Does morality have a biological basis?
An empirical test of the factors governing moral sentiments relating to incest

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Kin-recognition systems have been hypothesized to exist in humans, and adaptively to regulate altruism and incest avoidance among close genetic kin. This latter function allows the architecture of the kin recognition system to be mapped by quantitatively matching individual variation in opposition to incest to individual variation in developmental parameters, such as family structure and co-residence patterns. Methodological difficulties that appear when subjects are asked to disclose incestuous inclinations can be circumvented by measuring their opposition to incest in third parties, i.e. morality. This method allows a direct test of Westermarck's original hypothesis that childhood co-residence with an opposite-sex individual predicts the strength of moral sentiments regarding third-party sibling incest. Results support Westermarck's hypothesis and the model of kin recognition that it implies. Co-residence duration objectively predicts genetic relatedness, making it a reliable cue to kinship. Co-residence duration predicts the strength of opposition to incest, even after controlling for relatedness and even when co-residing individuals are genetically unrelated. This undercuts kin-recognition models requiring matching to self (through, for example, major histocompatibility complex (MHC) or phenotypic markers). Subjects' beliefs about relatedness had no effect after controlling for co-residence, indicating that systems regulating kin-relevant behaviours are non-conscious, and calibrated by co-residence, not belief.

Keywords: kin recognition; kin selection; incest; inbreeding; Freud; Westermarck

1. INTRODUCTION

Perhaps the most substantial debate in human biology is over the degree to which natural selection among our ancestors had consequences that still pattern modern human behaviour. On the one hand, several leading evolutionary biologists have argued that selection has shaped even so seemingly human-specific a phenomenon as morality (Darwin 1871; Williams 1966; Hamilton 1975; Wilson 1975; Dawkins 1976; Alexander 1979; Sober & Wilson 1998). By contrast, for almost a century the consensus among mainstream social scientists has been that the capacity for culture insulates almost all human behaviour from regulation by adaptively specialized neural circuitry—or even that the evolution of a culture-absorbing brain was accompanied by the erasure of specialized circuitry, turning the human mind effectively into a blank slate (e.g. Harris 1968; Geertz 1973; White 1975; Sahlins 1976). On this view, our evolved neurocognitive architecture resembles a tape recorder in that it is designed to register an environmental signal (ambient culture) without introducing any content of its own.

As developed by evolutionary researchers, a competing view is as follows. (i) The neurally based learning capacities of humans include specializations that evolved among our foraging ancestors to solve the specific adaptive problems posed by the statistical and causal structure of the ancestral world. (ii) Because these specializations constitute at least part of the circuitry through which learning and development proceed, they introduce evolved content into the mind (motivations, concepts, regulatory variables, etc.) that predisposes the individual to behave in ways that would have been adaptive given the recurrent statistical structure of the ancestral world. (iii) These specializations influence the content of cultural elements that are acquired from and transmitted to other individuals in a way that reflects, to some extent, the design and operation of these evolved problem-solving circuits (Tooby & Cosmides 1992).

These two views make contrasting predictions. The blank slate/cultural determinist view predicts the unbiased adoption of ambient cultural signals, with evolved functional specializations playing no role in fixing cultural content or regulating culturally significant behaviour. By contrast, an evolutionary view predicts that our universal architecture plays a part in generating the cultural baseline and—more importantly for this study—that individuals will exhibit lawful departures from the baseline given by ambient culture. These departures can be predicted in detail by analysing (i) the functional logic of the evolved neural specializations involved, as they operate on the inputs provided by (ii) the conditions that each individual faces during development.

This debate can only be meaningfully advanced through conducting empirical tests that contrast cultural determinist predictions with predictions derived from specific models of adaptive specializations. Moral phenomena are particularly well-suited to serve as an arena for resolving this question, because morality is held by many social scientists to be the paradigm case of a cultural domain, free of 'biological' regulation, yet it also involves types of behaviours (sexuality, infidelity, altruism, reciprocity, kin interactions, and so on) about which evolutionary biol-

02PB0795.1

ogists have developed clear predictions. In this study, opposition to incest is used as a means to test hypotheses about the existence and functional architecture of the human kin-recognition system, an otherwise difficult enterprise in a species where ethics forbid life-changing experimental manipulations. At the same time, a quantitative investigation into the developmental regulation of opposition to incest offers the broader opportunity to evaluate empirically the hypothesis that morality is un-influenced by human evolutionary biology.

(a) Incest avoidance in humans

For a century, theories regarding incest avoidance have been central to the social and psychological sciences (Freud 1918; Levi-Strauss 1969; Arens 1986). A unifying theme among scholars of otherwise divergent views has been the rejection of so-called biological explanations for incest avoidance, that is, a rejection of the hypothesis that the human neurocognitive architecture contains circuitry that evolved specifically to inhibit sexual activity among closely genetically related family members. Although non-evolutionary theorists have usually been willing to grant that sexual motivations may be part of our evolved architecture, they typically maintain that such motivations are relatively indiscriminate before cultural or moral norms mould and direct them. Hence, traditional theories have generally maintained that individuals are sexually attracted to family members unless and until external social forces intervene, in the form of ambient cultural signals or social reactions, to repress the attraction or to render it private (Freud 1918; Levi-Strauss 1969). Whether the prediction is that children start off endogenously neutral to the prospect of sex with close family members, or positively inclined, cultural determinists are united in believing that this initial orientation is overwritten by social signals originating outside of the conditioned individual (for reviews, see Arens 1986; Fox 1980).

By contrast, evolutionary researchers (e.g. Shepher 1971; Bevc & Silverman 1993; Wolf 1995; Lieberman *et al.* 2003; and many others) have hypothesized that the human neural architecture includes a specialized kin-recognition system that evolved among our hunter-gatherer ancestors to serve at least two independent functions: (i) to regulate the allocation of altruistic and competitive effort in accordance with the selection pressures described by inclusive fitness theory (Hamilton 1964); and (ii) to inhibit sex among reproductively mature close genetic relatives because children produced from such unions would be less healthy. This health impairment arises because such children would express far higher rates of deleterious recessives (e.g. Adams & Neel 1967; Bittles & Neel 1994) and possibly suffer more damage from infectious diseases because the antagonistic coevolution of genotype-sensitive parasites selects against more genetically homogeneous sets of kin (Tooby 1982; Penn & Potts 1999).

(b) Human kin recognition and the opposition to incest

The hypothesis that humans have a kin-recognition system is worth investigating because there is growing experimental, genetic and field evidence indicating that many other species, including mammals, may have such systems (e.g. Pusey & Wolf 1996; Penn & Potts 1999). Exper-imentation on non-human mammals suggests that such mechanisms commonly operate through an individual imprinting on targeted properties of those it was raised with early in life. Even kin-recognition systems that operate by monitoring the glycoproteins encoded by the major histocompatibility complex (MHC) appear to use familial imprinting on the MHC haplotypes of co-reared individuals, rather than matching to the haplotypes in the self (Yamazaki *et al.* 1988; Penn & Potts 1998, 1999).

A second source of support comes from anthropological research into the Westermarck hypothesis. In 1891, using surprisingly modern selectionist reasoning, Westermarck (1921) proposed that humans have a mechanism whose evolved function is to discourage incest. It was proposed to operate by causing children who are raised together to develop a sexual disinterest in or aversion to each other, which is beneficial because co-socialized children are usually closely related. Several studies have been conducted that ingeniously exploit unusual child-rearing conditions in several cultures as natural experiments to test for the presence of the Westermarck effect (Shepher 1971; Wolf 1995; see also McCabe 1983). The most striking results come from Wolf's study of the occasional Chinese and Taiwanese practice of adopting a female infant or child to become, on maturity, a bride for a son. Through a heroic compilation of data on such marriages, Wolf demonstrated that co-rearing pairs of unrelated children as future spouses increases divorce rates and lowers fertility in the subsequent marriage, which would be the observable consequence of the lowering of sexual desire predicted by the Westermarck hypothesis. The effect was most clearly detectable when co-rearing occurred during the first 3 years of life.

The first goal of the study reported here is to provide new lines of evidence that complement these earlier studies, using methods applicable to any human population. The study was designed to see whether Wolf's and Shepher's results generalized beyond their exceptional study populations (e.g. unrelated individuals raised together in kibbutz creches or in infant adoptions for future marriage). Second, because the function of a kin-recognition system is, after all, tracking genetic relatedness, we wanted to test whether the Westermarck effect could actually be documented among related individuals. Third, we wanted to test whether it operated within family structures that are more similar to ancestral family compositions, and more cross-culturally typical of modern household compositions as well (to develop analyses of the epidemiology of risk). Fourth, we wanted to test for the presence of additional design features that selectionist considerations suggest might be a part of the human kin-recognition system, such as sex differences in sensitivity and the use of co-residence cues after infancy.

Finally, we wanted to test Westermarck's original hypothesis about the source of moral sentiments regarding incest (Westermarck 1921). Westermarck argued that moral sentiments opposing incest in third parties were generated by the same evolved programme that generated the personal aversion to incest, and could therefore explain cultural prohibitions as well as individual aversion. Hence, for example, co-residence with an opposite-sex sibling should lead to greater opposition to sibling incest in others. Westermarck's hypothesis about moral senti-

ments was widely dismissed—without being tested—because his link from individual preference about one's own behaviour to objecting to others' conduct was not logically necessary (e.g. Freud 1918; White 1975). Whether or not this is necessary, there are several reasons why evolved machinery generating opposition to incest for oneself might also generate opposition to incest in others. For example, because such a system evolved in a small-scale social world where most third parties that an individual could influence were kin, the system might be designed to interfere with incest in both the self and others (Lieberman *et al.* 2003). Alternatively, it might generate opposition to third-party incest as a by-product of self-regulation (e.g. an incest avoidance system interacting with an empathy system). It is easy, for example, to evoke a contagion disgust reaction by showing subjects scenes of third parties ingesting polluting substances. Although evaluating alternative theories about these pathways, and indeed, the varied evolutionary (and non-evolutionary) theories about the nature and function of morality is beyond the scope of this study, the hypothesis that there is a relationship between incest avoidance for oneself and one's moral sentiments about incest in third parties is worth testing, and could open a window to the design of the human kin-recognition system.

Accordingly, the model being tested here is as follows. The human kin-recognition system includes circuits that are specialized to take certain cues as input that were reliably correlated with genetic relatedness ancestrally. It operates on these cues with neurally embodied procedures that are designed to produce a regulatory variable associated with each known individual whose magnitude corresponds to genetic relatedness (a *kinship estimator*). During the life of the individual, this magnitude, in turn, is taken as an input to procedures that regulate kin-relevant behaviours adaptively, including the allocation of assistance, inhibition of violence and sexual attraction or aversion.

More specifically, the kinship estimator should be one input feeding into the procedures that produce another regulatory variable, a *sexual value estimator*. The function of this magnitude is to regulate motivationally how to make trade-offs that include potential sexual behaviour with a specific individual, including how much effort to expend either to achieve or avoid a mating with a particular person. When the value is positive and high, the individual is motivated to expend substantial effort to obtain a mating with the person. When the value is negative and high (as is usually the case with incest inside the nuclear family), the individual is motivated to expend substantial effort to avoid such matings. In particular, when the kinship estimator between the self and a specific person is high, it should downregulate the sexual value estimator for that person correspondingly.

Kin recognition is a problem in Bayesian information engineering, and so a key question is, what cues did natural selection design the system to take as input? The recurrent statistical structure of the species' ancestral world created ecological relationships between cues and information that offered an array of possibilities (breast-feeding, mating behaviour, patterns of parental investment, eating together, etc.). The utility of different cues would vary on a perspective-specific basis (e.g. older siblings could potentially witness the birth and nursing of their younger siblings, but not the reverse). The evolution of a kin-recognition system depended on selection isolating cues that (i) provided probabilistic information that successfully predicted relatedness; (ii) were stable enough across generations to provide sufficient directional selection to build the adaptation; and (iii) could be detected at sufficiently low cost.

For children, one potential cue that fits these criteria well is the duration of co-residence during periods of parental investment. This is the cue that we concentrated on, given previous results. It would have been reliable because, among foragers, children maintain close association with their parents during childhood (and hence with their siblings). Moreover, the fusion–fission patterns of aggregation typical of foragers are shaped by a larger encompassing structure of adult relatedness (e.g. adult siblings and other close kin often prefer inhabiting the same bands, and if not, visit each other frequently, creating secondary patterns of relatedness-scaled exposure among cousins, aunts, uncles, nieces and nephews, and so on (see Kelly 1995)). As a result, the regularities of human motivational systems impose a relationship across generations in which the duration of childhood co-residence predicts greater genetic relatedness. If this is true, the relationship between genetic relatedness (which is unobservable) and the duration of co-residence (which is observable) should still be present even in modern environments (for parents, offspring, full or half-sibs; differences between ancestral and modern environments are likely to be greater for aunts, uncles, cousins and other members of the extended family).

If this model is correct, then clear relationships should be detectable between cues that the kin-recognition system uses to compute the kinship estimator, and the degrees of aversion (or attraction) that subjects feel towards sex with various individuals. Natural variation in household composition constitutes a natural experiment that allows quantitative relationships between possible cues and sexual aversion to be identified, and hence to test hypotheses about the cues that the human kin-recognition system uses. However, subjects' direct reports of their own opposition (or lack thereof) to incest with various family members are subject to methodological difficulties, including the sensitivity of getting subjects honestly to disclose such sentiments, the social undesirability of admitting attraction to incest, the fact that ceiling effects on fixed scales can mask major variation, and so on. By contrast, the measurement of moral opposition towards third-party incest, as distinct from personal incestuous inclinations, offers a way round these methodological problems. Subjects are more willing to report different intensities of response to various third-party moral transgressions. At the same time, this method allows the study to zero in on one of the most significant questions that biologists, psychologists and anthropologists have about morality: is an individual's morality adopted unchanged from the surrounding culture?

Accordingly, the design of this study involves using judgements by subjects of the moral wrongness of various acts by third parties to explore which cues are used by the kin-recognition system, and whether adaptively parameterized individual dispositions shape moral sentiments. Finally, if—as cultural determinists maintain—the human mind is designed to base its moral judgements on ambient

cultural signals, then there should be no systematic relationship between childhood co-residence with siblings and the opposition to incest.

Using this logic, the following study was designed and conducted.

2. METHODS

(a) *Subjects*

There were 186 subjects (102 female and 84 male), all undergraduates at the University of California, Santa Barbara (age (years) mean = 21.5, s.d. = 4.21, range of 18–47). They were recruited from undergraduate anthropology and psychology courses during the autumn quarter, 1997.

(b) *Material*

The survey developed for this study contained questions regarding family attributes, personal attitudes toward sexual behaviour, childhood activities with each sibling, and length and age range of co-residence with all family members. In addition, subjects were asked to rank-order 19 acts from least morally wrong to most morally wrong. All 19 items depicted third-party actions, including marriage and sex between family members as well as other social transgressions such as a husband killing his wife, smoking dope and child molestation. The scale of moral wrongness was designed to measure subjects' moral judgements of other people's behaviour. Males and females were presented with the same acts in the same randomized order. Only subjects who rank-ordered all 19 acts on the scale were included in the data analyses. The dependent measure was the average rank-order of the moral wrongness associated with both third-party sibling incestuous behaviours: consensual sex between a brother and sister and brother–sister marriage. We have labelled this variable MW_{sib}.

The independent measures indexed length of co-residence with opposite-sex siblings. In addition to the childhood age range of 0–10, which has been hypothesized to include the critical years for the development of a sexual aversion towards a sibling (Wolf 1995), we also focused on total length of co-residence between 0–18 to see whether additional years of co-residence beyond early childhood contribute to the level of moral wrongness associated with third-party sibling incestuous acts, MW_{sib}.

Because some subjects had more than one opposite-sex sibling, we created co-residence variables based on summing the years of co-residence that an individual experienced with all opposite-sex siblings. As before, one variable summed co-residence years that the focal individual experienced between the ages of 0 and 10 years, and the other between 0 and 18 years (e.g. a male with two older sisters who resided with each for all 18 years between *his* ages of 0 and 18 would register as co-residence of 36 years between the ages of 0–18, and co-residence of 20 years between the ages of 0–10). These composite co-residence variables were used in analyses involving third-party moral wrongness; additional analyses were performed that controlled for the independent effect of the number of opposite-sex siblings present in the family. This composite score was used because third-party moral wrongness more plausibly reflects total exposure to all opposite-sex siblings, and there were no grounds for selecting one particular sibling over another when there were more than one.

Another important variable was the coefficient of relatedness between siblings ($r = 0$ was assigned for step and adopted siblings; 0.25 for half-sibs, and 0.5 for full siblings). (For populations like ours, reported kinship reflects genetic relatedness in 95–98% of cases (MacIntyre & Sooman 1991; Sykes & Irven 2000), thus this variable indexes both genetic relatedness and subjects' beliefs about it.) Again, for moral wrongness analyses, we calculated a score for an individual that summed the coefficients of relatedness for all opposite-sex siblings.

To determine whether parental and personal attitudes toward sexual behaviour influence moral sentiments regarding third-party incest, we included in our analyses variables measuring perceived parental attitudes towards sexual behaviour and the subject's attitude towards sexual behaviour. All data analyses were carried out using SPSS. Unless stated otherwise, all analyses are one-tailed. The rs are all Pearson correlation coefficients, because these allow comparisons once other variables have been controlled for. Though data were normally distributed, the more conservative non-parametric Spearman rho statistics were also calculated and gave similar results: the effect sizes were greater than or equal to the comparable Pearson zero-order correlations.

(c) *Procedure*

Subjects were given an anonymous paper and pencil questionnaire to complete. Before any students filled out a survey, they were informed that many of the questions pertained to sexual behaviour between family members, and that they were free not to complete the survey. Participants were further asked to stop taking the survey if at any time they felt disturbed or upset by the content of the questions. As a precaution, the telephone number of the campus counselling centre was provided for all students.

3. RESULTS

(a) *Is length of co-residence correlated with degree of relatedness?*

Yes. Selection for a kin-recognition system that uses co-residence as a cue depends on there having been a substantial correlation between relatedness and co-residence. This assumption cannot be directly tested in ancestral populations, but one can see whether it holds today. It does: using each opposite-sex sibling pair as a data-point ($n = 157$), the correlation between length of co-residence between ages 0–18 and degree of relatedness was $r = 0.71$ ($p < 0.001$; for childhood years, 0–10, $r = 0.70$, $p < 0.001$). Because each sibling pair was a data-point, this correlation reflects both within- and between-family, variation—an appropriate measure, given that the function of the system is to discriminate degrees of kinship in the context of a multi-family network.

(b) *Does length of co-residence with opposite-sex siblings affect moral judgements regarding third-party sibling incestuous behaviour?*

Yes. There were significant positive correlations between co-residence and judgements of moral wrongness of third-party sibling incest (MW_{sib}) for all subjects with an opposite-sex sibling, as well as for males with sister(s) and females with brother(s) when analysed separately (see table 1, (*a*) entries). This held for both intervals of co-residence (0–10 and 0–18). The effect size was largest for men with sisters, computed over the 0–18 age interval ($r = 0.40$, $p < 0.001$).

The clearest effect of length of co-residence on MW_{sib} can be seen when subjects who did not reside at all with

Table 1. Moral wrongness associated with third-party sibling incestuous behaviours.

	total years of co-residence between ages 0–10	total years of co-residence between ages 0–18
(*a*) all subjects with an opposite-sex sibling (*n* = 112)	0.24**	0.29***
(*b*) controlling for sexual orientation (*n* = 112)	0.24**	0.29***
(*c*) controlling for degree of relatedness (*n* = 112)	0.16*	0.23**
(*d*) controlling for perceived parental attitude (*n* = 108)	0.30***	0.32***
(*e*) controlling for subject's sexual attitude (*n* = 110)	0.25**	0.29***
(*f*) controlling for number of opposite-sex siblings (*n* = 112)	0.22**	0.28***
(*a*) males with a sister (*n* = 46)	0.29*	0.40**
(*b*) controlling for sexual orientation (*n* = 46)	0.27*	0.39**
(*c*) controlling for degree of relatedness (*n* = 46)	0.19	0.37**
(*d*) controlling for perceived parental attitude (*n* = 45)	0.36**	0.48***
(*e*) controlling for subject's sexual attitude (*n* = 46)	0.27*	0.39**
(*f*) controlling for number of sisters (*n* = 46)	0.21	0.36**
(*a*) females with a brother (*n* = 66)	0.23*	0.23*
(*b*) controlling for sexual orientation (*n* = 66)	0.23*	0.23*
(*c*) controlling for degree of relatedness (*n* = 66)	0.17	0.18
(*d*) controlling for perceived parental attitude (*n* = 63)	0.23*	0.21*
(*e*) controlling for subject's sexual attitude (*n* = 64)	0.25*	0.24*
(*f*) controlling for number of brothers (*n* = 66)	0.24*	0.24*

* $p \leqslant 0.05$, ** $p \leqslant 0.01$, *** $p \leqslant 0.001$.

their opposite-sex sibling(s) are compared with subjects who did reside with their opposite-sex sibling(s). The moral wrongness judgements for sibling incest were, on average, two ranks higher for subjects who resided with their opposite-sex siblings than for those who did not (mean ± s.d. = 11.52 ± 2.55 versus 9.41 ± 3.32); this difference was significant ($t_{115} = 2.54$, $p = 0.006$, effect size $r = 0.23$).

It is possible that one's sexual orientation affects the degree of sexual aversion felt towards opposite-sex siblings. The correlations in table 1 ((*b*) entries) clearly show that the relationship between length of co-residence and MW_{sib} stays the same once sexual orientation is controlled for. Nevertheless, all subsequent data analyses control for this variable.

(c) *Which variable better predicts moral wrongness of third-party sibling incest: co-residence or degree of relatedness?*

Above, we showed that co-residence time for an opposite-sex sibling pair was highly correlated (0.71) with that pair's degree of relatedness. But degree of relatedness—itself an unobservable property—is also correlated with other potential cues to kinship: culturally transmitted beliefs about who counts as a sibling, the olfactory signature of an MHC similar to one's own, etc. If one of these other cues—and not co-residence—is a primary trigger for kin recognition, then degree of relatedness should predict moral wrongness of sibling incest even after the effects of co-residence are statistically removed.

It does not. There is a correlation between degree of relatedness and MW_{sib} ($r = 0.18$, $p = 0.028$, $n = 112$; this controls for sexual orientation), although one smaller than that for co-residence (0.18 versus 0.29). This effect disappears entirely, however, once the effects of co-residence

are statistically removed (controlling for co-residence for ages 0–18: $r = -0.07$, $p = 0.24$; for ages 0–10: $r = -0.01$, $p = 0.48$). In other words, degree of relatedness does not independently predict moral wrongness for sibling incest.

By contrast, length of co-residence continues to predict MW_{sib}, even after the effects of degree of relatedness are statistically removed (see table 1, (*c*) entries). Indeed, controlling for this variable reduces the effect sizes by very little: they are 78–82% of the size of the simple correlations, depending on whether one is looking at all subjects (0.23 versus 0.29), or at men and women separately.

Thus, whereas both predictor variables—co-residence and degree of relatedness—show a simple correlation with MW_{sib}, the simple correlation for degree of relatedness was spurious—a by-product of the fact that the two predictor variables were correlated with one another. Of these two key variables, co-residence is the only one that independently predicts judgements regarding the moral wrongness of sibling incest.

(d) *Do additional years of co-residence beyond childhood contribute to sentiments of moral wrongness for sibling incest?*

Yes, at least for males. Inspection of table 1 shows that the correlation coefficients between MW_{sib} and co-residence are consistently stronger for the entire co-residence period (subject's age 0–18) than for the childhood years (subject's age 0–10). However, this trend, which holds for all subjects taken together, is driven primarily by male responses.

The longer the time interval assayed, the more likely it is that it includes the presence of a second or third opposite-sex sibling. So, does co-residence between the ages 0–18 predict MW_{sib} better than between 0–10 merely because having more opposite-sex siblings produces a stronger aversion to sibling incest in general? (After all,

we asked about third-party moral wrongness, not about the subject's feelings *vis-a-vis* a particular sibling.) No. The number of opposite-sex siblings was not significantly correlated with MW_{sib} for either males ($r = 0.14$, $p = 0.18$) or females ($r = 0.06$, $p = 0.33$). In fact, controlling for the effects of co-residence removed all positive correlations between sibling number and MW_{sib}: male $r = 0.01$; female $r = -0.11$.

By contrast, the correlation between 0–18 co-residence and MW_{sib} remains stable, even after the effects of sibling number *per se* have been statistically removed (male partial $r = 0.36$ (compared with 0.39); female partial $r = 0.24$ (compared with 0.23)). Inspection of the (f) entries in table 1 shows that, when the number of opposite-sex siblings is controlled for, the 0–18 correlations remain higher than those for 0–10, especially for males. Further evidence that the stronger effects of 0–18 co-residence are not due to having more siblings is provided by looking at subjects who have just one opposite-sex sibling: for 0–18, $r = 0.23$ ($p = 0.02$, $n = 77$), whereas for 0–10, $r = 0.17$, ($p = 0.07$).

Interestingly, stronger correlations between 0–18 are consistently found for males with a sister, but not for females with a brother. Do additional years of co-residence beyond childhood affect males and females in the same way? We tested this by seeing whether length of co-residence between 11–18 correlates with MW_{sib} once the effects of co-residence between 0–10 are statistically removed. Co-residence after the age of 10, controlling for childhood co-residence, predicts sibling incest moral wrongness judgements for males ($r = 0.37$, $p < 0.01$), but not for females ($r = 0.03$, $p = 0.415$).

Taken together, these results provide converging lines of evidence that, in males, post-childhood years continue to regulate negative sentiments regarding third-party sibling incest. This is not because these years bring additional siblings *per se*, but because they provide additional kinship-relevant information.

(e) Does co-residence predict sibling incest moral wrongness even when no other cues to siblinghood exist?

Perhaps the purest test of the Westermarck hypothesis involves people who have opposite-sex siblings, none of whom are genetically related to them (i.e. all are step or adoptive). With genetic relatives, there could be multiple cues to siblinghood, any one of which is sufficient to trigger the development of sibling incest aversion: a similar MHC, a similar face, or the explicit social information from others about common parentage. But these cues are absent or reversed in step and adoptive siblings. Does length of co-residence still predict moral wrongness, even when no other phenotypic cues to siblinghood exist?

Yes. Thirteen subjects (10 men and 3 women) had opposite-sex siblings, none of whom were genetic relatives. For these 13, the correlation between length of co-residence with opposite-sex siblings and MW_{sib} was high: $r = 0.61$ ($p = 0.013$). This shows that length of co-residence predicts moral wrongness even when one explicitly knows that the sibling is not related, and even when there are no phenotypic cues to siblinghood.

(f) Can cultural transmission explain individual differences in moral sentiments regarding third-party sibling incest?

According to cultural explanations of the origin of moral sentiments regarding incest, the surrounding social and cultural environment determines one's attitudes towards sexual behaviour. There are two main avenues of cultural transmission: vertical (parent to child) and horizontal (peer).

(i) Vertical cultural transmission model

This model predicts that children will adopt parental attitudes toward sexuality (including sibling incest). Indeed, looking at all subjects in our sample (regardless of familial composition), subjects' and perceived parents' attitudes towards sexuality were significantly correlated, $r = 0.26$, $p < 0.001$, $n = 180$.

If vertical transmission were the primary cause of attitudes towards sexual behaviour (including incest), then the more restrictive parental attitudes towards sexual behaviour, the more restrictive subjects' attitudes should be—and, consequently, the more morally wrong subjects should find incestuous behaviour. Indeed, there is a marginal effect of this kind: the more restrictive was parental attitudes towards sexual behaviour, the more morally wrong subjects found sibling incest ($r = 0.15$, $p = 0.063$, $n = 108$). However, restrictive parental attitudes were also positively correlated with sibling co-residence (0–18: $r = 0.15$, $p = 0.064$; parents with more restrictive attitudes about sexual behaviour might be more likely to stay married, resulting in longer co-residence times for their children). This raises the question: do restrictive parental attitudes predict MW_{sib} after the effects of co-residence have been statistically removed?

No. Controlling for length of co-residence with an opposite-sex sibling, the relationship between parental attitudes and MW_{sib} drops and ceases to be significant (0–18: $r = 0.11$, $p = 0.14$, $n = 108$). Thus, parental attitude does not independently predict sibling incest moral wrongness.

By contrast, length of co-residence *does* independently predict sibling incest moral wrongness. In fact, once parental attitude towards sexual behaviour is controlled for, the correlation between length of co-residence and MW_{sib} becomes even stronger: $r = 0.32$ ($p < 0.001$), a 12% increase in effect size (see table 1, (d) entries). When this analysis is carried out for males and females separately, it is clear that this increase can be attributed to males alone. For females, there is not much change in the correlation between co-residence and MW_{sib} after controlling for parental attitudes. But for males, the effect size for 0–18 co-residence increased after controlling for parental attitudes by 22%; at $r = 0.48$, it is the largest correlation between co-residence and moral wrongness found in this study. These data suggest that, while parental attitudes might have some effect on moral norms, these effects were adding noise to the co-residence data, partially masking what turns out to be an even stronger relationship between co-residence and judgements of moral wrongness for sibling incest than at first appeared.

(ii) *Horizontal cultural transmission model*

A second route of cultural transmission is through the surrounding social environment, including one's peers. If peer attitudes have an effect, these would be reflected in the subject's own attitude toward sexual behaviour, and there would be a correlation between the subject's restrictiveness and that subject's judgements of moral wrongness for sibling incest.

However, looking at all subjects (regardless of family composition), there was no correlation between the subjects' attitudes towards sexual behaviour and MW_{sib} ($r = 0.02$, $p = 0.372$, $n = 179$). Moreover, once the subject's restrictiveness was controlled for, the correlations between co-residence with an opposite-sex sibling and MW_{sib} did not change for either interval of co-residence (0–10: $r = 0.25$, $p = 0.005$; 0–18: $r = 0.29$, $p = 0.001$ see table 1, (*e*) entries).

Taken together, these findings suggest that moral sentiments regarding incestuous acts are mediated by a different system from the one that governs culturally transmitted moral values.

(g) *Is the effect of co-residence with opposite-sex siblings on judgements of moral wrongness for sibling incest a by-product of some correlated attribute, such as having a more traditional family structure?*

As the Westermarck hypothesis predicts, length of co-residence with opposite-sex siblings was correlated with judgements of moral wrongness for sibling incestuous behaviour. As with any correlational study, however, one must consider the possibility that the apparent predictive power of opposite-sex sibling co-residence is an illusion—that it is correlated with some other variable that is the real cause of differences in moral judgements. For example, longer co-residence with opposite-sex siblings might be correlated with a more traditional family structure (sibling co-residence may be longer in families with no divorce), and something about growing up in a traditional family might cause harsher moral judgements about sibling incest.

This counter-hypothesis can be ruled out. Traditional family structure may predict length of sibling co-residence, but if it does, it does so for both opposite- *and* same-sex siblings (traditional or not, offspring gender is determined by a genetic coin flip). So, if traditional family structure were the real underlying predictive variable—and length of sibling co-residence merely indexes this variable—then length of co-residence between the ages 0–18 with *same-sex* siblings should also predict MW_{sib}. It does not: the correlation between length of co-residence with same-sex siblings and MW_{sib} was close to zero ($r = 0.01$, $p = 0.47$, $n = 113$ (all subjects with at least one same-sex sibling, controlling for sexual orientation)). By contrast, the analogous value for co-residence with opposite-sex siblings was $r = 0.29$ ($p = 0.001$).

4. CONCLUSION

Taken together, the data from this study directly support Westermarck's original hypothesis, that childhood co-residence with an opposite-sex individual predicts the strength of moral sentiments regarding third-party sibling incest. This relationship remained significant even after controlling for the effects of relatedness, sexual orientation, family composition, and parental and subject attitude towards sexual behaviour. Indeed, when all of these variables are entered into a stepwise multiple regression, length of co-residence is the only variable that significantly predicts moral wrongness of third-party sibling incest (for co-residence: beta = 0.34, $t_{106} = 3.64$, $p < 0.001$; for regression model: $F_{1,89} = 13.25$, $p < 0.001$; $R^2 = 0.11$). These results widen the evidentiary base supporting Westermarck's hypothesis by (i) measuring moral sentiments directly; (ii) showing that the effect applies to both genetic relatives as well as non-relatives; (iii) showing that the effect operates among kin within ordinary nuclear family households typical of most extant societies (see also Bevc & Silverman 1993, 2000); and (iv) documenting that co-residence remains a high-quality cue to genetic relatedness even in an industrial population. They complement rather than duplicate earlier results by Wolf (1995) and Shepher (1971), because these studies did not directly measure moral sentiments, but rather marital conduct and divorce rates among unrelated individuals raised in exceptional developmental environments.

These data also provide support for the hypothesis that an evolved human kin-recognition system exists, and that it uses the duration of co-residence (or something that covaries with it) as a central cue to compute a relatedness estimate for siblings. (Analyses of these data, to be reported elsewhere, also support the evolutionary prediction that the same computed variable in the human kin-recognition system regulates kin-directed altruism.) If there were other cues to relatedness being used by the kin-recognition system that were individually or aggregately as strong as co-residence, then reported relatedness would have trumped co-residence as a factor generating opposition to incest. Because the effect holds whether co-residing individuals are genetically related or not, these results undermine the hypothesis that human kin recognition—for siblings at least—involves using the MHC or phenotypic markers in oneself as a template for kin recognition. Moreover, in this dataset, conscious beliefs about relatedness had no independent effect after the duration of co-residence was controlled for. That is, it is the number of years during which a girl co-resides with a boy that matters, not whether she believes that he is her brother. This suggests that the flow of information is asymmetrical between the non-conscious sibling kin-recognition system and cultural beliefs. The kin-recognition system shapes beliefs about moral wrongness, but its motivational component appears to be somewhat resistant to revision by cultural beliefs as to who is a sibling.

Earlier studies have suggested that the first 3–6 years of life are the ones used by the Westermarck mechanism. By contrast, this study indicates that for males, but not females, additional years beyond the age of 10 significantly contribute to the moral wrongness associated with third-party sibling incestuous acts. We suspect this is evidence for sexual dimorphism in the motivational component of the kin-recognition system. Owing to the asymmetrical costs associated with inbreeding for females compared to males, decision rules governing when to categorize someone as a sibling should be biased such that minimal cues are sufficient to trigger the system in females (see

Lieberman *et al.* (2003) for discussion). From a signal detection standpoint, misses (categorizing a sib as unrelated) are more costly for females than false alarms (categorizing non-kin as a sib). By contrast, costs of inbreeding (misses) are less for males than for females and costs of false alarms are higher; therefore, the decision rules estimating kinship in males should be designed continually to reassess the likelihood of siblingship so as not to exclude a potential mating partner. Specifically, females may have already been exposed to enough co-residence information by the age of 10 to place co-residing males in the maximally suspect category, whereas the male system continues to use later years for updating and recomputing the kinship estimator.

These results cannot be easily reconciled with Freudian approaches, which implicate parent–offspring dynamics, not sibling co-residence, as the key variable creating incestuous wishes, their repression and their projection into cultural forms. More significantly, the evolutionarily predicted inter-individual variations in moral attitude cannot be easily accounted for by cultural determinist theories that posit that moral attitudes in individuals are immaculately conceived from ambient cultural attitudes, through a general learning capacity. Social science theories claiming that morality is free of biological regulation require revision. If the mind is not a blank slate, then theories of culture will have to accommodate this fact.

REFERENCES

Adams, M. S. & Neel, J. V. 1967 Children of incest. *Pediatrics* **40**, 55–62.

Alexander, R. D. 1979 *Darwinism and human affairs*. Seattle, WA: University of Washington Press.

Arens, W. 1986 *The original sin: incest and its meanings*. Oxford University Press.

Bevc, I. & Silverman, I. 1993 Early proximity and intimacy between siblings and incestuous behaviour: a test of the Westermarck theory. *Ethol. Sociobiol.* **14**, 171–181.

Bevc, I. & Silverman, I. 2000 Early separation and sibling incest: a test of the revised Westermarck theory. *Evol. Hum. Behav.* **21**, 151–161.

Bittles, A. H. & Neel, J. V. 1994 The costs of human inbreeding and their implications for variations at the DNA level. *Nature Genet.* **8**, 117–121.

Darwin, C. 1871 *The descent of Man, and selection in relation to sex*. London: Murray.

Dawkins, R. 1976 *The selfish gene*. Oxford University Press.

Fox, R. 1980 *The red lamp of incest*. London: Dutton.

Freud, S. 1918 *Totem and taboo*. (trans. A. A. Brill). New York: Moffat, Yard & Co.

Geertz, C. 1973 *The interpretation of cultures*. New York: Basic Books.

Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52.

Hamilton, W. D. 1975 Innate social aptitudes of Man: an approach from evolutionary genetics. In *Biosocial anthropology* (ed. R. Fox), pp. 133–155. New York: Halsted Press.

Harris, M. 1968 *The rise of anthropological theory*. New York: Crowell.

Kelly, R. 1995 *The foraging spectrum*. Washington, DC: Smithsonian Institution Press.

Lieberman, D., Tooby, J. & Cosmides, L. 2003 The evolution of human incest avoidance mechanisms: an evolutionary psychological approach. In *Evolution and the moral emotions: appreciating Edward Westermarck* (ed. A. Wolf & J. Takala). (In the press.)

Levi-Strauss, C. 1969 *The elementary structures of kinship*, revised edition. London: Eyre and Spottiswoode.

McCabe, J. 1983 FBD marriage: further support for the Westermarck hypothesis of the incest taboo? *Am. Anthropologist* **85**, 50–69.

MacIntyre, S. & Sooman, A. 1991 Non-paternity and prenatal genetic screening. *Lancet* **338**, 869–871.

Penn, D. J. & Potts, W. K. 1998 MHC-disassortative mating preferences reversed by cross-fostering. *Proc. R. Soc. Lond.* B **265**, 1299–1306. (DOI 10.1098/rspb.1998.0433.)

Penn, D. J. & Potts, W. K. 1999 The evolution of mating preferences and major histocompatibility complex genes. *Am. Nat.* **153**, 145–161.

Pusey, A. & Wolf, M. 1996 Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**, 201–206.

Sahlins, M. 1976 *The use and abuse of biology: an anthropological critique of sociobiology*. Ann Arbor, MI: University of Michigan Press.

Shepher, J. 1971 Mate selection among second generation kibbutz adolescents and adults: incest avoidance and negative imprinting. *Arch. Sexual Behav.* **1**, 293–307.

Sober, E. & Wilson, D. S. 1998 *Unto others*. Cambridge, MA: Harvard University Press.

Sykes, B. & Irven, C. 2000 Surnames and the Y chromosome. *Am. J. Hum. Genet.* **66**, 1417–1419.

Tooby, J. 1982 Pathogens, polymorphism and the evolution of sex. *J. Theor. Biol.* **97**, 557–576.

Tooby, J. & Cosmides, L. 1992 The psychological foundations of culture. In *The adapted mind* (ed. J. Barkow, L. Cosmides & J. Tooby), pp. 19–136. New York: Oxford University Press.

Westermarck, E. A. 1921 *The history of human marriage*, 5th edn. London: Macmillan.

White, L. 1975 *The concept of cultural systems*. New York: Columbia University Press.

Williams, G. C. 1966 *Adaptation and natural selection*. Princeton University Press.

Wilson, E. O. 1975 *Sociobiology*. Cambridge, MA: Harvard University Press.

Wolf, A. P. 1995 *Sexual attraction and childhood association: a Chinese brief for Edward Westermarck*. Stanford, CA: Stanford University Press.

Yamazaki, K., Beauchamp, G. K., Kupniewski, D., Bard, J., Thomas, L. & Boyse, E. A. 1988 Familial imprinting determines H-2 selective mating preferences. *Science* **240**, 1331–1332.