

---

---

## Original Articles

---

# Asymmetric Relations: Internal Conflicts and the Horror of Incest

David Haig

*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts*

---

**Incest can increase an individual's inclusive and individual fitness if the opportunity cost of incest is sufficiently small. As a corollary, genetic conflicts are possible between the two parties of an incestuous dyad if they have different opportunity costs. The opportunity costs of casual sex usually are greater for females than for males. Therefore, females are predicted to be more averse to incest than are males. Genetic conflicts also are possible between an individual's maternal and paternal genomes because of asymmetries of relatedness. Large asymmetries of maternal and paternal relatedness are present between half-siblings, and in the relationship of offspring to parents. These asymmetries raise the possibility of strong internal conflicts between an individual's maternal and paternal genomes over the costs and benefits of incest. Taboos and other social sanctions may serve to increase male opportunity costs and thus serve as a disincentive to incest. © 1999 Elsevier Science Inc.**

**KEY WORDS:** Incest; Genomic imprinting; Westermarck effect; Inclusive fitness.

---

**E**dward Westermarck (1921) wrote, "Taking, then, into consideration all the facts bearing on the subject which are known to me, I cannot but think that in-breeding generally is, in some way or other, more or less detrimental to the species. And here I find a quite sufficient explanation of the want of inclination for, and positive aversion to, sexual intercourse between persons who from childhood have lived together in that close intimacy which characterises the mutual relations of the nearest kindred. We may assume that in this, as in other cases, natural selection has operated, and by eliminating destructive tendencies and

Received July 9, 1998; revised November 6, 1998.

Address reprint requests and correspondence to: David Haig, Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A.

preserving useful variations has moulded the sexual instinct so as to meet the requirements of the species.”

Westermarck’s appeal to the good of the species was typical of the times, but his argument can easily be restated in terms of advantages to individuals or their genes. In this modernized version, sexual desire is lacking between close kin because incest produces offspring of reduced fitness. Therefore, individuals with an innate aversion to incest have left more descendants than individuals who lacked such an aversion. For Wilson (1998), incest avoidance is the category of human behavior that provides the fullest test of the hypothesis that widely distributed cultural traits confer Darwinian advantage on the genes that predispose them. In Wilson’s view, there is strong evidence for an evolved sexual desensitization toward individuals who were intimate companions during the earliest years of life. Needless to say, this is not a view that is unanimously held within the academic community [for reviews with diverse commentary, see Bixler (1981); Spain (1987); van den Berghe (1983)].

Defenders of an innate aversion to incest often start with a well-reasoned argument that humans are averse to sexual relations with siblings and then slip in the added claim that there is a similar aversion to incest between parents and offspring, without employing equal rigor to justify the additional hypothesis. Another tendency is to downplay potential conflicts of genetic interest between the two parties in an incestuous relationship [but see Barash and Waterhouse (1981); Waser et al. (1986)]. In this paper, I will present a series of explicit models that explore how large the reduction in offspring fitness would need to be if the costs of inbreeding were to explain a generalized aversion to sexual relations with a sibling, with a son or daughter, and with a parent. My principal aim is to be clear about what the underlying theory would predict if sexual aversions and desires were determined by the costs of inbreeding rather than to make a judgment on the larger question whether evolved aversions actually exist.

My analysis will emphasize a number of asymmetries present in incestuous relationships. The genetic costs and benefits of incest may be very different for the two principal protagonists. This asymmetry of fitness payoffs is a plausible evolutionary explanation for an asymmetry of sexual inclinations and aversions. Asymmetries of costs, benefits, and inclinations, when combined with asymmetries of power, are the principal reason why incest is a moral concern. My models will consider an additional asymmetry, of maternal and paternal relatedness, which is present in many interactions between kin. This asymmetry of relatedness, when combined with the asymmetry of costs and benefits, raises the theoretical possibility that incestuous desires could be the source of genetically mediated conflicts within individual psyches. The latter possibility has received little previous consideration, apart from a brief discussion by Trivers (1997).

## **A GENERAL MODEL**

Throughout this paper, I will make the simplifying assumption that incestuous couples are themselves outbred. Incest thus is assumed to be a rare event that does not run

in families. The principal protagonists of an incestuous dyad will be labeled  $A$  and  $B$  in this section, but will be labeled “father,” “mother,” etc., in subsequent sections.

Suppose that a child of an incestuous union has fitness  $x$  relative to unit fitness for an outbred child and is produced at an average cost of  $c_A$  outbred offspring for  $A$  and  $c_B$  outbred offspring for  $B$  [i.e.,  $c_A$  and  $c_B$  represent the opportunity costs of incest: Dawkins (1983)]. Thus, if  $c_A = 1$ ,  $A$  loses one outbred offspring for each inbred offspring, whereas if  $c_A = 0$ , incest has no effect on the number of children that  $A$  conceives with other partners. Given these definitions, the consequences of incest for the *individual fitnesses* of  $A$  and  $B$  are  $(x - c_A)$  and  $(x - c_B)$ , respectively. Incest increases  $A$ 's *inclusive fitness* if:

$$(x - c_A) + r_B(x - c_B) > 0 \quad (1)$$

where  $r_B$  is the probability that a gene in  $A$  is present in  $B$  because of identity by descent. In similar manner, incest increases  $B$ 's *inclusive fitness* if:

$$r_A(x - c_A) + (x - c_B) > 0. \quad (2)$$

A genetic conflict of interests is possible if  $(x - c_A)$  and  $(x - c_B)$  have opposite sign. Thus, a gene in  $A$  would benefit from incest at the expense of a gene in  $B$  if:

$$\frac{1}{r_B} > \frac{c_B - x}{x - c_A} > r_A, \quad (3)$$

when

$$x - c_A > 0 > x - c_B.$$

A genetic conflict also can occur within an individual if coefficients of relatedness differ for an individual's maternal and paternal genomes. If  $m_A$  is the probability that a maternal allele of  $B$  is present in  $A$ , and  $p_A$  is the corresponding probability for a paternal allele, then a maternal allele of  $B$  would benefit from incest at the expense of a paternal allele of  $B$  if:

$$m_A > \frac{c_B - x}{x - c_A} > p_A, \quad (4)$$

when

$$x - c_A > 0 > x - c_B.$$

This model (4) identifies three kinds of parameters that jointly determine the inclusive-fitness consequences of incest and therefore are relevant when considering the evolution of an innate aversion. These are coefficients of relatedness, opportunity costs, and the relative fitness of an incestuously conceived child. As always, when considering psychological adaptations, it is the value of these parameters in the evolutionarily relevant past (rather than their current values) that is pertinent.

In an ideal world, coefficients of relatedness could be obtained directly from Mendelian computations, but the psychological categories “mother,” “father,” “brother,” and “sister” need not correspond precisely to the kinship classification of

an omniscient geneticist. Persons who have lived together from childhood in the closest intimacy are not always sibs, but psychological mechanisms may be unable to recognize true degrees of relatedness. It is a wise child who knows his father, and uncertainty of paternity permeates degrees of relatedness to most kin.

The best available guide to the opportunity costs of incest in our evolutionary past are costs in the present, but even these are poorly known. The opportunity cost of incest is expressed above as the number of outbred offspring forgone per inbred offspring, but it should be emphasized that conception need not occur for incest to have a substantial opportunity cost (e.g., if potential husbands place a premium on virgin brides). The relative fitness of an inbred child is likewise uncertain, with the value of  $x$  for first-degree incest variously estimated as 0.58 (May 1979) and 0.8 (Bittles 1983). The purpose of this paper is to test the plausibility of arguments for an innate aversion to incest. Therefore, the models are concerned solely with genetic costs and benefits. These genetic costs are logically distinct from—and only imperfectly related to—the psychological costs of incest for actual humans.

## SIBLING INCEST

### Incest Between Full-Sibs

A child conceived as a result of sibling incest is simultaneously a daughter (or son) and a niece (or nephew) of its parents and thus will be called a niece-plus-daughter (or son-plus-nephew). For the sake of brevity, this section will use “daughter” to refer to an offspring of either sex and “niece” to refer to a sibling’s offspring of either sex. Suppose that each niece-plus-daughter is produced at an average cost of  $c_b$  outbred daughters for the incestuous brother and  $c_s$  outbred daughters for the sister. Offspring of first-degree incest (between full-sibs or between parent and offspring) will be assigned fitness  $m$  relative to unit fitness for an outbred child. The “relatedness” between full-sibs is one-half (independent of a gene’s parental origin). Therefore, a gene of the brother would benefit from incest if:

$$(m - c_b) + \frac{1}{2}(m - c_s) > 0. \quad (5)$$

Similarly, a gene of the sister would benefit from incest if:

$$\frac{1}{2}(m - c_b) + (m - c_s) > 0. \quad (6)$$

Incest increases the brother’s inclusive fitness but decreases that of his sister if:

$$2 > \frac{c_s - m}{m - c_b} > \frac{1}{2}. \quad (7)$$

Conditions (5)–(7) are derived from conditions (1)–(3) by substituting  $c_b$ ,  $c_s$ ,  $m$  for  $c_A$ ,  $c_B$ ,  $x$ . Two special cases will be considered:

1. If  $c_b = c_s = 1$ , each sibling is faced by a choice between an inbred niece-plus-daughter or an outbred niece plus an outbred daughter (Dawkins 1983). For both

- siblings, incest would increase their inclusive fitness only if children of incest were more fit than outbred offspring ( $m > 1$ ). Therefore, natural selection will favor genes that cause siblings to avoid incest, because children of incest are less fit than outbred offspring ( $m < 1$ ). This seems to be the implicit model of many verbal discussions of the evolution of incest avoidance.
2. If  $c_b = 0$  and  $c_s = 1$ , the genetic costs and benefits differ for brothers and sisters. From the brother's perspective, incest substitutes an inbred niece-plus-daughter for an outbred *niece*. From the sister's perspective, an inbred niece-plus-daughter replaces an outbred *daughter*. The brother's genes benefit if  $m > 1/3$ , whereas the sister's genes benefit if  $m > 2/3$ . The model of Taylor and Getz (1994) of the evolution of sibmating corresponds to case 2 when the sister's genotype determines whether or not incest occurs. Their conclusion that an allele for obligate outbreeding is stable to invasion when  $s < 1/3$  is equivalent to my conclusion that a sister's genes benefit from incest when  $m > 2/3$ . Their analysis is much more complete and sophisticated than the analysis presented here, and it should be consulted for a discussion of complications that are sidestepped by my simpler (but more general) model.

The sex that suffers greater opportunity costs (usually females) will be the sex that is more averse to incest. If so, brothers are more likely to experience sexual desire toward sisters than vice versa, and a sister's aversion to incest need not be reciprocated. Even if inbred offspring have greatly reduced fitness, a brother's genes may benefit from incest with his sister provided that incest has a minor impact on his other reproductive opportunities. Thus, a brother's disinclination to "marry" his sister, or fall romantically in love with her, should be distinguished from whether or not he is averse to intercourse that does not involve commitment nor renunciation of other sexual partners.

### Incest Between Half-Sibs

Suppose that incest occurs between maternal half-sibs. An individual's maternal alleles have probability one-half of being present in a maternal half-sib, but this probability is zero for the individual's paternal alleles. From the perspective of the half-brother's maternal genome, half-sib incest is profitable if:

$$(n - c_b) + \frac{1}{2}(n - c_s) > 0. \quad (8)$$

Similarly, the half-sister's maternal genes would benefit from incest if:

$$\frac{1}{2}(n - c_b) + (n - c_s) > 0. \quad (9)$$

The only change from conditions (5) and (6) is that  $m$  (the fitness of an offspring of full-sib incest) is replaced by  $n$  (the fitness of an offspring of half-sib incest). Therefore, if  $n > m$  (and  $c_b$  and  $c_s$  remain unchanged), the conditions under which incest with a maternal half-sib increases the inclusive fitness of maternal alleles are less restrictive than the equivalent conditions for full-sib incest (8,9).

By contrast (10), maternal half-sibs are unrelated paternally. Therefore, a half-brother's paternal alleles will benefit from any increase in the half-brother's individual fitness without regard to the opportunity cost for the half-sister. That is, if:

$$n - c_b > 0. \quad (10)$$

For the half-sister's paternal genes to benefit, incest must likewise increase her individual fitness:

$$n - c_s > 0. \quad (11)$$

These relationships can be illustrated by considering the special cases of the previous section. (1) For  $c_b = c_s = 1$ , incest benefits maternal and paternal alleles of both siblings if  $n > 1$ . (2) For  $c_b = 0$  and  $c_s = 1$ , paternal genes of the half-brother benefit if  $n > 0$ ; maternal genes of the half-brother benefit if  $n > 1/3$ ; maternal genes of the half-sister benefit if  $n > 2/3$ ; and paternal genes of the half-sister benefit if  $n > 1$  (11).

Because maternal half-sibs are first-degree relatives maternally, but they are unrelated paternally, the half-sib relationship creates an asymmetry of costs and benefits between an individual's maternal and paternal genes. Thus, incest would increase the inclusive fitness of a half-brother's paternal alleles but decrease the inclusive fitness of his maternal alleles whenever:

$$\frac{1}{2} > \frac{n - c_b}{c_s - n} > 0, \quad (12)$$

when

$$n - c_b > 0 > n - c_s.$$

Condition (12) specifies a zone of potential conflict between maternal and paternal alleles over the desirability of incest with a half-sister.

Inclusive fitness theory, by itself, has little to say about how such internal conflicts are resolved. The simplest resolution would occur if all relevant genes are functionally unimprinted (i.e., if the genes' expression is independent of their parental origin). Natural selection then would attach equal weight to costs (and benefits) when an autosomal gene is maternally derived and when it is paternally derived (Haig 1997). Therefore, an unimprinted gene expressed in males that promoted incest with a half-sister would be favored by natural selection if:

$$\frac{n - c_b}{c_s - n} > \frac{1}{4}. \quad (13)$$

This is simply an expression of Hamilton's rule using the average coefficient of relatedness for a half-sib (one-quarter) (13).

The evolutionary prediction as to how internal conflicts of interest will be resolved is unclear if some genes play imprinted "conditional strategies," favoring incest when paternally derived but not when maternally derived (Haig 1997). One possibility is that one or more genes can impose their "preference" with a *fait accompli* or veto (Haig 1992): a paternal allele would have an effective *fait accompli* if it could cause sexual attraction when incest benefits paternally derived genes; a ma-

ternal allele would have an effective veto if it could block sexual attraction when incest is costly for maternally derived genes. Perhaps the most interesting possibility is that no gene can consistently preempt the decision of the genetic collective, and the conflict of interests remains unresolved as an internal ambivalence [or intrapsychic conflict: Trivers (1997)].

### Incest Between “Sibs” of Uncertain Relationship

Westermarck (1891) argued that “there is no innate aversion to marriage with *near relations*,” rather “there is an innate aversion to sexual intercourse between persons living very closely together from early youth, and that, as such persons are in most cases related, this feeling displays itself chiefly as a horror of intercourse between near kin.” Suppose that, during the evolutionarily relevant past, individuals who belonged to the psychological category “sib” had probabilities  $k_1$  of being a full-sib,  $k_2$  of being a paternal half-sib,  $k_3$  of being a maternal half-sib, and  $k_4$  of being a step-sib ( $k_1 + k_2 + k_3 + k_4 = 1$ ). If so, the paternal genes of a “brother” would benefit from incest with a “sister” if:

$$k_1 \left[ (m - c_b) + \frac{1}{2}(m - c_s) \right] + k_2 \left[ (n - c_b) + \frac{1}{2}(n - c_s) \right] + \quad (14)$$

$$k_3(n - c_b) + k_4(1 - c_b) > 0.$$

Condition (14) simplifies to:

$$\bar{m} - c_b > \frac{k_1}{2}(c_s - m) + \frac{k_2}{2}(c_s - n) \quad (15)$$

where

$$\bar{m} = k_1 m + (k_2 + k_3)n + k_4.$$

The left-hand side of condition (15) is the expected individual-fitness benefit that a “brother” obtains from conceiving a child by a “sister.” The right-hand side takes account of costs to the “sister” only when the “sibs” share the same father (i.e., are full-sibs or paternal half-sibs). Similarly, the maternal genes of a “brother” would benefit from incest if:

$$\bar{m} - c_b > \frac{k_1}{2}(c_s - m) + \frac{k_3}{2}(c_s - n). \quad (16)$$

In this case (16), the right-hand side takes account of costs to the “sister” only when the “sibs” share the same mother. Thus, costs and benefits to the individual fitness of the “brother” are included in the calculations, regardless of his true relatedness to his “sister,” whereas costs and benefits to the individual fitness of the “sister” do not appear in the calculations if she has zero paternal relatedness for his paternal genes or zero maternal relatedness for his maternal genes. Equivalent conditions are easily derived for the genetic interests of the “sister” (not shown).

The conditions favoring incest have been presented as if there were only a single psychological category of “sib.” However, during the evolutionarily relevant past, the

probabilities  $k_1$ ,  $k_2$ ,  $k_3$ , and  $k_4$  may have been systematically different for different kinds of “sibs.” For example, average paternal coefficients of relatedness might decrease as the age difference between “sibs” increases. If so, similar calculations of costs and benefits could easily be performed for each separate category of “sibs.”

## FATHER–DAUGHTER INCEST

Suppose that a child conceived during the course of an incestuous relationship between a father and daughter is produced at a cost of  $c_d$  outbred offspring for the daughter and  $c_f$  outbred offspring for the father. For simplicity, I will assume that a daughter’s incest with her father does not affect her mother’s individual-fitness returns from offspring other than the daughter. Further suppose that the father is the daughter’s genetic father with probability  $k$ , but is an unrelated male with probability  $(1 - k)$ . In the former case, their child will be assigned fitness  $m$  because the degree of inbreeding is the same as for full-sib incest. In the latter case, the child is genetically outbred and will be assigned unit fitness. On average, the genes of the father will benefit from incest if:

$$(\bar{m} - c_f) + \frac{k}{2}(m - c_d) > 0, \quad (17)$$

where

$$\bar{m} = (1 - k) + km.$$

For genetic fathers ( $k = 1$ ), condition (17) is essentially the same as condition (5), with father and daughter substituted for brother and sister. There is no conflict between the father’s maternal and paternal genomes with respect to incest with a daughter, because both are equally related to the daughter and her offspring. Similarly, a brother is equally related to his full-sisters via his mother and father.

From the genetic perspective of a parent, the costs and benefits of incest with an offspring resemble those of incest with a full-sib. But, from the separate perspectives of an offspring’s maternal and paternal genomes, incest with a parent has quite different consequences from incest with a full-sib. A daughter’s paternal genes are equally likely to be present in one of her own gametes and one of the gametes of her genetic father. Therefore, a paternal gene of the daughter would benefit from incest if:

$$k(m - c_f) + (\bar{m} - c_d) > 0. \quad (18)$$

By contrast, a daughter’s maternal genes are absent from her father. Consequently, such genes would benefit from incest only if incest increases the daughter’s individual fitness.

$$\bar{m} - c_d > 0. \quad (19)$$

If gene expression is unaffected by parental origin, this internal conflict can be resolved by “averaging” (18) and (19). A daughter’s genes would benefit (on average) if:

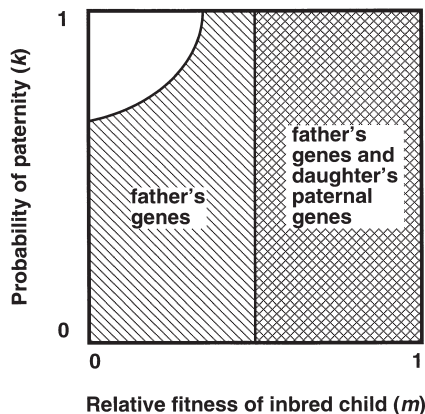
$$\frac{k}{2}(m - c_f) + (\bar{m} - c_d) > 0. \tag{20}$$

Condition (20) restores the symmetry between parent–offspring and full-sib incest. Whether averaging is justified as a basis for making behavioral predictions is, in part, an empirical question about the rarity or ubiquity of imprinted genes affecting the relevant behaviors.

Consider the special case where the father’s opportunity cost is zero ( $c_f = 0$ ) but the daughter’s opportunity cost is the replacement of an outbred offspring by an inbred offspring ( $c_d = 1$ ). If  $k = 1$ , the father’s genes benefit from an incestuous conception when  $m > 1/3$ , because of the father’s higher relatedness to a son-plus-grandson than to a grandson. If  $k < 2/3$ , the father’s genes benefit from incest even if an inbred child has zero fitness ( $m = 0$ ), because the genetic benefit of gaining an outbred son (if the daughter is the child of another man) outweighs the loss of a grandson (if she is his child). For this special case, the probability of paternity ( $k$ ) cancels out when considering the daughter’s genetic interests: the paternal genes of the daughter benefit from incest if  $m > 1/2$ ; her maternal genes benefit if  $m > 1$ ; and her maternal and paternal genomes are in conflict for  $1 > m > 1/2$ . These relationships are illustrated in Figure 1. If the interests of maternal and paternal alleles are averaged, the daughter’s genes benefit if  $m > 2/3$  (Smith 1979).

Step-fathers and step-daughters are genetically unrelated individuals ( $k = 0$ ) and their offspring do not suffer from inbreeding depression. In purely genetic terms, step-fathers and step-daughters are no different from any other unrelated male and female. Therefore, incest will benefit the genes of a step-father or step-

**FIGURE 1.** The genetic beneficiaries of father–daughter incest when the father’s opportunity cost is zero and the daughter’s opportunity cost is the replacement of an outbred offspring by an inbred offspring. The father’s genes benefit from incest, except in the top left-hand corner, where inbreeding depression is severe and the probability that the daughter is some other man’s child is small. The daughter’s paternal genes benefit from incest when  $m > 1/2$ , but her maternal genes benefit when  $m > 1$  (beyond right-hand side of figure).



daughter if it increases their respective individual fitnesses. Moral concerns about such relationships focus on asymmetries of power and betrayals of trust. In general, the genes of fathers have greater incentives for incest as their confidence of paternity decreases, because the probability that any resulting child will be inbred decreases, as does the probability that the father will experience an inclusive-fitness cost from reductions in the daughter's individual fitness.

## MOTHER–SON INCEST

An individual's mother usually is not in dispute. Suppose that the child of an incestuous relationship between mother and son has relative fitness  $m$  and is produced at an opportunity cost of  $c_n$  outbred offspring for the son and  $c_m$  outbred offspring for his mother (of which a proportion  $p$  are full-sibs of the son). On average, a gene of the mother would benefit from incest if:

$$(m - c_m) + \frac{1}{2}(m - c_n) > 0. \quad (21)$$

Condition (21) resembles condition (5) for full-sib incest and condition (17) for father–daughter incest, because all three describe costs and benefits of first-degree inbreeding.

A son's maternal genes are equally likely to be present in one of his mother's gametes or one of his own gametes. Therefore, his maternal genes will benefit from incest whenever the sum of the effects on his mother's and his own individual fitness is positive.

$$(m - c_m) + (m - c_n) > 0. \quad (22)$$

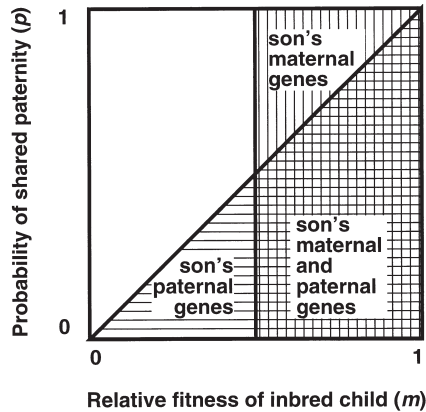
Condition (22) is the counterpart of condition (18) for father–daughter incest. By contrast, a paternal gene of the son would benefit from incest if:

$$(m - c_n) - pc_m > 0. \quad (23)$$

That is, the individual-fitness benefit to the son must be greater than the opportunity cost to the mother weighted by the probability that the mother's outbred offspring would have the same father as the son. If the son's own father is dead or absent, the son's paternal genes attach no weight to effects on the mother's reproduction with a subsequent partner.

Whether the son's maternal or paternal alleles benefit from incest varies in complex ways. Consider the special case in which incest involves no opportunity cost for the son ( $c_n = 0$ ) but, from the mother's perspective, replaces an outbred daughter ( $c_m = 1$ ) with an inbred daughter-plus-granddaughter. In this case, genes of the mother benefit if  $m > 2/3$ ; maternal genes of the son benefit if  $m > 1/2$ ; and paternal genes of the son benefit if  $m > k$ . In the absence of genomic imprinting, the son's genes would benefit, on average, if  $m > (1 + p)/3$ . These relationships are illustrated in Figure 2.

The relationship between father and daughter is genetically symmetric with the relationship between mother and son. Conditions (17)–(19) differ from conditions



**FIGURE 2.** The genetic beneficiaries of mother–son incest when the son’s opportunity cost is zero and the mother’s opportunity cost is the birth of an inbred rather than an outbred offspring. The son’s paternal genes benefit when  $m > k$  (horizontal hatching) and his maternal genes benefit when  $m > 1/2$  (vertical hatching). The mother’s genes benefit from incest if  $m > 2/3$ .

(21)–(23) because my model of father–daughter incest includes a parameter  $k$  to represent uncertainty of paternity, whereas my model of mother–son incest includes a parameter  $p$  to represent a correlated cost to the son’s father of the mother’s opportunity cost of incest.

## TABOOS

Previous sections have considered only the genetic interests of the principal protagonists, but these individuals are embedded in a wider social context, and other members of society also may have an interest in whether or not incest occurs.

Incest has consequences for the inclusive fitness of other family members. For example, the interests of a mother’s genes with respect to incestuous relations between a son and a daughter are intermediate between the interests of the son’s and the daughter’s maternal genes (because the mother is equally related to both). If the son and daughter have different fathers, the genetic interests of the son’s paternal relatives are aligned with the genetic interests of the son, and the genetic interests of the daughter’s paternal relatives are aligned with those of the daughter. In the case of father–daughter incest, the mother and her kin will have different inclusive fitness interests from the father and his kin.

Incest also may have consequences for nonrelatives. Other potential sexual partners of a daughter (and their relatives) generally will have an interest in the suppression of sibling or paternal incest, as will the community as a whole if there are social costs of raising inbred children.

Frazer (1910) argued that the almost universal occurrence of incest taboos contradicted Westermarck’s hypothesis of an innate aversion for sexual relations with

close kin. In Frazer's view, "law only forbids men to do what their instincts incline them to do; what nature itself prohibits and punishes, it would be superfluous for the law to prohibit and punish." The possibility that males sometimes have incestuous inclinations that run counter to the interests of other members of society is a plausible explanation for the institution of incest taboos. The associated punishments and social disapprobation increase the opportunity costs for potentially incestuous males and provide a powerful disincentive to incest.

## THE DIVIDED SELF

The maternal alleles of a child have a relatedness of one to the child's mother and a relatedness of zero to the child's father, whereas the paternal alleles of the child have a relatedness of zero to the mother and one to the father. The traditional way to calculate a coefficient of relatedness in such cases has been to average maternal and paternal relatedness (when these differ) and obtain a *coefficient of average relatedness*. Thus, the relatedness of a child to its parents has been calculated as one-half, the same as the relatedness of the parents to the child. However, it should be noted that these coefficients reflect different kinds of uncertainty. The parents' relatedness to the child is one-half because of the uncertainty of Mendelian segregation (each parental allele has a 50% chance of being transmitted to the child), whereas the child's relatedness to the parents is one-half because of uncertainty whether an allele is maternally or paternally derived.

The discovery that some genes in the mammalian genome carry an imprint of their parental origin that determines when, where, and whether the gene is expressed has called into question the validity of using coefficients of average relatedness (Haig 1997). If sexual partnerships were dissolved after the birth of each child, there would be the potential for strong genetic conflicts within the child over how much of its own individual fitness the child should sacrifice for the benefit of a parent, say the father. A paternal allele of the child is present as a single copy in both child and father, and it should be evolutionarily indifferent about whether a benefit is conferred on the child or the father. On the other hand, a maternal allele of the child is absent from the father. Therefore, no benefit to the father, no matter how large, could compensate a maternal allele for any cost to the child, no matter how small. This internal conflict is mitigated by prolongation of the sexual relationship between the child's father and mother because then the parents' residual reproductive values are correlated.

Much then hangs on the importance of genomic imprinting in brain function. If imprinting is unimportant, evolutionary models can use coefficients of average relatedness and discount the possibility of internal conflict. However, a number of recent studies have found significant effects of imprinting on brain function and development (Allen et al. 1995; Keverne et al. 1996; Skuse et al. 1997). If evolutionary conflicts are played out within the individual, many of the issues that have been the province of behavioral ecology (credible signaling, reciprocity, reputation, etc.) are transferred within the body into the realm of neurology and endocri-

nology. At the present time it is unclear how such conflicts will be expressed in external behavior and subjective experience.

This paper has considered three relationships in which there is symmetry of maternal and paternal relatedness (full-sib to full-sib, father to daughter, mother to son) and three in which there is asymmetry (half-sib to half-sib, daughter to father, son to mother). Father–daughter incest is consistently found to be the most traumatic form of incestuous abuse for female victims (Finkelhor 1979; Russell 1986). On average, abuse was perceived as more traumatic when there was some degree of ambivalence on the victim’s part than when the abuse was completely unwanted (Russell 1986: 48). Whether strong internal genetic conflicts are perceived as particularly traumatic remains, at the moment, no more than an interesting speculation. I have found no studies that address differences in the emotional response to full-sib and half-sib incest.

Incest between half-siblings, and incest between parent and child, have been used in this paper to illustrate how asymmetries of maternal and paternal relatedness can result in genetic conflicts within individuals. However, analogous conflicts arise in many other situations. For example, if a parent (say a mother) takes a new partner, the children of a previous union could experience an internal genetic conflict with respect to parental care lavished on children of the new relationship rather than themselves. The new children are just another set of siblings (relatedness one-half) from the perspective of the older children’s maternal genes but are nonrelatives (relatedness zero) from the perspective of the older children’s paternal genes.

Discussion has so far been restricted to a consideration of inclusive-fitness effects for autosomal genes, but inclusive-fitness calculations sometimes will differ for autosomal and sex-linked genes. For example, the coefficient of paternal relatedness to a full-sib of the opposite sex is one-half for autosomal loci but zero for sex-linked loci, because a brother inherits his father’s Y chromosome whereas his sister inherits her father’s X, thus creating the possibility of internal conflicts between autosomal and sex-linked genes.

## DISCUSSION

There cannot be a universal aversion to incest—experienced by all humans, at all times—because sexual relations between close relatives are not unknown. Finkelhor (1979) administered a questionnaire to New England college students about childhood sexual experiences: 14% of 530 female respondents reported a “sexual experience” with a brother and 1% a sexual experience with a father; 6% of 266 male respondents reported a sexual experience with a sister, but none reported a sexual experience with either parent. Five percent of college students who responded to another questionnaire reported a “consummatory act” with a sibling that involved some form of male penetration or attempted penetration (Bevc and Silverman 1993). Russell (1986) analyzed 930 interviews with San Francisco women in which 2% reported “sexual abuse” by a brother; 3% sexual abuse by a biological father; and 2% sexual abuse by a nonbiological father. Russell ascribed the differences in incidence between her study and that of Finkelhor to the latter’s broader definition

of a sexual experience and to possible differences between responses to questionnaires and interviews.

Data on the frequency of incestuous acts address the question how often men and women feel sexual attraction to close kin only indirectly, because not all sexual relations are desired by both parties, and because not all sexual desires are consummated. The opportunity costs of casual sex are generally greater for females than for males (Trivers 1972). Therefore, females are predicted to be the sex that is more averse to incest. The detailed responses to Finkelhor's and Russell's surveys provides evidence for such a difference between the sexes. In both studies, most incestuous acts were unwanted by females and initiated by males [also see Phelan (1995)]. Thus, most women and girls appear to be averse to incest, but a similar aversion is absent in (at least) a proportion of men and boys. Quantitative data on sexual attraction, rather than sexual acts, is limited. An exception comes from a study of incest offenders in which 11% of the control group of nonincestuous fathers reported some degree of sexual arousal in response to their daughters (Williams and Finkelhor 1995). Given the nature of the question, this figure is unlikely to be an overestimate.

Perhaps the strongest evidence that mechanisms exist that (for the most part) suppress sexual relations between siblings comes from studies that find sexual desire is reduced between unrelated individuals who have been raised together from infancy, even though sexual relations between such individuals is not socially proscribed. These studies find a diminution of desire in both males and females [see Wolf (1995) for a review of the substantial anthropological evidence on this question].

The degree of relatedness of brother to sister (full-sibs) is the same as the degree of relatedness of father to daughter. Therefore, if natural selection has favored a diminution of desire of brothers for sisters, it also could have favored a diminution of desire of fathers for daughters (assuming that the opportunity costs of incest were similar for brothers and fathers). Sexual arousal of fathers in response to daughters is not uncommon (Williams and Finkelhor 1995), but a comparison of fathers with step-fathers provides evidence for a relative suppression of sexual acts. In the study by Russell (1986), "*one out of approximately every six women who had a stepfather as a principal figure in her childhood years was sexually abused by him before she reached the age of fourteen.*" As a consequence, "*women who were raised by a stepfather were over seven times more likely to be sexually abused by him than women who were raised by a biological father*" (emphases in original). In the multivariate analysis of Finkelhor (1984), the presence of a step-father was the strongest correlate of a daughter's victimization.

The evolutionary models of this paper demonstrate that genes of "fathers" with lower confidence of paternity gain relatively greater benefits from incest with "daughters." Therefore, a reduced probability of paternity is predicted to increase a male's predisposition toward incest. There are little data to test this hypothesis, except in the case of step-fathers (see earlier). From a purely genetic perspective, a step-daughter is an unrelated female over whom a step-father may have considerable powers of coercion. A higher incidence of incest also is predicted between half-

sibs (and step-sibs) than between full-sibs, but I know of no data that systematically test this hypothesis.

Incest between mothers and sons is very much rarer than incest between fathers and daughters. Mothers would appear to have little interest in sexual relations with sons, and sons little interest in sexual relations with mothers (although there is little direct evidence on this question). The mother–son and father–daughter relationships differ in the nature of opportunity costs and in the uncertainty of paternity present in the father–daughter relationship. This suggests that the principal evolutionary reason why fathers are more predisposed to sexual relations with offspring than are mothers is that opportunity costs have been lower for fathers and that a father cannot be certain of his paternity.

The reason why sexual aggression by sons toward mothers is so rare is less clear. One factor may be the internal conflict within the son's genome between his maternal and paternal alleles. A son's paternal alleles are equally likely to be present in his own gametes and his genetic father's gametes. When there is a high probability that a mother's future offspring will have the same father as the son, the son's paternal alleles gain more from the father conceiving a child because this avoids the costs of inbreeding. Another factor may be the age-related decline in female fertility that reduces the desirability of the mother as a sexual partner by the time her sons are sexually mature.

The author thanks Louis Culot, Martin Daly, Lucas Mix, Peter Taylor, Margo Wilson, and an anonymous reviewer, who all made helpful comments that improved the manuscript.

---



---

## REFERENCES

- Allen, N.D., Logan, K., Lally, G., Drage, D.J., Norris, M.L., and Keverne, E.B. Distribution of parthenogenetic cells in the mouse brain and their influence on brain development and behavior. *Proceedings of the National Academy of Sciences USA* 92:10782–10786, 1995.
- Barash, D.P., and Waterhouse, M. Comments on Bixler. *Current Anthropology* 22:643–644, 1981.
- Bevc, I., and Silverman, I. Early proximity and intimacy between siblings and incestuous behavior: a test of the Westermarck theory. *Ethology and Sociobiology* 14:171–181, 1993.
- Bittles, A.H. The intensity of human inbreeding depression. *Behavioral and Brain Sciences* 6:103–104, 1983.
- Bixler, R.H. Incest avoidance as a function of environment and heredity. *Current Anthropology* 22:639–654, 1981.
- Dawkins, R. Opportunity costs of inbreeding. *Behavioral and Brain Sciences* 6:105–106, 1983.
- Finkelhor, D. *Sexually Victimized Children*. New York: Free Press, 1979.
- Finkelhor, D. *Child Sexual Abuse*. New York: Free Press, 1984.
- Frazer, J.G. Totemism and Exogamy. *A Treatise on Certain Early Forms of Superstition and Society*, (Vol. IV). London: Macmillan, 1910.
- Haig, D. Intra-genomic conflict and the evolution of eusociality. *Journal of Theoretical Biology* 156:401–403, 1992.
- Haig, D. Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proceedings of the Royal Society of London B* 264:1657–1662, 1997.
- Keverne, E.B., Fundele, R., Narasimha, M., Barton, S.C., and Surani, M.A. Genomic imprinting and the differential roles of parental genomes in brain development. *Developmental Brain Research* 92: 91–100, 1996.
- May, R.M. When to be incestuous. *Nature* 279:192–194, 1979.

- Phelan, P. Incest and its meaning: the perspectives of fathers and daughters. *Child Abuse and Neglect* 19: 7–24, 1995.
- Russell, D.E.H. *The Secret Trauma*. New York: Basic Books, 1986.
- Skuse, D.H., James, R.S., Bishop, D.V.M., Coppin, B., Dalton, P., Aamodt-Leeper, G., Bacarese-Hamilton, M., Creswell, C., McGurk, R., and Jacobs, P.A. Evidence from Turner's syndrome of an imprinted X-linked locus affecting cognitive function. *Nature* 387:705–708, 1997.
- Smith, R.H. On selection for inbreeding in polygynous animals. *Heredity* 43:205–211, 1979.
- Spain, D.H. The Westermarck–Freud incest-theory debate. *Current Anthropology* 28:623–645, 1987.
- Taylor, P.D., and Getz, W.M. An inclusive fitness model for the evolutionary advantage of sibmating. *Evolutionary Ecology* 8:61–69, 1994.
- Trivers, R.L. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871–1971*, B. Campbell (Ed.). Chicago: Aldine-Atherton, 1972, pp. 136–179.
- Trivers, R.L. Genetic basis of intrapsychic conflict. In *Uniting Psychology and Biology*, N. Segal, G. Weisfeld, and C. Weisfeld (Eds.). Washington, DC: American Psychological Association, 1997, pp. 385–395.
- van den Berghe, P.L. Human inbreeding avoidance: culture in nature. *Behavioral and Brain Sciences* 6: 91–123, 1983.
- Waser, P.M., Austad, S.N., and Keane, B. When should animals tolerate inbreeding? *American Naturalist* 128:529–537, 1986.
- Westermarck, E. *The History of Human Marriage*. London: MacMillan, 1891.
- Westermarck, E. *The History of Human Marriage, (Vol. I)*, 5th ed. London: MacMillan, 1921.
- Williams, L.M., and Finkelhor, D. Paternal caregiving and incest: test of a biosocial model. *American Journal of Orthopsychiatry* 65:101–113, 1995.
- Wilson, E.O. *Consilience*. New York: Knopf, 1998.
- Wolf, A.P. *Sexual Attraction and Childhood Association*. Stanford: Stanford University Press, 1995.