brother-sister mating, (a) when male survival to reproductive age is negligibly small, or (b) when male and female demographic parameters are comparable, and the reproductive value of a newborn female is larger when she inbreeds than when she outbreeds.

Extra Mating Model

This model restricts the gene-culture coevolutionary model of Aoki and Feldman (1997) to the special case of genetically determined behavior, but at the same time extends it by incorporating the possibility that an incestuous male (i.e., a male who has mated with his sister) may forfeit further breeding opportunities. Details, including methods of analysis, can be found in their paper.

Each mated pair produces one daughter and one son. All outbred offspring survive to reproduce, but a fraction d of inbred offspring die prematurely. Hence, d is the inbreeding depression. All surviving A_1 females and a fraction $1 - \alpha$ of surviving A_2 females are out-

breeders (where α is assumed to be small). The remaining fraction α of surviving A_2 females prefers to mate with their brothers. Each such female can do so only if her brother has survived. Else, she outbreeds with probability b and refrains from mating with probability $1-b$. A fraction g of males who have mated with their sisters forfeit further breeding opportunities. All other males compete equally for the outbreeding females.

The major prediction of this model is that genotype A_1 will be replaced by genotype A_2 , whence a low rate of brother-sister mating will evolve, if

$$3d < 1-g. \quad (1)$$

In jargon, fixation of A_1 is unstable if $3d < 1-g$, and fixation of A_2 is stable if $3d < 1-g$. Note that inequality (1) does not depend on the parameters b and α (provided α is small). Rather it depends only on the magnitude of the inbreeding depression, d , and the probability that incestuous males can mate with outbreeding females, $1-g$.

An incestuous male is by definition assured one mating with his sister. If $g = 0$, he can also compete for the outbreeding females on an equal footing with the other males. In this case, inequality (1) reduces to $d < 1/3$, which agrees with the heuristic condition obtained by Smith (1979) and Maynard Smith (1980). The inclusive fitness argument used by these authors can be adapted as follows. The relatedness between brother and sister is approximately $1/2$, since incestuous matings are rare (i.e., α is small). Hence, recalling that each female when mated bears 2 offspring, the inclusive fitness of a female who mates with her brother is $2[1-d + (1/2)(1-d)]$, and that of a female who outbreeds is 2. Therefore, an incestuous female has a higher fitness than an outbreeding female if $2[1-d + (1/2)(1-d)] > 2$, namely $d < 1/3$.

As the value of g increases, the condition (1) clearly becomes more stringent. In particular, when $g = 1$ (e.g., with enforced monogamy) it cannot be satisfied. Hence, we have rigorously re-derived the well-known result that a low rate of brother-sister mating may be tolerated in a polygynous (but not a strictly monogamous) species (Smith 1979; Maynard Smith 1980; Waser et al. 1986). In addition, it is necessary that the inbreeding depression be less than $1/3$. Interestingly, the average inbreeding depression due to nuclear family incest in 38 species of mammals in captivity is, coincidentally, 33 percent, as pointed out by Ralls et al. (1988). The corresponding estimate in humans is about 29 percent (Adams & Neel 1967). Moreover, humans are mildly polygynous (Alexander et al. 1979).

A low rate α of brother-sister mating is likely not an evolutionarily stable strategy (Aoki & Feldman 1997). However, a suitably low rate corresponds to a random mating strategy, which is a readily implemented behavior. By contrast, for most values of α it is difficult to imagine a simple strategy that would result in this probability of brother-sister mating.

Head Start Model

This model is motivated by the heuristic model of Keller and Arcese (1998), who argue that the song sparrow, by mating with a full sib rather than an unrelated partner, may get a head start in reproduction and thus enjoy a greater lifetime reproductive success. These authors describe a model in which full sibs are available as mates from the first breeding year, but to mate with an unrelated partner requires waiting until the second breeding year.

In order to formulate a tractable model in terms of population genetics and demography theory, we have made several assumptions: there are three age classes, mates are of the same age, full-sib matings between yearlings produce inbred offspring, all other pairs are randomly formed and regarded as unrelated, the number of clutches produced equals the number of available females (female demographic dominance), clutches have an even sex ratio at birth, polygyny occurs when there is a shortage of males, but strict monogamy is enforced when males are in excess. In addition, we introduce the following parameters.

The three age classes are labeled 0, 1, and 2. Female and male survival probabilities from age i to age $i + 1$ are p_i and q_i (where $i = 0, 1$). A yearling female can mate with her brother (born in the same clutch), producing a clutch of size $f_1(1-d)$. If both members of an incestuous pair survive to age 2—where in a polygynous mating the death of the male partner implies the simultaneous dissolution of more than one pair—they produce a clutch of size $f_2(1-d)$. All single two-year-old females and a fraction w_f of widows mate at random. Competing for these females are all single two-year-old males and a fraction w_m of widowers. Each such mating between unrelated individuals results in a clutch of size f_2 . Hence, the parameter d is the inbreeding depression—specifically, the reduction in live births and the increase in infant mortality. All f_1 females and a fraction $1 - \alpha$ of f_2 females forgo mating until age 2 (where α is assumed to be small). The remaining fraction α of f_2 females mate as yearlings with their brothers, who are always available provided $q_0 > 0$.

The model is too complex to permit a thorough analysis. Therefore, we have limited our task to asking when fixation of A_2 (i.e., the equilibrium at which all individuals are of genotype A_2) is stable. (See Appendix for an outline of the approach taken.) Fixation of A_2 is said to be stable if evolutionary forces will cause A_1 individuals—introduced at low frequency into a population where A_2 individuals are in the majority—to decrease. Instability, on the other hand, implies that the A_1 individuals will increase, whence the equilibrium cannot be reached. Thus, the behavior associated with genotype A_2 , namely, a low rate of full-sib mating, can evolve only if fixation of A_2 is stable.

We find that there is a strong dependence on q_0 , the male survival probability from age 0 to age 1. First, assume that q_0 is of the same order of magnitude as αp_0 . In this case, premature death strikes many more males than females, so that the sex ratio among reproductives is low. Then, fixation of A_2 is stable if

$$q_0 < \alpha p_0 [1 + (1-p_1)w_m]/2, \quad (2)$$

and unstable if the inequality is reversed. Although we report condition (2) for completeness' sake, we are unable to interpret it heuristically.

Next, consider the case where q_0 is of the same order of magnitude as p_0 , a situation often applying to birds and mammals. Then, in contrast to (2), stability of fixation of A_2 is more likely for larger values of q_0 . In particular, when the demographic parameters are the same in both sexes (i.e., $p_0 = q_0$, $p_1 = q_1$, and $w_f = w_m$), we obtain as the condition for stability

$$p_0 f_1 (1-d) (p_0 p_1 f_2 / 2)^{1/3} + p_0 p_1 f_2 [q_1 (1-d) + (1-q_1)w_f] > p_0 p_1 f_2. \quad (3)$$

The meaning of inequality (3) is intuitively clear when we note that $(p_0 p_1 f_2 / 2)^{1/3}$ is approximately the growth rate of a population dominated by two-year-old outbreeders (since α is small). Hence, the left-hand side is proportional to the reproductive value of an incestuous female of age 0. Similarly, the right-hand side is proportional to the reproductive value of an outbreeding female of age 0. When the former exceeds that latter, we expect a low level of brother-sister mating to evolve.

Inequality (3) differs from the heuristic formula (A1) of Keller and Arcese (1998) in two ways. First, it is the reproductive value rather than the net reproduction rate (i.e., lifetime reproductive success) that is relevant. Note the weight $(p_0 p_1 f_2 / 2)^{1/3}$ on offspring produced by yearlings. Second, the fertility of an incestuous female in her second breeding year depends on the fate of her mate. If he survives (with probability q_1) she produces $f_2(1-d)$ offspring. If he dies (with probability $1-q_1$) she remates with probability w_f producing f_2 outbred offspring.

This model was motivated by inbreeding in birds and is obviously too crude to apply directly to humans. In particular, humans do not produce clutches, so that brother and sister would usually be separated in age. Nevertheless, the model has the merit of providing rigorous theoretical support for the claim that a low rate of full-sib mating may evolve if it permits a head start in reproduction. We have already noted the evidence for the lower age at marriage in brother-sister unions. The effect of the inbreeding depression, d , is to reduce the likelihood of incest being favored, but it is not clear that the critical value of $1/3$ (predicted by the extra mating model) has any special meaning here.

The Westermarck Hypothesis and the Incest Taboo

Westermarck (1891: 320) proposed that "there is an innate aversion to sexual intercourse between persons living closely together from early youth." In particular, full sibs reared together are expected to avoid mating with each other. Avoidance is also predicted when unrelated boys and girls are reared together in the same household. Thus, Wolf's studies on

the Chinese custom of sim-pua are believed to support the Westermarck hypothesis. The sim-pua (i.e., “little daughter-in-law”) is a girl who is adopted, often as an infant, into a family with a young boy, to be his future bride. Compared to other arranged marriages, the fertility of this type of marriage (i.e., “minor marriage”) is low, and the divorce rate is high (Wolf 1966, 1968, 1970, this volume).

In a recent book, Wolf (1995: 259) discusses the “different degrees of [inborn] sensitivity to the experience of being reared with a potential sexual partner.” A minority of “couples reared for minor marriages were not sexually indifferent to each other, not even when they were brought together as early as one or two years of age” (Wolf 1995: 253). In other words, although the Westermarck hypothesis would appear to be valid on average, there is substantial variation among couples. We are tempted to attribute a part of the atypical responses to the presence of a small fraction of women who are prepared to mate with their brothers.

Our models predict that, under certain conditions possibly applying to humans, females would have evolved to accept brothers at a low (but nonzero) rate. However, the small fraction of females in which this preference is expressed can mate with brothers only if they are available. In humans, brothers are nearly always proscribed by the incest taboo. The minor marriage is a very special situation in that the cohabiting brother equivalent is the socially sanctioned spouse.

If it is true that humans have not evolved to avoid brother-sister mating completely, then it is easier to explain the nearly universal occurrence of the taboo against brother-sister mating (Murdock 1949). For if “the law only forbids men to do what their instincts incline them to do” (Frazer 1910, cited in Wolf 1995: 11), at least some humans must by nature be incestuous. The rules are then interpretable as an attempt by the “non-inclined” majority to suppress the “inclined” minority. Thornhill (1991) holds the view that natural selection should have completely eliminated incestuous tendencies. Consistent with this position, she claims that the majority of societies in the ethnographic present do not have rules against nuclear family incest. Although we are not competent to judge the overall truth of this surprising claim, the Tallensi, who are classified by Thornhill as lacking a taboo, do in fact proscribe brother-sister mating. Thus, according to Fortes (1936: 244), “Tallensi agree that to copulate with one’s ‘sister’ is prohibited.”

Appendix

This appendix outlines the approach used in the head start model to analyze the stability of the equilibrium at which genotype A_2 is fixed. The basic variables are the numbers of mating types as distinguished by age, relatedness, and genotypes of partners, and the numbers of clutches produced by such matings. First, we obtain the stable demographic distribution assuming that genotype A_2 is fixed. The characteristic polynomial will be called $\phi(\lambda)$.

Next, we do a local stability analysis in the frequencies of the variables involving the rare genotype A_1 . Call the characteristic polynomial $\psi(\lambda)$. Then, $\phi(\lambda)$ and $\psi(\lambda)$ each possess one positive eigenvalue, which is dominant. Moreover, the equilibrium is stable if the dominant eigenvalue of $\phi(\lambda)$ exceeds the dominant eigenvalue of $\psi(\lambda)$. The approximate eigenvalues can be obtained by perturbation in the small parameter α .

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