

Original Article

Beyond Westermarck: Can Shared Mothering or Maternal Phenotype Matching Account for Incest Avoidance?

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Abstract: Westermarck's Hypothesis (WH) is widely accepted amongst evolutionary scientists as the best explanation of human incest avoidance. Although WH may account for incest avoidance between co-reared kin, it cannot explain other forms of incest avoidance, and therefore, cannot account for the differential incidence of sibling-sibling, mother-son, father-daughter and other forms of incest. WH also face problems adequately accounting for phenomena within its explanatory domain. Neither of the studies widely thought to corroborate WH (the Israeli kibbutz and Taiwanese simpua marriage studies) provides a genuine test of it, and the results of experimental thought to confirm WH are vitiated by methodological problems. The present paper considers two alternatives to WH: the shared mother hypothesis (SMH) and the maternal phenotype-matching hypothesis (MPMH). SMH states that human infants imprint on their mother, who then treat as kin those individuals towards whom their mother behaves in a kin-like or mate-like manner. MPMH states that humans unconsciously use the maternal phenotype as a visual template for estimating coefficients of relatedness, and that these estimate regulate altruistic and mating behavior. Both SMH and MPMH are able to account for the kibbutz and simpua marriage data, and entail additional epidemiological and experimental predictions. SMH and MPMH have greater explanatory power than WH, and MPMH has greater explanatory power than SMH.

Keywords: Inbreeding, incest, paternal uncertainty, phenotype matching, Westermarck.

Introduction

During the second half of the 19th century, anthropologists began to conjecture that the incest taboo originated as a way of guarding against the deleterious effects of inbreeding (e.g., Morgan, 1877). However, this explanation rested on the implausible idea that prehistoric peoples intentionally established the incest taboo as a form of genetic hygiene (Wallace, 1983; Wolf, 2004). In 1891, the Finnish philosopher and social anthropologist Edvard Westermarck proposed that incest avoidance is based on an instinctual rather than a

consciously calculated response to the danger of inbreeding depression (Westermarck, 1891, 1921, 1926, 1934). He reasoned that because inbreeding is “detrimental to the species” (1891, p. 352) and our aversion to it is probably an outcome of natural selection. This hypothesis makes sense only if our ancestors possessed some means of determining which individuals are their close genetic relatives, and Westermarck accordingly argued that humans respond to extended childhood co-residence as an indication of genetic kinship. “Generally speaking,” he wrote, “there is a remarkable absence of erotic feelings between persons living very closely together from childhood....

Nay more, in this, as in many other cases, sexual indifference is combined with the positive feeling of aversion when the act is thought of. This I take to be the fundamental cause of the exogamous prohibitions. Persons who have been living closely together from childhood are as a rule near relatives. Hence their aversion to sexual relations with one another displays itself in custom and law as a prohibition of intercourse between near kin” (Westermarck, 1926, p. 80).

Of course, this is not always the case: an adopted child is not the sibling of the other children with whom he or she co-resides. Nature sometimes makes mistakes, but if the benefits exceed the costs (in this case, as long as the benefits gained from avoiding sex with siblings exceed the cost of lost mating opportunities with pseudo-siblings), then natural selection can do its work. A good deal hangs on the word “can” in the preceding sentence. Westermarck’s Hypothesis (hereafter WH) is a strong hypothesis—a very strong hypothesis, and natural selection may have structured human mating behavior in the way that it describes. But then again, she may not have.

Discussion

A careful reading of the passage excerpted from Westermarck in the preceding section reveals that WH consists of at least three component-hypotheses, which Durham (2004) calls “the aversion hypothesis”, “the adaptation hypothesis”, and “the expression hypothesis”. The aversion hypothesis states that protracted childhood coresidence inhibits sexual desire and promotes sexual aversion. The adaptation hypothesis states that the biological function of incest avoidance is to prevent the deleterious consequences of inbreeding (we can ignore Westermarck’s claim that this is “for the good of the species”).

Finally, the expression hypothesis states that cultural taboos against incest are a collective expression of individual aversive feelings. They are not rules to prevent people from acting on their desires. Instead, they express the repugnance to incest felt by most people.¹ These three components are logically distinct, and should be evaluated separately. For instance, it might be true that childhood association causes sexual aversion, but false that the adaptive function of this is to prevent deleterious consequences of inbreeding, and a nuanced assessment of WH must take these distinctions into account. Strictly speaking, we should perhaps speak of the Westermarck *Hypotheses* rather than the Westermarck *Hypothesis*, and it is important to be explicit about which of the component hypotheses one is concerned with. In this paper, will use the terms “Westermarck’s Hypothesis” and “WH” to designate the aversion hypothesis.

However, because of the specific focus of this paper, I will use the terms “Westermarck’s Hypothesis” and “WH” to designate the aversion hypothesis.

WH is not a thesis about incest avoidance per se. It is specifically concerned with sibling incest. Advocates of WH sometimes overlook this. “Defenders of an innate aversion to incest,” writes Haig, “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” (Ihanus, 1999, p. 84). Along the same lines, Ihanus remarks that:

Westermarck speaks vaguely about “persons who have been living closely together from childhood.” We should note, therefore, that his model does not explain parents’ sexual aversion towards their children, since of course they have not lived with them since their *own* childhood (Ihanus, 1999, p. 193).

If WH only explains incest avoidance between individuals brought up in sibling-like relationships, its truth entails that other mechanisms *must* be invoked to explain other forms of incest avoidance. We will need a different story—or several different stories—to account for incest avoidance between parents and offspring, uncles and nieces, grandparents and grandchildren, and so on. This, by the way, demonstrates the fallaciousness of the oft-repeated claim (e.g. Ridley, 1993; Wilson, 1998; Wolf, 1995) that the putative empirical validation of Westermarck’s hypothesis demonstrates that Freud’s account of incest-avoidance was wrong. Freud’s thesis may well be wrong, but we cannot logically conclude this from the (alleged) correctness of WH. At best, Westermarck may have shown that Freud was wrong about *sibling* incest, but sibling incest does not exhaust the possibilities of human inbreeding.

The explanatory limitations of WH are routinely ignored in much of the pro-Westermarck literature. For example, Ridley (1993) states that WH predicts that “if incest does occur, it will prove to be between parent and child, and specifically between father and daughter, because a father is past the age at which familiarity breeds aversion and because men usually initiate sex” (p. 284). But the prediction that father-daughter incest is the most common form is not deducible from WH. It is deduced from WH in conjunction with the principle that men usually initiate sex. This general notion is more plausibly and powerfully formulated in terms of parental investment theory (Trivers, 1972). Parental investment theory proposes that members of the sex that pays the higher reproductive costs will be discriminating when selecting mates. In our species, females pay higher reproductive costs than males. Females also pay higher opportunity costs than males, because a woman who becomes pregnant through incestuous copulation cannot simultaneously outbreed, whereas a male that impregnates a woman via incestuous copulation can simultaneously outbreed. The risk of inbreeding depression weighs more heavily on mothers, daughters, and sisters than on fathers, sons, and brothers, and one would consequently expect males to be more inclined towards incest than females, because they have far less to lose (see Moore, 1992; Walter and Buyske, 2003).

It is clear that, contrary to some of the claims that have been made about it in the literature, WH—at least in its traditional form - cannot provide a comprehensive

explanation for incest avoidance. It *may* account for incest avoidance between co-reared kin, but it does not have the theoretical resources to explain other forms of incest avoidance, and, therefore, cannot on its own account for the differential incidence of sibling-sibling, mother-son, father-daughter and other forms of incest.

The popularity of WH is partially based on the fact that it accounts for inbreeding avoidance between siblings in many non-human species (e.g., Pusey, 2004). This continuity is certainly suggestive, but it should not cause us to forget that there are also significant discontinuities between species, and it may be that *Homo sapiens* has found a different pathway to the fitness-enhancing goal of inbreeding avoidance. It also should be borne in mind that evidential support for a scientific hypothesis falls short of warranting acceptance of it.

Those who believe that WH accounts for incest avoidance in our own species have not recklessly extrapolated from nonhuman cases. Their endorsement of WH flows primarily from studies of pseudo-siblings, with inferences that turn on the potential for the Westermarck effect to misfire, resulting in false judgments of kinship and therefore sexual aversion between pseudo-siblings. The most famous, and probably the most powerful support for WH comes from studies of individuals brought up in age-graded peer groups on Israeli kibbutzim. Prior to the 1970s, children raised in kibbutzim were separated from their parents a few weeks after birth and brought up in age-graded peer groups of six to eight children who lived together in a *kvutza* (children's home). Children in a peer group performed most of their daily activities together. They even slept together in dormitories, attended by a *metapelet* (female caretaker). Day-to-day contact between parents and children was restricted to one or two hours at the end of the working day. WH predicts that under these circumstances members of the same peer-group will develop sexual aversions to one another, and this prediction is corroborated by empirical data. Surveys of second-generation kibbutzniks reveal that sexual relationships or marriage between peer-group members are virtually nonexistent (Shepher, 1971, 1983; Spiro, 1958; Talmon, 1964).

The other main source of empirical support for WH comes from Taiwanese *simpua* ("little bride") marriages, in which infant girls are adopted and raised in the households of the boys whom they will eventually be required to marry. This is similar to the normal situation of an adopted child, but with one crucial distinction: there is no attempt to dissuade the girl and boy from being attracted to one another. Wolf found that high levels of divorce, infidelity, and infertility plague marriages contracted in this way, and he attributed these difficulties to sexual aversions between husband and wife in consequence of their having been raised as pseudo-siblings (Wolf, 1966, 1968, 1970; Wolf and Huang, 1980). He found that these negative effects only occur if the *simpua* bride is adopted before her third birthday, which led him to believe that the first three years of life are a sensitive period for imprinting on siblings.

Various methodological and interpretative criticisms have been leveled against the claim that the kibbutz and *simpua* marriage data are best accounted for by WH (e.g., Hartung, 1985; Kirkpatrick, 1972; Walter and Buyske, 2003). I will not review these here, but I will advance a hitherto unrecognized objection to the probity of the kibbutz studies. Recall that children raised on kibbutzim were largely segregated from their biological families. As a result, they had much more contact with their same-age peers than they did

with their parents and genetic siblings. According to the Westermarck hypothesis, members of age-graded peer-groups were functional kin and therefore developed sexual aversions towards one another. But what does this imply about the relationship between these children and their actual siblings? If WH is correct, the attenuated relationship between these children and their genetic siblings should, all things being equal, result in an elevated rate of actual sibling-sibling incest, as compared to the rate of incest between co-reared siblings. The *ceteris paribus* clause is included to cover the possibility that there may be other variables at work to inhibit incest between these individuals. Of course, if such countervailing factors are present in the case of kibbutzniks, it is reasonable to assume that they are also present in relationships between co-reared siblings, and may undermine the extent to which WH can account for incest aversion between co-reared siblings. Alternatively, it might be that confounding variables such as social learning inhibit incestuous acts without inhibiting sexual desire between non-co-reared siblings, in which case WH would predict elevated levels of sexual desire between non-co-reared siblings.

If WH accounts for avoidance of incest between pseudo-kin it cannot coherently account for incest-avoidance between actual kin in these circumstances. So, if it turns out that there are elevated levels of sexual desire or elevated rates of incest between kibbutz-reared siblings as compared to co-resident siblings, this would provide impressive empirical support for WH, but if such evidence is lacking, WH is called into question.

There is a more general methodological problem that haunts both of these studies: neither of them directly tests Westermarck's hypothesis about sibling incest. WH makes claims about the absence of sexual desire between kin, claims that are simply not addressed by studies that examine marriages, or the lack of them, between co-reared non-kin. Generalizing from pseudo-kin to kin assumes that the two cases are comparable in all relevant respects, but there is evidence that argues against this assumption. Separated relatives (for example, adoptees) once reunited sometimes experience a powerful sexual attraction to one another (Erickson, 2004; Greenberg and Littlewood, 1995; Krista, 2003). According to Greenberg and Littlewood (1995) this phenomenon, which is called Genetic Sexual Attraction (GSA), occurs in over 50% of relatives reunited after early separation. GSA both supports and detracts from the cogency of WH. On the one hand, it demonstrates a clear relationship between early co-residence and incest avoidance. Reunited relatives do not have an opportunity to develop sexual aversions that would have protected them from incestuous passion. On the other hand, it suggests that inhibitions against incest must operate against an especially potent prior attraction: sexual feelings experienced by reunited relatives are often especially intense, suggesting that sexual aversions between co-reared non-kin and co-reared kin are not entirely comparable.

To the best of my knowledge, Bevc and Silverman (Bevc and Silverman, 1993, 2000; Silverman and Bevc, 2004) are the only researchers who have tested WH using actual cases of sibling incest. Bevc and Silverman investigated three samples. Sample (a) consisted of individuals who had engaged in attempted or successful genital intercourse with a sibling, sample (b) consisted of individuals who had engaged in post-pubertal non-procreative sex with a sibling, and sample (c) consisted of individuals who did not have sexual relations of any kind with a sibling. They found a correlation between childhood separation between siblings and genital intercourse, but no correlation between childhood co-residence and

non-procreative sexual activity. They also found a positive rather than a negative correlation between the degree of childhood intimacy and non-procreative incestuous activity, which disconfirms the hypothesis, derived from WH by Fox (1962, 1980), that childhood intimacy results in sexual indifference or aversion. The studies by Bevc and Silverman suggest that the Westermarck effect may play a more modest role in human inbreeding avoidance than has hitherto been assumed. Childhood association between siblings appears to inhibit specifically procreative sexual activity, but it does not inhibit sexual *desire*, as Westermarck claimed, and therefore casts doubt on the assumption by earlier researchers that the absence of marriage, or marital unhappiness, is an index of the absence of sexual desire.

Experimental approaches provide another avenue for testing WH. To date, there have been two important studies along these lines (Fessler and Navarete, 2004; Lieberman, Cosmides and Tooby, 2003). Lieberman, Cosmides and Tooby set out to investigate the connection between feelings of aversion to sibling incest *per se* and childhood co-residence with a sibling of the opposite sex. They asked American undergraduates about their attitudes towards third-party incest on the assumption that their answers would reflect their first-person attitudes towards engaging in incest with an opposite-sex sibling. Comparing responses with subjects' autobiographical data revealed a significant correlation between the amount of time spent in co-residence with an opposite-sex sibling and the tendency to morally condemn third-party incest. As predicted by parental investment theory, the effect was stronger for females than for males. Fessler and Navarete (2004) replicated these results in a study of 233 American undergraduates using an analogous method. Both groups of investigators interpreted their findings as corroborating WH.

Groundbreaking though these studies are, inferences made by the investigators are open to question on three major counts. First, it is not clear that aversion to the thought of others committing incest is an accurate indicator of an aversion to engaging in incest oneself. Lieberman, Cosmides and Tooby note this difficulty, which was first raised decades ago by Westermarck's critics, and reasonably note that the relationship *might* hold. However, that the relationship "might" hold is too delicate a support to bear the full epistemic weight of their claims. Second, even if we can infer disapproval of first-party incest from subjects' moral condemnation of third party incest, we cannot reasonably infer that subjects did not have incestuous *desires*. After all, it is possible (and indeed common) to morally disapprove of one's own desires. Third, even if subjects are not aware of incestuous desires, but are conscious only of repugnance and disapproval, it is possible that they are self-deceptively unaware of desiring that which they condemn. The classic study by Adams, Wright, and Lohr (1996) focusing on aversion to homosexuality provides an interesting and useful comparison. These investigators found that homophobic males who reported that they were repelled by homosexual activity nonetheless showed signs of sexual arousal when viewing films of male-on-male sexual activity. If Adams, Wright, and Loar had contented themselves with subjects' verbal reports of their conscious attitudes, they would have reached a different conclusion. Self-reports may not be reliable tools for accessing emotionally charged aspects of human nature that are likely to arouse mental conflict. It is possible that some form of self-deception was at work in subjects' and physiological measurements of their responses to reading the incest vignette might either

strengthen or undermine their case. The studies by Lieberman, Cosmides, and Tooby and by Fessler and Navarete suggest that sibling co-residence during childhood is correlated with the tendency to express moral disapproval of third-party sibling incest. Whether this is best accounted for by WH, or simply indicates a causal relationship between sibling co-residence and moral disapproval of sibling incest (possibly coupled with self-deception) is not yet clear.

Acceptance of a scientific hypothesis is evidentially warranted only if it explains and correctly predicts more observations than its rivals do. It is important, then, to generate plausible alternatives to WH and find ways to pit the hypotheses against one another in *experimentae crucis*. In the remainder of this paper, I introduce two contenders that not only explain the kibbutz and *simpua* marriage data, but also make additional predictions and are free from some of the explanatory constraints inherent in WH.

Both hypotheses draw on the phenomena of maternal certainty and paternal uncertainty. Judgments of relatedness between mothers and infants are far less likely to be in error than any other judgments of kinship. Women are sometimes sexually unfaithful to their partners, and secretly have intercourse with other men. It follows that no man can be certain that he conceived his mate's children. A woman can be certain that any child to whom she gives birth is genetically her child. A woman can be certain that her children are related to her by a coefficient of at least .5 ("at least" because if they are the product of an incestuous mating, r will be greater). Men have no guarantee that their mate's children are related to them at all. Given that motherhood is virtually certain, the most effective kin-identification strategy for a human infant would be to first identify its mother, and then use this identification to extrapolate to other kin. This is the basis for an alternative to WH that I call the Shared Mother Hypothesis (SMH).

The offspring of many mammals learn to identify their mother shortly after birth, and it is reasonable to conjecture that, like them, some mechanism causes a human infant to identify an adult as its mother. This mechanism would need to be sensitive to the quality and quantity of the infant's interactions with the mothering person during a critical period of development. Having identified its mother, it may be that the infant's mind is designed to be responsive to mate-like and kin-like interactions between its mother and others. Given that anyone whom one's mother treats in a mate-like fashion during early childhood is likely to be one's father, and anyone whom one's mother treats in an offspring-like fashion during early childhood is likely to be one's sibling, these early impressions might form the basis for post-pubertal sexual aversions to ostensible kin. So, unlike WH, SMH explains why sons are averse to sexual relations with their mothers, and daughters with their fathers. Lieberman, Tooby and Cosmides (2007) have recently advanced a strikingly similar hypothesis to partially account for sexual aversion between siblings.ⁱⁱ

How does SMH handle the kibbutz and *simpua* marriage data? The *simpua* marriage data are straightforward. Both prospective husband and adopted future bride share the same "mother" during the critical first three years of life. SMH predicts that this is sufficient to cause them to inhibit sexual attraction to one another. Encompassing the kibbutz data is a little more difficult, but also more interesting. Remember that from an early age, kibbutz children were required to live in a *kvutza* under the care of a *metapelet*—a female caretaker—and had little contact with their own parents. It is not far-fetched to suggest that

these children maternally imprinted on their *metapelet* rather than on their genetic mothers. This would imply that, in consequence of the offspring-like relationship between the *metapelet* and the other children, all of the children in the peer group would respond to one another as siblings. Descriptions of the behavior of kibbutz children dovetail with this hypothesis. For example, Spiro (1958) writes in his classic *Children of the Kibbutz* that:

Since the typical nurse is nurturer and comforter, it is small wonder that, as one nurse expressed it, “The children are very tied to the people who take care of them.” There are times when a child may prefer his nurse to his own mother. Moreover, there is evidence to indicate that some children would like to combine mother and nurse in one person. Children, for example, will unwittingly address the nurse as “Mother,”.... Sometimes children deliberately put the nurse in the place of either parent. One nurse reports that her charges often tell her, “You are my mother”.... The children not only love their nurse, but they are jealous of the love that she displays towards other children. One of the few sources of competition within the *kevutza* is competition over the nurse; for from the earliest ages, the children attempt to monopolize her attention, her affection, or her lap (pp. 72-74).

Alternatively, it might be that these children were thrown into a state of *maternal uncertainty*. The lack of a single, consistent, unambiguously maternal figure might create a situation in which most of the adults in the kibbutz environment are treated as potential kin, resulting both in high levels of in-group altruism and a global tendency toward sexual aversion. This would explain an aspect of Shepher’s data that is inconsistent with WH. According to Shepher (1983):

Marriage at Ya’ara revealed [that].... No one married within the peer group. There were no marriages between the peer groups either, except in one case in which the male had joined the kibbutz at the age of seven. Most marriages were to partners outside the kibbutz, either from other kibbutzim or from the cities (p. 57).

WH predicts sexual aversions between members of the same *kvutza* but not between members of different *kvutza* within the same kibbutz. In contrast, the version of SMH invoking maternal uncertainty predicts both.

SMH may also be consistent with the studies by Lieberman, Tooby, and Cosmides (2003) and Fessler and Navarete (2004). If the results of these studies are construed as showing a correlation between sibling childhood co-socialization and sexual aversion they might equally be interpreted as showing a correlation between siblings’ childhood experience of a common maternal figure and sibling sexual aversion.

As attractive as SMH seems, it also has significant shortcomings. One of these is the failure to explain parents’ avoidance of incest with their offspring, and significantly older siblings’ avoidance of incest with younger siblings. Also, like WH, SMH does not have the resources to explain the differential incidence of father-daughter, sibling-sibling and mother-son incest, unless we complicate the theory by stipulating that the mother’s behavioral markers of one’s probable father and siblings activate different intensities of sexual aversion. These problems are similar in kind, if not in degree, to the shortcomings of WH: although SMH accounts for everything that WH accounts for, plus a bit more, there are additional significant features of the incest story that are addressed by neither

hypothesis.

If one were to go about designing an incest-avoidance mechanism, what would be the best way to proceed? What would be the optimal design for such a mechanism? Given that the risk of inbreeding depression is proportional to the size of the coefficient of relatedness, we would want a mechanism that calibrates the intensity of sexual aversion to the size of the coefficient of relatedness. For this to happen, we would need to design a mechanism that is sensitive to degrees of relatedness, a mechanism able to adjust the intensity of sexual avoidance to the probable coefficient of relatedness (r) of the parties concerned. Let us call this the “naïve model” of incest-avoidance. The behavioral consequences of this arrangement would be consistent with what we know about the epidemiology of incest. Although there are no reliable figures on the relative incidence of different forms of incest, sexual relations between cousins are more common and more widely tolerated than sexual relations between parents and offspring or between siblings. However, the model fails when we try to make more fine-grained predictions. Given that parents are related to their offspring and siblings are related to one another by an average r of .5, we would expect mother-son, father-daughter and sibling-sibling incest to be equally common, but they are not. Father-daughter incest is thought to be the most common of the three, mother-son incest the least common, while sibling-sibling incest occupies an intermediate position (Justice and Justice, 1979; Seemanova, 1971; Weinberg, 1955).

One way to reconcile the naïve model with reality is to introduce supplementary hypotheses. For example, we might invoke Parental Investment Theory to account for the differential incidence of father-daughter and brother-sister incest on the one hand, and mother-son incest on the other. We would then require an additional hypothesis—for example, WH—to account for the (purported) differential frequency of father-daughter and brother-sister incest. This account would fulfill its explanatory aim at the price of invoking three distinct incest avoidance mechanisms operating in tandem. Although there is no reason a priori to rule out explanatory models invoking multiple causal mechanisms, it is a time-honored scientific rule of thumb that simple hypotheses are preferable to complicated ones with the same explanatory/predictive power. All things considered, then, the best account of incest avoidance should be the simplest one with the greatest explanatory power. The naïve model of incest avoidance is complicated by the fact that assessments of relatedness are not always straightforward. In species with internal fertilization, cryptic ovulation and in which females engage in extra-pair mating—species like our own—judgments of paternity are precarious. A woman can be certain that she is related to her offspring by an average coefficient of relatedness of at least .5, and her offspring can have the same degree of confidence in their relatedness to her. This contrasts sharply with the situation of the male, who can never be certain that his mate’s children are related to him at all. Paternal uncertainty has a knock-on effect on other kin relationships. Most immediately, it impacts on considerations of relatedness between siblings. Barring adoption, each of us can be certain that we are related to our mother’s other children by at least .25, but the fact that we cannot be certain of having the same father renders the likely degree of relatedness indeterminate. Similar considerations apply to grandparents, uncles, aunts, cousins, and so on. Given this uncertainty, it becomes important to recognize the distinction between genuine incest and ostensible incest (hereafter, o-incest). The only

forms of heterosexual incest that are *not* merely ostensible are mother-son and grandmother-grandson incest. Full sibling incest is ostensible because, given the uncertainty about their paternity, siblings cannot know whether they are related by an average coefficient of .5 (uterine-agnatic) or .25 (uterine *or* agnatic). Ostensibly uterine siblings (maternal half-siblings) can count on being related to one another by at least .25 and possibly by .5 (due to paternal uncertainty, they might in fact be full siblings). Agnatic siblings (paternal half-siblings) however, have an average coefficient of relatedness of either .25 or 0. Ostensibly full siblings might even be related to one another by a factor greater than .5 if they are products of an incestuous mating between their mother and one of her kin!ⁱⁱⁱ

Given that the risk of inbreeding depression in an offspring is proportional to the degree of relatedness between its parents, it follows that paternal uncertainty also makes for uncertainty about the likelihood of inbreeding depression in consequence of ostensible full sibling incest and ostensible father-daughter incest. In light of this, we would want to design an incest-avoidance mechanism capable of more nuanced responses to potential mates than either the childhood-familiarity-breeds-sexual-contempt mechanism suggested by Westermarck or SMH are capable of. Such a mechanism—or suite of mechanisms—would have greater biological utility than just determining whom to avoid mating with. Judgments of relatedness are also vital for determining the circumstances under which acts of altruism are likely to enhance one's inclusive fitness.

In Haldane's classic formulation of the genetics of altruism he invites the reader to “suppose that you carry a rare gene which affects your behavior so that you jump into a flooded river and save a child, but you have one chance in ten of being drowned, while I do not possess the gene, and stand on the bank and watch the child drown.”

If the child is your own child or your brother or sister, there is an even chance that the child will also have this gene, so five such genes will be saved in children for one lost in an adult. If you save a grandchild or nephew the advantage is only two and a half to one. If you only save a first cousin, the effect is very slight. If you try to save your first cousin once removed the population is more likely to lose this valuable gene than to gain it.

This sounds a good *prima facie* argument for the plausibility of the existence of cognitive mechanisms geared towards estimating coefficients of relatedness. However, in his very next breath, Haldane goes on to express skepticism about this very possibility.

But on the two occasions when I have pulled possibly drowning people out of the water (at an infinitesimal risk to myself) I had no time to make such calculations. Paleolithic men did not make them. It is not easy to see how, except in small populations, such genes could have been established. Of course the conditions are even better in a community such as a beehive or ants' nest, whose members are all literally brothers and sisters. (Haldane 1955, p. 44).

What is the evidential basis for Haldane's claim that Paleolithic men did not calculate their coefficients of relatedness with potential beneficiaries of altruistic acts? Perhaps what he had in mind is that it is simply implausible to think that prehistoric hominins *consciously* worked out degrees of relatedness before acting. However, conscious calculation is not the

only possibility. If Haldane were faced with the dilemma of rescuing either one of his own children or rescuing the child of a stranger, I bet that he would feel an overwhelming urge to save the life of his child, and that he would allow the stranger's child to drown. I do not think, though, that he would consciously work out the relevant coefficients of relatedness before leaping into the water! From his subjective vantage point he would simply act on the basis of his feelings, but from a more objective, biological standpoint, these feelings are biased in favor of Haldane's reproductive success. This admittedly crude example suggests that there may be non-conscious mechanisms at work when genetic relatedness biases our attitudes towards others. More specifically, there may be unconscious cognitive mechanisms that automatically estimate degrees of relatedness without conscious effort or awareness. Shifting the focus from altruism to incest-avoidance, it is obvious that a species equipped with systems for discriminating probable degrees of relatedness would have some protection against costs incurred by paternal uncertainty, which would cause individuals to forego mating opportunities with individuals who might otherwise be regarded as out-of-bounds. If this is right, and if such system exists, we should expect the relative frequency of the various forms of incest to inversely mirror the actual, rather than the merely ostensible, degree of relatedness between partners. Factoring in paternal uncertainty, we can predict the relative incidence of 5 forms of o-incest: mother-son, uterine-agnatic sibling, uterine sibling, agnatic sibling, and father-daughter incest. The reliability maternal relatedness makes it virtually certain that mothers are related by .5 to their sons. Ostensibly uterine-agnatic siblings are likely to related by either .5 or .25, depending on whether *in fact* they possess a common father. I say 'are likely' because it is possible for siblings to be fathered by a genetic relative of either their mother or their ostensible father. I will ignore these complexities in the present discussion. Ostensibly uterine siblings are related by either .25 or .5, depending on whether they were in fact fathered by different males. Fathers and their ostensible daughters are related either by .5 or not at all. Finally, agnatic siblings are related either by a factor of .5 or—thanks to paternal uncertainty—not at all. These relationships are displayed in Table 1. When two figures appear in the 'relatedness' column, the first corresponds to r in circumstances of genuine paternity and the second to r in circumstances of merely ostensible paternity.

Table 1: Relatedness, Risk and Probable Relative Frequency of Incest

Type	Relatedness	Risk	Frequency
Mother-Son	$r = .5$	Greatest	Least
Uterine-agnatic siblings	$r = .5$ or $.25$		
Uterine siblings	$r = .25$ or $.5$		
Father-Daughter	$r = .5$ or 0		
Agnatic siblings	$r = .25$ or 0	Least	Greatest

How does this model line up with reality? Although there are no reliable data on the epidemiology of incest, it is widely thought that mother-son incest is least frequent, father-daughter incest the most frequent, and sibling incest intermediate between the two. There is a widely accepted biological theory that can *almost* account for the broad

consistency between these coefficients of relatedness and accepted views on the relative incidence of various forms of incest. We need only invoke WH in conjunction with parental investment (PI) theory. WH would inhibit sexual activity between co-reared siblings, and PI would account for the low incidence of mother-son incest as compared to father-daughter incest. However, WH plus PI cannot account for the differential incidence of father-daughter incest as compared to sibling-sibling incest. This might be remedied by adding the principle that fathers are more dominant than sons, and are thus more able to override the female reticence postulated by PI. I will henceforth refer to the conjunction of WH with parental investment theory and paternal dominance as WPD.

The obvious alternative to WPD is that there may *in fact* be a causal relationship between inbreeding-avoidance and the discrimination of degrees of relatedness. WPD clearly specifies three independently plausible and evidentially well-supported biological principles, but it also invokes more mechanisms to account for the effect than the hypothesis that incest avoidance is directly linked to perceived degrees of relatedness. The latter approach uses just one principle to explain far more, but—at least at this point in the discussion—it is unacceptably vague. To have grounds for taking it seriously we must (a) provide an empirically tested or testable account of the mechanism for detecting degrees of relatedness, and (b) deduce from it a set of empirically testable predictions, which, if corroborated, would exclude the competing hypothesis. Several of these predictions have already been itemized in Table 1, which specifies distinctions between the relative incidence of three forms of sibling incest that are not predicted by WPD. Below are five additional predictions, none of which can be deduced from WPD.

First, in populations where non-incestuous extra-pair copulations are prevalent, and paternal uncertainty is consequently high, the rate of o-incest between fathers and daughters and between siblings will be higher than in populations where extra-pair copulations are less prevalent (controlling for the rate of extra-pair copulations in the population as a whole).

Second, there is a negative correlation between paternity confidence in a given population and the incidence of father-daughter, agnatic sibling and agnatic-uterine sibling o-incest, but *not* with uterine sibling and mother-son incest.

Third, the lower the level of paternal confidence in a population, the less altruistically fathers are inclined to behave towards their ostensible offspring, and the lower the inclination for ostensible full siblings to behave altruistically towards one another. However, there should be no diminution in altruistic behavior between a mother and her offspring, or between uterine siblings as compared to populations with lower levels of non-paternity. We would also expect to find a higher than normal level spousal violence (as a mate-guarding effort) than is found in populations with higher levels of paternal confidence. The correlation between incest and familial “dysfunctionality” has been noted in the clinical literature (Erickson, 2005), but whereas it has been assumed that the latter causes the former, the kin discrimination hypothesis suggests that the causal relation may run in the opposite direction.

Fourth, if WH is the best explanation of sibling incest avoidance, the incidence of incest between uterine and uterine-agnatic siblings should be similar. In contrast, the present hypothesis predicts that incest between uterine siblings is substantially more

frequent than incest between uterine-agnatic siblings. Both hypotheses predict that the highest rate of sibling incest is between agnatic siblings (see Shepher, 1983).

Fifth, because there are two degrees of paternal uncertainty separating paternal grandfathers from their granddaughters, but only one degree of paternal uncertainty separating maternal grandfathers from their offspring, the present hypothesis predicts that paternal grandfathers engage in incestuous acts with their granddaughters more frequently than maternal grandfathers do (controlling for female dispersal).

If incest avoidance is mediated by kin recognition mechanisms, how might these operate? Visual or olfactory phenotype matching are possibilities (Hauber and Sherman, 2001; Lacy and Sherman, 1983). The idea that olfaction plays a role in human kin recognition is centuries old. “Nature itself,” wrote Peter Damian in the 12th century, “...exudes a sort of odor of natural community that exists between relatives” (Damian, 1844-64). There is evidence that phenotypic olfactory matching plays a role in human kin recognition (Mateo and Johnston, 2000; Porter and Moore, 1981; Porter, 1998-99, Weisfield, Czilli, Phillips, Gall and Lichtman, 2003). Weisfield et al. also showed olfactory recognition of relatedness of opposite-sex but not same-sex siblings, an aversive olfactory response between opposite-sex siblings and father-daughter pairs, and discrimination between full and half-siblings. Porter (1991) has shown that mothers can recognize the smell of their children when they are only one day old. However, it is not clear that olfactory recognition is a form of phenotype matching. It may be that we learn to recognize kin by their smell rather than learning by their smell that they are kin. The prospects for visual phenotype matching are more promising. Theoretically, our visual acuteness and our use of vision to mediate social perception (e.g., facial expressions of emotion) gives visual phenotype matching a measure of *prima facie* plausibility as a mechanism for estimating coefficients of relatedness. More importantly, there is a growing body of research suggesting that *Homo sapiens* use visual cues for making judgments about kinship. Maternal relatives tend to remark on the visual resemblance between the newborn and father, as if to convince the latter that the offspring is his (Daly and Wilson, 1982; McLain et al., 2000; Regalski and Gaulin, 1991). Several studies show that males are inclined make investment decisions on the basis of unconsciously discriminated facial resemblance to themselves (DeBruine, 2002, 2004, DeBruine, Jones and Perrett, 2005, Platek et al., 2002, 2003, 2004, 2005). Platek and his coworkers simulate relatedness by morphing photographs of children’s faces to resemble experimental subjects. They found that resemblance influences male subjects when simulated $r \geq .25$. A study by Burch and Gallup (2001) suggests a direct correlation between paternal physical abuse and facial resemblance. DeBruine (2005) has demonstrated that when one modifies a photograph of a member of the opposite sex to make them resemble the subject, the face is rated as trustworthier but less sexually attractive. This is precisely what the hypothesis that kin recognition is mediated by visual phenotype matching would lead one to expect. When we see a member of the opposite sex whose face resembles our own sexual desire is inhibited and altruistic impulses are augmented.

In experimental protocols like those used by Platek and DeBruine, in which photographs of faces of third parties are morphed to resemble the subjects it is reasonable to ask *whose* phenotype subjects are matching the faces with. If visual phenotype matching

is an adaptation, we should not assume that it is directly self-referential. It is unlikely that ancestral humans had access to accurate information about their own facial appearance. The first artificial mirrors, made of polished obsidian, were produced around 6200 BC at Çatal Hüyük in what is now Turkey (Pendergrast, 2003), and there were no artificial mirrors available earlier in prehistory when our ancestors would have evolved the capacity for visual phenotype matching. Might they have acquired a conception of their own facial appearance by gazing at their reflections in the natural mirror of still water? Platek (2003) argues that this is unlikely both because water is rarely sufficiently still enough to produce a high-fidelity image, and water's motion and murkiness normally distort the reflection. Platek notes that the water-reflection hypothesis may account for selection against mirror self-recognition in gorillas, as those animals that stayed by the waterside to gaze at their image were at risk of predation by crocodilians. Even today, several thousand sub-Saharan Africans are devoured by crocodiles every year (Hart and Sussman, 2005) and watering holes are also magnets for dangerous terrestrial predators. Ancestral humans may have spent as little time as possible lingering beside still water. Platek suggests that hominins may have learned what they look like by touching their own faces or by proprioceptive responses from the underside of the face. Active intermodal mapping has been invoked to account for autoscopic hallucinations and infants' ability to imitate others (Humphrey, 2005). The intermodal mapping hypothesis predicts that people who have never seen their reflection in a mirror will not be surprised when they see their reflection for the first time. The anthropologist Edmund Carpenter gives an account of such an experience in his fieldwork with the Biame, a remote tribe in New Guinea. The Biame did not live near still water, and although some men possessed mirror shards, which they used as reflectors, the shards were far too small to enable self-recognition (Carpenter, 1975). Carpenter writes that Biame tribesmen's first experience of their reflections in large mirrors "suggested this was a wholly new experience for them.... They were paralyzed: after their first startled response – covering their mouths and ducking their heads – they stood transfixed, staring at their images, only their stomach muscles betraying great tension...." (Pendergrast, 2003, p. 368). Carpenter's observations suggest that the intermodal mapping hypothesis may be incorrect.

A second alternative to WH, which I call the Maternal Phenotype Matching Hypothesis (MPMH), may have greater explanatory power than either WH or SMH. The hypothesis states that incest avoidance may be mediated by unconscious estimates of r based on the degree visual phenotypic resemblance between a potential sexual partner and one's own mother.

Let us suppose that kin discrimination is mediated at least in part by a form of visual phenotype matching that is not self-referential. How might it work? One possibility is for individuals to use family resemblance as a guide to genetic kinship by taking the facial appearance of close kin as a reflection of their own phenotype. On the face of it, this proposition sounds circular: the idea of "family resemblance" presupposes an awareness of kinship and so cannot be invoked as a means of discriminating kinship. Notwithstanding this objection, family resemblance can be used as a guide to kinship if at least one close relative is first identified by means other than phenotypic resemblance, and others are identified as kin by comparison with *this* individual's phenotype. Because of paternal

uncertainty, fathers would provide an uncertain standard for phenotypic comparison, and the knock-on effect of paternal uncertainty would also make siblings poor visual prototypes for judgments of kinship. By contrast, mothers provide a much more reliable reflection of one's own phenotype. Comparing the face of a prospective mate or coalition partner with one's mother's face may have been the best means available to our ancestors for visually discriminating degrees of relatedness. Siblings could then be identified on the basis of the phenotypic resemblance to one's mother.

If this is right, what might appear to be self-referential visual phenotype matching may be maternal-referential visual phenotype matching. In other words, although virtually all modern populations have access to artificial mirrors, the visually-sensitive cognitive mechanisms selected to mediate kin-recognition in the service of inbreeding avoidance may be sensitive *only* to the maternal phenotype. The maternal phenotype-matching hypothesis has both epidemiological and experimental ramifications. Epidemiologically, in addition to entailing the predictions already itemized, it predicts that paternal single-parent families with closely-spaced siblings there should, in cases where the mother has been absent from early in the elder sibling's life, be a greater incidence of sibling-sibling incest than in circumstances where the mother is present (the ideal test-cases would be heterosexual twins whose mother died or defected soon after their birth). Experimentally, MPMH suggests a novel interpretation of and improvement upon DeBruine's protocol. DeBruine morphed photographs of faces of persons of the opposite sex to resemble her subjects, and discovered a positive correlation between resemblance and perceived trustworthiness and a negative relationship between resemblance and sexual attractiveness. If the maternal phenotype-matching hypothesis is correct, then DeBruine's results may be attributable not to the resemblance between subjects and faces morphed to resemble them, but rather to the resemblance between the morphed faces and the faces of subjects' mothers. Replicating DeBruine's study using faces morphed to resemble subjects' mothers would allow a test of this hypothesis. If the maternal phenotype-matching hypothesis is correct, maternally morphed faces should elicit responses that are similar to but stronger than those elicited by the original protocol (sexual aversion varying negatively and trustworthiness varying positively with resemblance). Morphing faces to resemble subjects' fathers should not elicit significant effects.

Among the explanatory advantages of MPMH are its ability to account for the experimental results garnered by Platek and DeBruine, and its ability to predict differential rates of incest corresponding to widely accepted views on the relative incidence of father-daughter, sibling-sibling, and mother-son incest. One weakness of the hypothesis is that MPMH does not provide an explanation of why daughters do not pursue sexual relations with their fathers. Theoretically, fathers could compare their daughters' phenotypes with that of their own mother, but there is unlikely to be any special resemblance between a girl's maternal and paternal phenotypes. Some additional incest-avoidance hypothesis would have to be invoked to account for this. MPMH additionally predicts that the rate of incest between full siblings and maternal siblings should be equally infrequent, but that incest between paternal half-siblings should be considerably more common. It also predicts that children adopted at a young age are likely to have strong sexual aversions towards their adoptive siblings, but that adoptive siblings are less likely to be averse towards

sex with the person who has been adopted (in consequence, sex between “siblings” in cases where one has been adopted is likely to involve coercion of the adopted sibling). Finally, MPMH predicts that in cases of genetic incest, we are likely to discover either that the object of incestuous desire happens not to resemble the maternal phenotype (either due to genetic luck-of-the-draw or facial disfigurement) or that the perpetrator suffers from a deficit in the ability to identify subtle patterns of facial similarity.

If we are to give any *prima facie* credence to MPMH it must also be able to make sense of the kibbutz and *simpua* marriage data. It is difficult to make sense of the kibbutz data in light of MPMH unless we make the assumption already mooted in the discussion of SMH that child-rearing practices in the kibbutzim induced a state of maternal uncertainty in children. If this is right, kvutza children may have been unable to imprint on a single individual as mother and did not have a clearly defined maternal prototype to use as a phenotypic template for discriminating other kin. The hypothesis is not that kvutza children did not know who their parents were. Of course they did. My point is that the conditions that normally activate maternal imprinting mechanisms may not have been present, and under these circumstances sexual avoidance of everyone in the community might be the default position. Interpreting the *simpua* marriage data in terms of MPMH is both more straightforward and leads to a striking empirical prediction. The adopted future bride would presumably use her adoptive mother’s phenotype as a template for judging kinship, misidentify her prospective husband as a sibling (a person resembling her “mother”) and develop a sexual aversion towards him. But the picture looks very different from the prospective husband’s point of view. Using his actual mother’s phenotype, he would correctly identify his prospective bride as non-kin, and would not be expected to develop sexual aversions towards her (or, if there are secondary mechanisms at work, would not be expected to develop a sexual aversion towards her that is as powerful as the aversion that she develops towards him). Notwithstanding these explanatory virtues, if the studies by Lieberman, Tooby and Cosmides (2003) and Fessler and Navarete (2004) are best interpreted as showing a correlation between childhood co-socialization and sexual aversion, this result is unaccounted for by MPMH.

Conclusions

Scientific reasoning rests on the practice of testing competing hypotheses, and it violates sound scientific principle to accept as warranted an hypothesis that has not been tested against plausible competitors. Although widely embraced by evolutionary scientists, the Westermarck Hypothesis has not been so tested. Careful examination shows both that (a) the Westermarck Hypothesis cannot, on its own, account for all or even most of the data on human incest avoidance, and that (b) there are at least two competing hypotheses that may better account for the data, both of which entail empirical predictions that diverge from those deduced from the Westermarck Hypothesis. Of these the Maternal Phenotype Matching Hypothesis is the more powerful, and can be experimentally tested using variations on existing protocols.

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ⁱ Shortly after its introduction, the British anthropologist Sir James Frazer disputed Westermarck's thesis. "The law," he wrote, "only forbids men from doing what their instincts incline them to do.... Instead of assuming, therefore, from the legal prohibition of incest that there is a natural aversion to incest, we ought rather to assume that there is a natural instinct in favor of it." (Frazer, J.G., 1910, p. 97). Freud (e.g., 1913) agreed with Frazer, adding that human beings are both attracted to and repelled by incest, and that both

the attraction and the repulsion are biological dispositions (Badcock, 2002; Sulloway, 1979). Thornhill (1991) argues that in most societies incest taboos are restricted to preventing matings between cousins and in-laws. They thus pick up where the natural aversion to inbreeding leaves off.

ⁱⁱ Debra Lieberman called my attention to this paper just as I was making the final revisions to the present paper. A detailed discussion of the relationship between our hypotheses will be reserved for a future publication.

ⁱⁱⁱ The idea that paternal uncertainty may play a role in incest was apparently first mentioned by Joseph Shepher (1983) and elaborated more fully by David Haig (1999).