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Incest Aversion

The Evolutionary Roots of Individual Regulation

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To Lou Frances and Ines Adélia
for giving meaning to my life.

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“I am indebted to my father for living, but to my teacher for living well”. Just a few years back I was thinking I would not pass the entry exam to study psychology, let alone pass the courses should I be accepted. Right now I am finalizing my doctoral thesis in psychology. Things change. And the change can be rapid if the circumstances are right. In my case the catalyst for change is without the shadow of a doubt my supervisor, Professor Pekka Santtila. Without your guidance, patience, positive attitude, and your exceptional capacity to make complex issues easy to understand, I would not have ventured into conducting research, an activity I now deeply cherish. Over hours and hours of conversation and coffee, data files and disputes, experiments and encouragement, I have learned immensely. And I have come to learn that enjoying what one does and doing it as well as one can is “living well”. It has always been incredibly fun to work in your good company. I am also glad to have had Professor Kenneth Sandnabba as my supervisor. When it has been necessary to switch perspective in order not to get too deeply buried in my own line of reasoning you have with enviable ease provided the refreshing perspective my work has needed.

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List of Original Publications

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II. Antfolk, J., Karlsson, M., Bäckström, A., & Santtila, P. (2012). Disgust elicited by third-party incest: The roles of biological relatedness, co-residence, and family relationship. *Evolution and Human Behavior*, *33*, 217-223.[1.]

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V. Antfolk, J., Lindqvist, H., Albrecht, A., & Santtila, P. (2014). Self-reported availability of kinship cues during childhood is associated with kin-directed behavior in adulthood. *Evolutionary Psychology*, *12* (1), 148-166.

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Definitions

Inbreeding avoidance: This term is used to describe the general lack of inbreeding observed in many species, including humans. Inbreeding is considered a biological phenomenon referring to the result of actual reproduction between close relatives.

Incest aversion: This term is used to describe the general lack of sexual interest or direct aversion towards having sex with purported relatives, regardless of whether this sexual activity results in reproduction or not. Incest aversion thus describes a psychological construct.

Opportunity cost: This term is used to describe a situation in which a (simultaneous or sequential) choice between different mating opportunities is made. If the value of the best alternative reproduction is forgone by this choice, the choice incurs an opportunity cost on reproduction.

Svensk sammanfattning

Den evolutionära förklaringen till den allmänt utbredda incestaversionen, dvs. motviljan för sex med nära släktingar, försöker besvara såväl frågan om *varför* incestaversionen gynnats i det naturliga urvalet som frågan om *hur* denna aversion regleras på individuell nivå. Eftersom inavlade barn har en försämrad biologisk duglighet än andra barn, medför kostnaderna av denna icke-optimala reproduktion ett selektionstryck mot inavel. Eftersom kvinnor i allmänhet satsar mer biologiska resurser på sina barn än vad män gör, är kostnaderna generellt sett högre för kvinnor än för män. Eftersom det endast är fertila kvinnor som riskerar satsa resurser i en inavlad avkomma förväntas även fertila kvinnor ha högre incestaversion än icke-fertila kvinnor.

Kostnaderna av inavel begränsas dock inte till enbart de individer som har incest. Eftersom alla våra biologiska släktingar sannolikt delar våra alleler, medför inavel mellan dem kostnader även för oss. Detta betyder att en allel som påverkar en motvilja för andras incest, dvs. en motvilja för incest mellan våra släktingar, kan spridas i populationen. Dessutom förväntas styrkan av motviljan för att själv ha incest och motviljan för andras incest spegla duglighetskostnaderna. Duglighetskostnaderna som en viss situation medför beror till exempel på släktskapsgraden mellan de inblandade. I regel kan människor inte vara helt säkra på huruvida en annan individ verkligen är en släkting eller inte. Säkerheten om släktskap grundar sig i hög grad på tillförlitliga (men felbara) signaler om biologiskt släktskap, såsom att bo tillsammans i barndomen eller att se ens mamma ta hand om en annan, yngre individ. Flera av dessa signaler är dessutom internt sammanbundna och kan förutsätta en lyckad identifikation av sina egna föräldrar.

Studier har visat att människor känner motvilja för andras incest även om dessa individer inte är ens egna släktingar. Den psykologiska mekanism med vilken sådana situationer bedöms är dock okänd. Enligt den otestade teorin om självreflekterande empati bedöms sådana situationer genom att man själv föreställer sig ha sex med motsvarande släkting och känslan som väcks i denna process ger därefter emotionell information till bedömningen av andras incest.

Även om man har funnit stöd för en del av dessa antaganden är flera av dem fortfarande otestade. Därför testades följande antaganden i en serie av fem studier:

I studie I testade vi huruvida duglighetskostnaderna förutsäger styrkan av incestaversion. Vi fann att oavsett om respondenten var beskriven som inblandad eller inte, speglade incestaversionen och aversionen gentemot andras incest de biologiska kostnaderna av incest.

I en tilläggsanalys visade vi också att kvinnor har högre incestaversion än män.

I studie II testade vi om aversionen gentemot andras incest reflekterar duglighetskostnaderna för dem som är inblandade i inaveln även när dessa individer inte var släkt med försöksdeltagaren. Som stöd för detta antagande fann vi att biologisk (jämfört med social) incest, föräldra-barn (jämfört med syskon) incest och incest mellan individer som hade bott (jämfört med inte bott) tillsammans medförde en starkare aversion.

I studie III testade vi effekten av fertilitet på incestaversion och fann att kvinnor i (jämfört med kvinnor utanför) den fertila fasen av menstruationscykeln hade högre incestaversion och att denna effekt var starkare i de situationer som kvinnorna själva beskrevs som delaktiga i incesten.

I studie IV testade vi teorin om att andras incest bedöms genom självreflekterande empati. I tre delstudier fann vi att självreflektion var positivt associerat med styrkan av aversion gentemot andras incest.

I studie V testade vi om släktskapssignaler i barndomen reglerar styrkan av incestaversion. Vi fann att den självrapporterade förekomsten av sådana signaler förutsade säkerheten på släktskap och incestaversion till föräldrar i vuxen ålder.

Fann vi stöd för antaganden om både de ultimata och proximala mekanismerna som reglerar styrkan av incestaversion på individnivå. Vidare fann vi stöd för teorin att andras incest bedöms genom självreflekterande empati. Resultaten från dessa studier har också betydelse utanför evolutionspsykologin eftersom de kan användas för att styra datainsamlingar i utredningar av misstänkta sexuella utnyttjanden inom familjen. Resultaten understryker även vikten av att beakta biologins roll i familjepolitiken.

Summary

The evolutionary explanation of the aversion generally felt toward having sex with close kin (i.e., incest aversion) seeks to answer both *why* natural selection has favored incest aversion and *how* this is put to effect on an individual level. Since inbred children are less biologically fit than outbred children, the cost of producing sub-optimal offspring suggests a selection pressure against inbreeding. The costs are generally higher for women than men. This is because women generally invest more resources in producing and raising a child. Furthermore, as only fertile women risk investment in an inbred child, fertile women are expected to have a higher incest aversion than women who are not fertile.

The cost of inbreeding is, however, not limited only to the individuals engaged in the sexual union. As all our biological relatives are likely to share our alleles, inbreeding between them is also costly to us. Thus, an allele that underlies third-party aversion (i.e., an aversion toward our relatives engaging in incest) can spread in the population. Furthermore, the strength of both incest aversion and third-party aversion is expected to reflect fitness costs. The fitness cost of an inbreeding situation depends on, for example, the degree of relatedness between the two individuals engaged in the sexual union. In general, humans cannot be certain about whether another individual actually is a relative or not. Therefore the certainty or relatedness depends largely on reliable (but fallible) indicators of biological relatedness, such as co-residence in childhood or seeing a younger individual nursed by one's mother. Several of these indicators are interdependent and may depend on a first step, such as successful recognition of one's parents.

Studies show that humans react with aversion to third-party incest also when this involves individuals unrelated to the observer. The psychological mechanism with which such situations are evaluated is, however, unknown. The untested egocentric empathy model of third-party evaluations suggests that such situations are processed emotionally through self-reflection (imagining oneself having sex with one's own relative) and the emotion elicited by this process serves as input in the third-party judgment.

Although some of these assumptions have been confirmed by empirical tests, several remain untested. Thus, in a series of five studies we tested these assumptions:

In Study I we tested whether fitness costs predict the strength of incest aversion. We found that irrespective of self-involvement, incest aversion and third-party aversion reflect the costs of inbreeding.

In Study II we tested if third-party aversion reflects the fitness cost to those engaged in an inbreeding union even if these individuals were unrelated to the participant. In line with this assumption, we found that biological (vs. socio-legal) incest, parent-child (vs. sibling) incest, and incest between individuals described as having (vs. not having) co-resided was found more aversive.

In an additional meta-analysis we showed that women have a higher incest aversion than men.

In Study III we tested the effect of fertility on incest aversion and found that women in (vs. women outside) the fertile phase of the menstrual cycle were more aversive to incest and that this effect was stronger for situations in which the women themselves were described as being involved in the incest.

In Study IV we tested the egocentric empathy model of third-party aversion. In three studies we found that self-reflection was positively associated with the strength of third-party aversion.

In Study V we tested whether kinship indicators in childhood regulate incest aversion. We found that the self-reported availability of such indicators predicted certainty in relatedness and incest aversion to parents in adulthood.

In sum, we found support for the assumptions regarding both the ultimate mechanisms in the evolution of incest aversion and the proximate mechanisms governing the manifestation of this aversion on the individual level. Furthermore, we found support for the egocentric empathy model of third-party incest aversion. The results also have implications outside evolutionary theory: they may guide the gathering of data in investigations of alleged familial sexual abuse and also underline the importance of biology in family policy in general.

1 Introduction

1.1 Questions Concerning the Origin of Inbreeding avoidance

Why do brothers typically not have sex with their sisters? How come children typically do not find their parents sexually attractive? The first of these questions refers to *inbreeding avoidance*; the fact that, like many other species, humans avoid having sex with close relatives. The second of these questions refers to the fact that humans tend not to feel sexual attraction to family members. This can be labeled *incest aversion* and is expected to be a psychological mechanism explaining a part of human inbreeding avoidance. When asked these types of questions, many would reject them as purely nonsensical, saying it is *obvious* family members do not have sex and that it is equally *obvious* that members of the same family do not feel sexual attraction towards each other. Indeed, it is certainly true that in most—but not all— cases family members do not have sex; neither do they find each other sexually attractive. So, why ask such questions? First of all, the nearly universal nature of these two phenomena, *inbreeding avoidance* and *incest aversion*, is in itself not an answer to the question *why* these phenomena exist. On the contrary, the fact that family members almost universally shun each other as sexual partners requires an explanation. In fact, one could argue that few things better illustrate the need for an explanation than the common tendency to refute these questions in the first place. One reason to ask such questions is to better understand the mechanisms involved in the development of incest aversion between family members. By understanding why family members tend to feel no sexual attraction towards each other, and by understanding the normal development of this aversion over the course of life, we can gain some understanding of what has gone wrong when familial sexual abuse—a special case of incest—occurs, and with sufficient knowledge we may even be able to prevent such abuse from occurring. Another reason to ask these questions is to better understand how humans differentiate between family members and other individuals, and, more generally, to improve our understanding of the structure and function of the human family. While questions about human incest aversion have been approached from a number of theoretical viewpoints (See Wolf & Durham, 2004 for an overview), arguably no other theoretical framework has provided as many testable predictions and yielded as much useful knowledge as evolutionary theory. Interestingly, evolutionary theory may also be able to provide answers to another set of equally intriguing questions: Why do we judge *others* who engage in incest? How does the aversion I feel towards the thought of having sex with a close relative affect the way I judge others engaging in incest? Not only do people avoid engaging in incest themselves, they also tend to moralize and judge others who do. Most societies have normative prescriptions against incestuous unions, for example, banning marriage between cousins or siblings (e.g, Durham, 1991). The link—should there be one—between the personal tendency to avoid inbreeding and the tendency to morally condemn and be disgusted by others engaging in incest is certainly an interesting one.

Evolutionary psychology has begun to unravel the mysterious origins of the horror of sexual intercourse between close relatives, providing ultimate answers to *why* natural selection has favored inbreeding avoidance and also providing some answers regarding the proximate mechanisms, that is, answering *how* this is put to effect. Therefore, I set out to find some missing pieces from the puzzle regarding human incest aversion. In a series of seven studies described in five publications, we tested a number of predictions regarding incest aversion from the following understanding of evolutionary theory:

1.2 The Evolutionary Explanation of Inbreeding Avoidance

Inbreeding avoidance has been observed in a large number of species and across various taxa (e.g., Pusey & Wolf, 1996; Thornhill, 1993), including such diverse species as the field cricket (Bretman, Wedell, & Tregenza, 2004), the great tit (Szulkin & Zelazowski, 2009), the rhesus macaque (Manson & Perry, 1993), and our close relative, the chimpanzee (Pusey, 1980). Inbreeding avoidance is also almost universally observed across human cultures (Thornhill, 1991). This universality is, in itself, evidence of inbreeding avoidance having an extensive evolutionary history. Although parts of the natural history of inbreeding avoidance may be shared between species, ecological differences between species are also known to lead to different types of adaptations. Concerning incest aversion phylogenetic accounts are difficult to establish. Because incest aversion is a psychological construct it is difficult to measure in the animal world and therefore there is very little available information regarding the presence or absence of a similar aversion in animals.

Apart from understanding the human phylogeny, understanding the human environment is of paramount importance for sorting out the particularities of human inbreeding avoidance and incest aversion. Like in all evolutionary analyses, we need to analyze mechanisms both at the *ultimate* and *proximate levels* to understand a particular phenomenon. Ultimate mechanisms describe the environmental and biological forces crafting a given trait within a species while proximate mechanisms describe the immediate environmental, physiological, or psychological factors underlying a trait and its development in the individual (Mayr, 1961; Tinbergen, 1963). For instance, the evolutionary explanation of inbreeding avoidance requires both an understanding of *why* inbreeding avoidance has evolved and *how* it is manifested at the individual level.

1.2.1 The Evolution of Sexual Reproduction and Genetic Relatedness

Because inbreeding entails sexual reproduction between relatives, the first natural step in understanding it is to look at two phenomena: sexual reproduction and genetic relatedness.

In the beginning there was no sexual reproduction. According to the Red-Queen hypothesis (Bell, 1982; Hamilton, 1990; Tooby, 1982; Van Valen, 1973) sexual reproduction has evolved as a means to counteract detrimental parasitic influence through continuous recombination of the organism's genome. In this arms race between an organism and their parasites, the increased genomic heterogeneity that meiotic recombination of two dissimilar parental genomes provides can lead to an improved immunological defense against parasites (e.g., Kuma, Iwabe, & Miyata, 1995). Genomic dissimilarity, in turn, is a function of the relatedness between two parental genomes, so that the less related they are, the more dissimilar they are, and the more immunologically advantageous is their recombination for future generations.

Genetic relatedness can be defined as the increase in the probability of sharing an allele copy compared to the base-line probability of allelic similarity between two individuals randomly chosen from the populations (Grafen, 1985; Mitteldorf & Wilson, 2000; Queller & Goodnight, 1989). This definition allows for estimating the degree of relatedness between two given individuals. If the degree of relatedness between two randomly drawn individuals in the population is set to zero, then a pair of actual individuals can be either positively related (i.e., share more alleles than expected by chance) or negatively related (i.e., share less alleles than expected by chance; e.g., Gardner & West, 2004; Krupp, DeBruine, Jones, & Lalumière, 2012). In the case of family members, individuals tend to be positively related due to common descent. From a focal person's point of view, a sibling, a parent, and a child have a degree of relatedness (r) of .5 to the focal person, while this coefficient gradually decreases for half-siblings, uncles, aunts, nieces, nephews and grandparents ($r = .25$) and first-degree cousins ($r = .125$). However, not all family members are blood-relatives. For instance, the degree of relatedness for adopted and step relatives is zero ($r = .0$), that is, the baseline probability of sharing a gene with a random member of the population.

Sexual recombination opens up the possibility of combining genomes between individuals that are more or less genetically similar. To the extent that pathogens thrive in more similar genetic environments that persist over generations, this creates a selection pressure to avoid genetically similar mates.

1.2.2 Inbreeding Depression in Humans

Darwin's (1859) theory of natural selection defines the process of adaptive change as driven by the differential reproductive success of individual organisms or groups of organisms to the extent this reproductive success reflects specific genotypes (e.g., Maynard Smith, 1989). Put another way, evolutionary success is measured as the quantity of alleles transmitted to subsequent gene pools (relative to the quantity of other allele-types). As a child born to a brother and his sister are genetically more similar (*r* = .75) to both its parents than is a child born to less related parents, inbreeding seems to represent a particularly successful reproductive strategy. There are at least two reasons why this is not the case: First, if an individual produces one offspring with, say, a sibling, the inbred daughter is a niece/daughter (for simplicity, the terms used for the offspring refer only to the female sex) to both its parents and that the relatedness between each parent and the niece/daughter is (*r* = 0.75). However, if this offspring replaces an outbred daughter for each parent, each parent loses one direct offspring (*r* = 0.5) and, adding to that, the inclusive fitness of a niece (*r* = .25; e.g., Dawkins, 1979; Kokko & Ots, 2006). In this particular situation, other things being equal, inbreeding and outbreeding are equivalent. Additionally, one has to remember that the biological fitness of the offspring also matters. An inbred child is more likely to suffer disease and death than an outbred child (e.g., Adams & Neel, 1967; Bittles & Neel, 1994). This decrease in fitness is usually referred to as *inbreeding depression* (δ). If this decrease in fitness outweighs the benefit of transmitting an increased number of alleles, natural selection is expected to have selected against, and not in favor of, inbreeding. The lowered biological fitness of inbred offspring is due to the increased biochemical similarity between close kin. Kin are more likely than non-kin to share identical harmful recessive alleles that would be expressed in a common offspring, having a negative impact on the offspring's immunological plasticity, and consequently on the offspring's health (Charlesworth & Charlesworth, 1987; 1999; Ralls, Ballou, & Templeteon, 1988; Tooby, 1982). Further, the higher the degree of relatedness between the two parents, the more dramatically decreased is the fitness in inbred offspring. The excess pre-adult mortality in offspring of first-degree cousins has been estimated at 5-10%, and for offspring to siblings or child-parent unions, the increase is about fourfold (Bittles & Neel, 1994; Morton, Crow, & Muller, 1956). This would estimate δ to be in the range of .2 to .4 in inbreeding between first-degree relatives.

Excessive outbreeding can also be costly. This can be the case if, for instance, individuals are adapted to local conditions and the dispersal of individuals reflects relatedness or if outbreeding risks breaking down co-adapted gene-complexes

(Bateson, 1978; Frankham, 1995). From these two independent selection pressures an optimal balance between outbreeding and inbreeding could be expected. In fact, a study on the reproductive success of couples of various degrees of relatedness estimated unions between third ($r \approx .0078$) and fourth degree ($r \approx .0020$) cousins as the most successful (Helgason, Pálsson, Gudbjartsson, Kristjánsson, & Stefánsson, 2008). In sum, sex with *close* kin is disadvantageous and natural selection is expected to have crafted human sexuality so as to exclude sexual interest between highly related individuals.

1.2.3 Inclusive-Fitness Theory and the Opportunity Costs of Inbreeding

The cost of inbreeding is not limited only to the individuals engaged in the sexual union. The cost of inbreeding reaches beyond these two individuals and also affects their relatives. This is because an individual's reproductive success is not limited to the number or the biological fitness of his or her *own* offspring. Rather, reproductive fitness is measured by the total number of allele copies that an individual transmits to subsequent generations, either through direct descendants or indirectly, through offspring of relatives. This view is captured by *inclusive-fitness theory* (Hamilton, 1964), which shows how alleles resulting in aiding kin can spread in the population. The implications of inclusive-fitness theory on kin-directed altruism and inbreeding avoidance are profound: Inclusive-fitness theory can explain why we are altruistic toward kin other than our own offspring. As our siblings and cousins (and their offspring) have an increased probability of sharing copies of the alleles underlying our altruistic behavior, investing in their well-being and reproductive success increases the probability that these alleles will be furthered to future generations. Similarly, alleles contributing to *not* acting in a manner that is harmful to close kin can also spread in the population. For example, inclusive-fitness theory predicts that in estimating the cost of inbreeding to an individual, we also have to include the inclusive cost inbreeding has to the individual with whom he/she shares this sexual union. To test whether kin-selection has played an important role in crafting human inbreeding avoidance, we need to derive and test predictions from inclusive-fitness theory. To do this we first need to define the inclusive-fitness effects of inbreeding.

One important thing to consider in defining the effects of inbreeding is the *opportunity cost.* As the number of offspring an individual successfully can produce and raise is limited, the degree to which producing an inbred offspring (and raising this offspring to nutritional independence) affects the possibility of producing and raising outbred offspring. The effect of having an inbred offspring on the possibility of having outbred offspring can be defined as the opportunity cost of inbreeding. In fact, inbreeding is evolutionarily costly only if having an inbred child decreases the opportunity to have a more biologically fit child, and this opportunity cost is larger than the fitness gained through producing an inbred child (e.g., Dawkins, 1983; Haig, 1999).

Following Haig's (1999) model this can be expressed in the following way: Let us assume that the fitness of, for example, a child from a sibling inbreeding is expressed as x. Since x is lower than the fitness of an optimally bred child, the inbred child is produced at some opportunity cost c_A to its parent A and c_B to its parent B. Hence, the fitness consequences of inbreeding to parent A can be expressed as $(x - c_A) + r_B(x - c_B)$, where r is the coefficient of relatedness between A and B. From the point of view of parent B, the fitness consequences can be modeled as $(x - c_B) + r_A(x - c_A)$. In the case of brother-sister incest, r would be .5, meaning that in accordance to inclusive-fitness theory half of the cost to the sister (B) is added to the direct cost for the brother (A) in the first example. In the second example, half of the cost to the brother (A) is added to the direct cost for the sister (B) (See Figure 1.)

In the above examples, the costs to the brother (C_A) and to the sister (C_B) are assumed equivalent. We need to, however, consider an asymmetry between the sexes. The minimum parental investment in offspring is generally higher for women than for men (Trivers, 1972). Women minimally invest nine months of gestation and often some time breastfeeding. During this time fertility is repressed. On the other hand, men need minimally invest nothing more than the metabolic resources and the time needed for copulation. This means that, on average, the opportunity costs of engaging in inbreeding are larger for women than for men. Translating this to our example above, c_A is generally smaller than c_B. However, in the case of inbreeding the total cost to the male needs to include the inclusive cost he suffers via his relative, the female (and *vice versa*). To further exemplify the implications of this model, we can assume the inbred offspring's fitness to be 30% lower than of that of a child with the optimal fitness 1. Subtracting this fitness decrease from the optimal fitness, the fitness of an inbred child is 0.7 ($1- \delta = 0.7$). We further can assume that this inbred child is produced and raised at some opportunity cost to its parents, brother *A* and sister *B*. If the inbred child's mother (sister *B*) loses one child with optimal fitness for each inbred child, her opportunity cost is 1. The cost to the brother is on average lower than to the sister: given egalitarian parenting, we can in this example assume his opportunity cost to be modestly decreased to, say, 0.8. Then this model would give that for the brother, the cost of inbreeding with his sister is $(0.7 – 0.8) + .5(0.7 – 1.0) = - 0.25$. For the sister the cost of inbreeding is $(0.7 – 1.0) + .5(0.7 - 0.8) = - 0.35$. The negative but asymmetric values indicate that, for both sexes, the opportunity costs outweigh the fitness gain of having an inbred child. This, in turn, suggests an adaptive value of avoiding inbreeding for both sexes. If the value were positive, inbreeding would, evolutionarily speaking, be beneficial.

Inclusive-fitness theory has another important implication in this context: Inbreeding between two individuals is costly to biologically related bystanders. To demonstrate this, consider the following example that illustrates how inbreeding between two individuals not only bears fitness costs to them, but also to their relatives (e.g., a sister of the sibling pair used in the above example).

Although the sister of the sibling pair does not herself engage in inbreeding, she suffers inclusive-fitness costs by losing outbred nieces/nephews. In this case these inclusive-fitness costs are suffered both via her brother and via her sister. We can thus extend the model given by (Haig, 1999) to describe the fitness consequences to a related bystander (common sister *C*). From the perspective of C, the fitness costs of inbreeding between *A* and *B* can be modeled as $r_{AC}(x - c_A) + r_{BC}(x - c_B)$, where the costs to the sister and the costs to the brother are first weighted by the degree of relatedness of *C* to *A* and the degrees of relatedness of *C* to *B* respectively, and then summed. (See Figure 2).

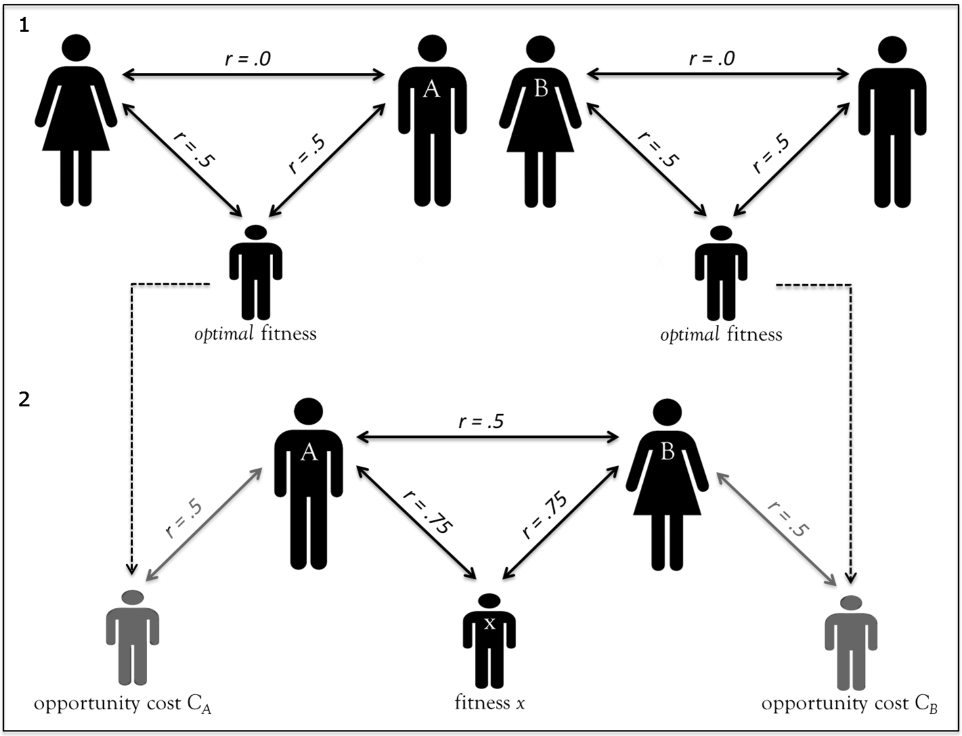


Figure 1. Schematic description of the fitness costs to a male A and his sister B engaging in inbreeding from an inclusive-fitness perspective. The two panels, the upper Panel 1, and the lower Panel 2, describe alternative mating possibilities. In Panel 1, A and B both mate with individuals unrelated to them producing offspring of optimal fitness. In Panel 2, A and B mate with each other producing an offspring with (reduced) fitness *x*. This production of the inbred child affects, to an unknown degree, the number of outbred children with optimal fitness A and B can produce over their lifetime. This is defined as opportunity costs C_A and C_B.

Using the same values as above, the cost to sister of inbreeding between *A* and *B* would be .5(0.7 - 0.8) + .5(0.7 - 1.0) = - 0.20.

In this manner, the costs of inbreeding can be mathematically described from an inclusive-fitness perspective, with the limitation that the exact opportunity costs have not been estimated.

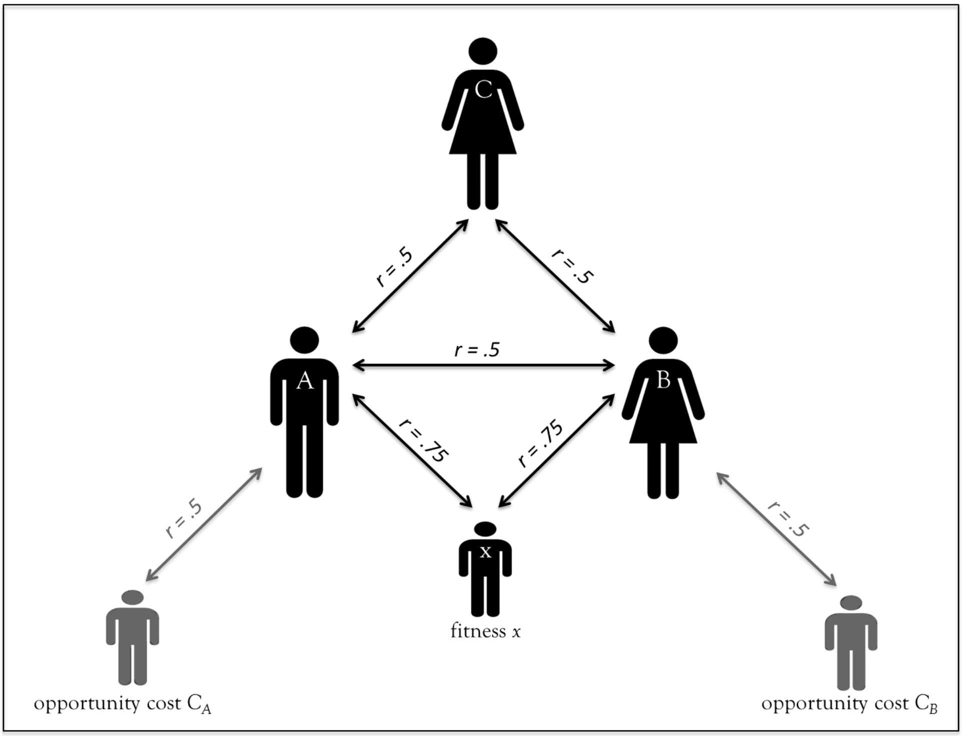


Figure 2. Schematic description of the fitness costs to a common sister *C* in the case her brother *A* and a sister *B* engage in inbreeding. Again the opportunity costs of inbreeding between *A* and *B* are measured as a relative decrease compared to optimal breeding described in Panel 1 in Figure 1.

1.2.4 Variations in Opportunity Costs

Opportunity costs make up an important part of the model described above. Opportunity costs are, however, not evenly distributed across populations, individuals, and situations. In fact, a number of factors are thought to affect the magnitude of the individual opportunity costs associated with inbreeding. First, as we have seen above, an asymmetry between the sexes has to be considered. Based on parental investment theory (Trivers, 1972), we should expect women to be more averse to incest than men. A second factor affecting the opportunity costs are individual differences in the ability to access optimal partners. Human mating is a non-random process (e.g., Barber, 1995; Bereczkei & Casanaky, 1996; Darwin, 1871; Symons, 1979), and some individuals possess more characteristics that are generally valued in a mate or sexual partner (e.g., Bailey, Durante, & Geary, 2011; Edlund & Sagarin, 2010; Starratt & Shackelford, 2012). As a general rule, individuals with low mate value have sexual access to fewer individuals than do individuals with high mate value. This, in turn, means that individuals with a low mate value suffer a lower opportunity cost from inbreeding than do individuals with high mate value. (In our example, *c* is higher for individuals with a high mate value than individuals with a low mate value). Third, population size and population viscosity (i.e., the average genetic similarity between two randomly selected individuals in a population; e.g., Mitteldorf & Wilson, 2000), also affect opportunity costs. Using computerized modeling, Denic, Agarwal and Nagelkerke (2012) illuminated the effects of access to unrelated partners on inbreeding avoidance, showing that when the population size decreases and the relatedness between individuals in this populations increases, inbreeding is, on average, associated with lower opportunity cost. For instance, on a small island where contact with other populations is limited, genetic similarity in a population can be quite high. Under such circumstances, a strict avoidance of sex with closely related individuals would lead to few mating opportunities and reduce the chance of reproduction. However, also in this case, more distant relatives should be preferred over closer relatives, all else equal.

1.2.6 The Ovulatory Shift and Opportunity Costs of Inbreeding

One specific case of variation in the cost of engaging in sub-optimal sexual behavior is the change in fertility across the female menstrual cycle. This change directly regulates the fitness costs (and benefits) of sexual behaviors. During the menstrual cycle, with an average length of 29 days (e.g., Fehring, Schneider, & Raviele, 2006), a woman's most fertile phase—the time period during which the likelihood of conception is highest—takes place in the late follicular phase, about five days before ovulation (Mihm, Gangooly, & Muttukrishna, 2011; Wilcox, Weinberg, & Baird, 1995). Given the narrow window of fertility, it has been hypothesized that evolution crafted female sexual psychology to take advantage of sexual opportunities when fertile versus when not. Indeed, sexual willingness does seem to increase during the late follicular phase as evidenced by, for example, an increase in bodily ornamentation (Durante, Li, & Haselton, 2008; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007), sexual desire (Warner & Bancroft, 1988), and partnered sexual behavior (Burleson, Trevathan, & Gregory, 2002; Matteo & Rissman, 1984). As pointed out by Thornhill and Gangestad (2008), however, the function of female estrus is not to indiscriminately obtain sperm for fertilization, but to obtain sperm from men, who, relative to other men, may offer increased genetic fitness in offspring. Hence, behaviors and partners associated with relative fitness gains should become increasingly appealing in comparison to behaviors and partners associated with relative fitness costs. Consequently, behaviors and partners that, in the case of conception, are linked to sub-optimal reproduction should be more intensely avoided during the fertile phase. Indeed, research supports these assumptions. For example, women in the late follicular phase have an increased preference for indicators of genetic quality in men using a variety of measures such as preferring the scent of dominant (Havlicek, Roberts, & Flegr, 2005) and symmetric men (Gangestad & Tornhill, 1998), preferring masculine faces (Penton-Voak et al., 1999), and preferring behaviors such as dominance, male intrasexual competitiveness (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004), and creativity (Haselton & Miller, 2006). Conversely, there is also evidence that women in the late follicular phase show increased sensitivity toward stimuli and sexual behaviors associated with direct fitness costs (e.g., Roberts et al., 2008). For instance, women in the follicular phase show increased handgrip strength after contemplating sexual assault scenarios (Petralia & Gallup Jr, 2002), suggesting increased defensive responsiveness to potential rape-situations during the fertile period. Lieberman and colleagues (2011) reported that women who are fertile are less likely to associate with male kin as compared to female kin, a behavior that decreases the likelihood of inbreeding. Taken together, the empirical literature shows that variations in fertility during the menstrual cycle moderate women's sex-related cognitions and emotions, favoring behaviors and traits that promote fitness, and avoiding behaviors that do not.

1.2.6 Direct and Collateral Kin and Kin Bias

Finally, we should not expect degree of relatedness to be the only factor to take into account. Although we, on average, share the same amount of alleles with both direct kin (i.e., parents and children) and collateral kin (i.e., siblings) we should not expect kin-selection to treat these as equivalent groups. In fact, several studies have shown preferential investment in direct kin over collateral kin (Judge & Hrdy, 1992; Webster, 2004; Webster, Bryan, Crawford, McCarthy, & Cohen, 2008).

One reason for this could be that an allele underlying a strong preference for investment in collateral kin is, if it is to develop at the expense of investment in direct kin, unlikely to spread in the population. The spread of such an allele is obviously restricted by the decreased survival of direct offspring. In other words, an allele motivating siblings to invest in each other while not motivating them to invest in their respective children, would, so to speak, have no future generations to be transmitted to. Alleles motivating investment in children at the expense of investment in our siblings is not an equally dramatic problem. It is actually just half the drama, as an allele is twice as likely to spread via an own offspring ($r = .5$) than through a nephew or a niece ($r = .25$). This is actually defined in Hamilton's (1964) inclusive-fitness theory, where an altruistic allele can spread in the population if the benefit of investing in kin (multiplied with the degree of relatedness between actor and recipient) is larger than the cost to the participant. Both the benefit and the cost are defined as lineal reproduction in inclusive-fitness theory.

Another factor that has to be considered is that competition between relatives may tilt the balance of kin-selection. Kin compete about resources and there the degree of this completion in asymmetrically distributed among kin dyads (Griffin & Stuart A. West, 2002; Haig, 2009; West, Murray, Machado, Griffin, & Herre, 2001). For instance, competition between siblings is expectedly higher than competition between parents and their offspring due to the siblings having a decreased age difference. Furthermore, parents invest in their offspring, of which there is often more than one. Each offspring has a lot to gain from a parent investing in them. The investment of parents in a sibling (which all other things being equal has an equal value to the parent) limits the maximum investment in each direct offspring. If, for instance, an individual has one sibling, this individual can expect to obtain 1/2 of his parents' investment. From this individual's perspective, inbreeding with a parent would give the parent another offspring (a child/grandchild to the parent and a sibling/child to the focal person) and thus change the denominator. In this case the maximum investment he could obtain from his parent would be 1/3.

Both these constraints to kin-selection predict that parent-child inbreeding should be considered more costly than sibling inbreeding.

1.3 The Proximate Mechanisms of Inbreeding Avoidance

While the theoretical considerations described above are important for understanding the ultimate evolutionary causes of inbreeding avoidance, they do not inform us about how inbreeding avoidance is manifested on an individual level in humans. To address the proximate mechanisms employed in this individual manifestation, we need to direct our gaze to human circumstances. Inbreeding avoidance can be achieved without a psychological capacity to discriminate kin from non-kin. For instance, in many bird species, the rate of inbreeding is decreased by dispersal of kin. When two related birds disperse and become separated by a large geographical distance, the risk of them mating with each other is decreased (Moore & Ali, 1984). Dispersal does not require more than that the sexes have different migration patterns. However, in species where kin interact after reaching sexual maturity, kin cannot be completely avoided. Instead, there must exist some specific mechanism by which kin are not considered potential mating partners. In humans, where kin interact throughout the life-cycle and do so extensively, the human family unit and its structure may offer a good starting point for understanding the proximate mechanisms involved in the development of human inbreeding avoidance.

1.3.1. The Human Family and its Evolutionary Function

Inbreeding certainly is a family matter. Understanding *how* we avoid our family members as mates (while the same family members are the objects of a wide range of positive affection) quite naturally requires an understanding of the family structure. The evolutionary analysis of the human family starts off with the supposition that the genetic relatedness of family members explains the structure and function of families (e.g., Emlen, 1997). The human family is also characterized by increased interaction between affines, such as mates or in-laws. These individuals usually have one evolutionary interest in common, the successful development of one or more individuals, to whom all other family members are related (with the obvious exception of step-, foster-, and adoptive relatives; e.g., Bar-yam & Darby, 1997; Kaplan, Hill, Lancaster, & Hurtado, 2000). Thus, families are characterized by increased genetic relatedness and increased interaction between family members. In humans, childhood extends over many years, during which one's parents may have more than one child at a given point in time. This means, that a child is not only in direct contact with its parents, but also often with one or more siblings. Moreover, although the contact diminishes later in life, human families are distinguished by the fact that contacts with parents and siblings continue into adulthood. This prolonged and continuous contact is also of importance in understanding the developmental mechanisms involved in human inbreeding avoidance as, for example, any mechanism (e.g., dispersion) that would diminish this contact and thereby diminish positive investment in one's family members, would not be optimal. Rather the operating mechanism needs to be specific enough to successfully inhibit sexual contact while not decreasing other types of contact between family members.

1.3.2 Kin Recognition and Human Inbreeding Avoidance

This far we have made one important simplification: We have assumed that the semantic categories ("sibling", "brother", "niece" etc.) truly reflect degrees of relatedness. The reality is that, apart from mothers who can be certain about their child being their own biological relative, human relations are uncertain and probabilistic in nature. In our evolutionary background, there were no means to know whether another individual was kin or not. Although kin-selection does not necessitate *kin recognition* (i.e., the ability to *identify* another individual as kin), kin recognition is thought to be an important proximate mechanism in the individual development of kin-directed behavior in humans (e.g., Krupp, DeBruine, & Jones, 2011; Nakagawa & Waas, 2004; Penn & Frommen, 2010; Tal & Lieberman, 2007), including human inbreeding avoidance. In the case of psychological aversion (or motivation) to inbreeding, the degree to which one individual *believes* himself to be related to another individual must be included. For example, if a man is completely certain a woman is his full sister, the motivation to avoid inbreeding should be higher than if the man is in doubt about his relatedness to the woman. Considering this, one important mechanism that in human incest aversion is the ability to recognize kin and the subjective certainty in relatedness to another individual.

As so called green-beard effects (i.e., where a single allele produce a phenotypic trait, a capacity to recognize this trait [and thereby the same underlying allele], and finally, lead to selective treatment of the individual with this trait; e.g., Dawkins, 1976; Hamilton, 1964), are believed to be rare in humans (e.g., Qirko, 2011), human kin recognition is thought to rest largely on environmental information. Environmental information used in kin-recognition can be either direct or indirect and contextual (Penn & Frommen, 2010). Direct kin-recognition in humans consists of, for instance, phenotype matching, where another individual’s phenotypic characteristics are compared to psychological kin templates that, in turn, can be either other-referent (i.e., based on information from already recognized kin) or self-referent (i.e., based on information about oneself; e.g., Krupp et al., 2011). Phenotype matching may serve in recognition of all types of kin (e.g., siblings, children, and parents). Concerning indirect and contextual kin recognition, the type of contextual information that provides reliable information about kinship depends on the type of kin to be recognized. An example of indirect, contextual kin recognition in humans is early co-residence.

Indeed, concerning direct kin-recognition studies have shown that facial similarity up-regulates incest aversion between siblings (DeBruine, 2005; DeBruine et al., 2011; Marcinkowska & Rantala, 2012; Marcinkowska, Moore, & Rantala, 2013), and there is some evidence that phenotype matching may be used also in other types of family dyads (e.g., Alvergne, Faurie, & Raymond, 2007, 2009, 2010; Cernoch & Porter, 1985; DeBruine, 2004, 2005; Dubas, Heijkoop, & van Aken, 2009; Marcinkowska & Rantala, 2012; Park & Schaller, 2005; Platek et al., 2003).

Concerning indirect, contextual cues, Westermarck (1891) proposed that when two individuals live in close propinquity during childhood, a natural aversion to sexual relationships between these individuals is activated, and, as such individuals tend to be genetically related, this aversion appears as an aversion to sex with blood-relatives. There is a large corpus of evidence in support of Westermarck's hypothesis regarding the effects of early co-residence (See Rantala & Marcinkowska, 2011 for a review). For example, studying archival data from about 15.000 Taiwanese arranged marriages, Wolf (1966, 1968, 1970, 1995) showed that when unrelated individuals grew up together to later enter marriage, the rates of divorce were higher, and the fertility rates were lower than in comparable arranged marriages, where the bride and the groom had grown up separately. This finding has been corroborated by data from Israeli kibbutzim, where individuals raised in the same groups tend to feel no sexual attraction towards each other in adulthood (Shepher, 1971, 1983; Spiro, 1958; Talmon, 1964) and in Lebanese (McCabe, 1983) and Moroccan (Walter, 1997) *Bint'amm* marriages, where two patrilineal cousins are raised together to later marry, resulting in higher divorce rates and lower fertility rates than in other comparable marriages. In two case-control studies, Bevc and Silverman (1993, 2000) showed that duration of co-residence with a sibling was negatively associated with the risk of engaging in sibling-incest. Maternal perinatal association, that is, observing a younger sibling receiving maternal care from a woman recognized as one's mother, also serves as an important cue of kinship and moderates the effect of co-residence (Lieberman, 2009; Lieberman, Tooby, & Cosmides, 2007).

Because in our evolutionary background, reliable information about one's own physical attributes may have been limited, other-referent kin-recognition is likely to play an important role in identifying one's kin. However, other-referent kin-recognition, whether direct or indirect, requires a start-off point. For example, for maternal perinatal association to reliably function as a kin-recognition cue of younger siblings, the common mother must successfully have been identified. This suggests that children's identification of their parents may be an important first step in the process of identifying various kin.

1.3.3 The Role of Disgust in Human Incest Aversion

The increased presence of kinship cues leading to a reduction in sexual interest between two individuals relies, at least, partly on an *aversive* reaction. This aversion Westermarck (Westermarck, 1891, p. 320) described as "the horror of intercourse between near kin". The emotion disgust seems to play an important role in incest aversion as well as in avoiding other sub-optimal sexual behaviors. Reacting with disgust to potentially harmful sexual behavior such as incest is thought to be a co-opted function of the primary role of the emotion disgust, namely protecting the organism from pathogens (Tybur, Lieberman, Kurzban, & Descioli, 2013). Indeed, there is a large body of research showing that disgust down-regulates sexual arousal (e.g., Borg & de Jong, 2012; Koukounas & McCabe, 2001; Malamuth & Check, 1980; Rempel & Baumgartner, 2003; Stark et al., 2005). Disgust has also been directly implicated in incest aversion. For example, a study by Ackerman and his colleagues (Ackerman, Kenrick, & Schaller, 2007) suggests that incest elicits disgust rather than other negative emotions. A recent study by De Smet and her colleagues (2014) also found that incest elicits disgust measured physiologically and a brain-imaging study by Lieberman and her colleagues (2008) also implicates disgust in incest aversion. Also, a victimization study quite interestingly showed that the most common feeling after incestuous sexual abuse was disgust (Sariola & Uutela, 1996). Thus, disgust seems to play an important role in down-regulation sexual interest between close kin.

1.4 Aversion to Third-Party Incest

A number of studies have shown that humans react aversively, feeling disgusted by *third-party incest*, that is, *other* persons engaging in incest (e.g., Fessler & Navarrete, 2004; Lieberman, Tooby, & Cosmides, 2003, 2007; Royzman, Leeman, & Sabini, 2008). These third-party evaluations (i.e., judgments of other persons engaging in incest) require explanation. It may seem odd that evolution would have crafted an aversion to witnessing unrelated *others* engaging in incest, as such incest does not appear to have any direct negative effect on the continuation of *our* alleles. In fact, our alleles could gain relative benefits of unrelated others engaging in incest, as alternative alleles likely to be present in such, to us unrelated, individuals would tend to decrease over time. However, an extension of incest aversion to reactions to *all* third-party incest could have evolved if populations were relatively small in our evolutionary background and the relatedness to other individuals, with whom an individual interacted, was high. In other words, in situations where the cost of false negatives (lack of aversion to *related* third-party incest) was outweighed by the benefit of false positives (aversion to *unrelated* third-party incest), the aversion to seeing other individuals engaging in incest could be an evolutionary byproduct.

Another explanation has been given by Aoki (2004), who argued that given that rules prescribing incest originated through cultural transmission between family members (where inbreeding is costly) and after that extended to encompass also others (that already were likely to have adopted similar rules), and given that such prohibitions were not costly, cultural transmission of norms against third-party incest could extend the aversion to incest between related others beyond its original inclusive-fitness function. This cultural transmission could be adaptive if there are societal costs (the summed costs of each individual in the population) of raising inbred children (Haig, 1999).

A proximate mechanism by which this extension could be achieved was proposed by Westermarck (1906), who, strongly influenced by Adam Smith's philosophy of the moral emotions, argued that when evaluating the behavior of others, humans, via "sympathetic sentiments", place themselves in the position of the other person and react as if they themselves would be engaging in the described behavior. Borrowing the terminology from Van Boven, Dunning, and Loewenstein (2000), Fessler and Navarrete (2004) later called this process *egocentric empathy*. As we cannot always be aware of the actual motives, sentiments, and beliefs of others, we may imply them from our own: When observing an individual acting in a given situation, the egocentric empathy model suggests that we image ourselves in a similar situation, and observe the emotional response this as-if process elicits in us. (See Figure 3 for a schematic description of the model).

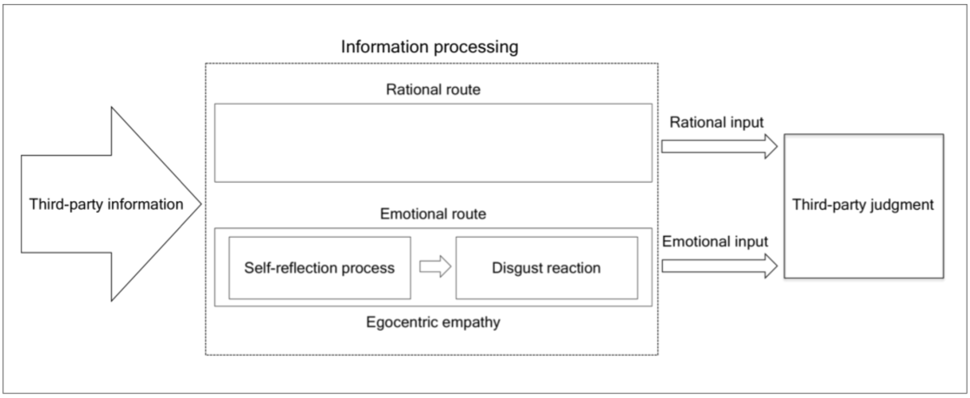


Figure 3. Schematic model of the egocentric empathy hypothesis of third-party judgments. In this model the information passes through an emotional route in which self-reflection elicits an emotional reaction. This emotional reaction then serves as emotional input into the judgment made.

In line with this model, Tybur and his colleagues (2013) recently proposed that disgust reactions may reflect the fitness costs associated with the observed behavior. Extending the emotion felt when self-reflecting third-party behavior, we can tag the behavior and endorse moral rules that are in line with our own behavioral propensities. This, in turn, could have an adaptive value. The adaptive value of this is that punishment and social exclusion (Haig, 2011) pose adaptive problems to individuals who risk being sanctioned by other group members and thereby lose access to the benefits of co-operation. Thus trying to influence moral rules in such a direction that they are in line with one's own behavioral propensities can be an efficient way to deal with this threat (Tybur et al., 2013).

A testable prediction can be derived from this line of thought: Third-party incest aversion should be correlated with the aversion to engage in incest oneself, and this correlation should be mediated through self-reflection. To date, no studies have been designed to test this prediction. However, moral psychology provides some interesting data in line with this theory. Empathy indeed seems to have an important role in third-party evaluations. Empathic accuracy (Ickes, 1997) or perspective taking (Higgins, 1980), which both describe the capacity to see things from another person's point of view, is fundamental in social interactions, including moral judgment. Attributing motives and beliefs to others' actions, has been shown to play an important role in moral judgment (e.g., Young, Cushman, Hauser, & Saxe, 2007; Zelazo, Helwig, & Lau, 1996). According to the dual-process model of moral judgments proposed by Greene and his colleagues (e.g., 2001; 2008), both emotional and rational processes are involved in moral judgment. While one part of moral judgments is rational, following, for example, utilitarian principles, another part of moral judgments tends to stem from our emotional reactions. For instance, the inability to interpret one's own emotions has been found to increase rational thinking in moral judgments (e.g., Koenigs et al., 2007; Valdesolo & DeSteno, 2006), suggesting that interpreting one's own emotional response is of importance in the shaping of moral judgment. Concerning the role of disgust in moral judgments, it has been found that smelling a disgusting odor (Schnall et al., 2008), experiencing disgusting tastes (Eskine, Kacinik, & Prinz, 2011), and inducing disgust under hypnosis (Wheatley & Haidt, 2005) increase the tendency to judge acts as morally wrong.

One interesting piece of information comes from the study of incest aversion itself. As mentioned above, studies show that across the menstrual cycle women regulate their *own* individual propensity to engage in various sexual behaviors, including incest. However, some studies also suggest that the variations in fertility during the menstrual cycle moderate judgments of *other* individuals' sexual behavior, suggesting that the variations in the strength of the personal aversion may extend to the judgment of others. In a study where women were asked to read a third-party sibling incest description, Fessler and Navarrete (2003) showed an increased disgust toward this description in fertile women. This observation cannot be explained by the adaptive value a fertility-dependent self-regulation could have. Thus, one important aspect in understanding the regulatory function embedded in the ovulatory shift is its specificity. It may be the case that the ovulatory shift extends to third-party incest, moderating women's cognitions and emotions also regarding sexual behavior that bears no direct risk to them themselves. However, as fertility variations within an individual do not *as such* moderate the costs inbreeding bears to others, the ovulatory-shift theory would suggest that the effects of fertility across the menstrual cycle are primarily self-regulatory. In other words, the effect of fertility should be *stronger* when regulating an individual's own propensity to engage in incest than when extended to others.

1.5 Gaps in the Incest-Aversion Literature

Although much is known about the ultimate forces shaping human incest aversion, at least one important question remains unaddressed. In the absence of empirical data to support or falsify predictions from inclusive-fitness theory, the effect of kin-selection processes in human incest aversion remains unknown. In fact, it could be argued that in the case of inbreeding avoidance, kin selection mechanisms are best studied in humans. Because the psychological construct of incest aversion can be measured irrespective of an individual's self-involvement, incest aversion can provide more data than simple avoidance, as avoidance is a behavior that does not extend to third-party situations. This is indeed an important question as inclusive-fitness theory provides possible answers to why we are aversive not only to having sex with kin, but also aversive to our kin having incest even without our own engagement. The limitations to a balanced kin-selection process, where direct and collateral kin are treated exactly the same, also require attention: In the case of inbreeding, these limitations include parental-investment differences (Trivers, 1972) and asymmetries in resource allocations

(Haig, 2009). In addition, it should be noted that, although the ovulatory-shift effect has been shown in many domains of sexual behavior, the evidence of its effect on incest aversion is limited. Moreover, nothing is known about whether this effect is specifically self-regulatory, or it extends to third-party incest aversion.

Regarding the proximate mechanisms involved in the individual manifestation of avoiding inbreeding with kin, there are an increasing number of studies investigating the use of various kin-recognition cues. However, as earlier mentioned, the possibility of children's identification of their parents acting as an important step in this process remains to a large degree untested. Empirical evidence concerning the cues used by children to identify their parents may be central to kin-recognition and its role in down-regulating detrimental behaviors and up-regulating investment to kin.

Finally, although testable assumptions about the processes employed in extending the individual aversion to encompass third-party incest can be found in the literature (Aoki, 2004; Tybur et al., 2013; Westermarck, 1906), to date, no studies have been designed to test these assumptions.

In sum, the questions regarding why incest is aversive, how this aversion manifests itself in the individual, and how judgment of others is connected to this individual aversion have not yet been fully answered.

2 Aims and Research Questions

The present thesis had five main aims. The first aim was to investigate whether the strength of incest aversion followed predictions from inclusive-fitness theory, so that the higher the fitness costs implied to a participant from a given incest situation (either involving the participant themselves or only individuals related to the participants), the stronger the aversion. This aim was addressed in **Study I**. The second aim was to investigate whether humans are sensitive to factors that affect fitness costs to *others* engaging in incest. Thus, in **Study I,** we also wanted to see whether in situations where individuals unrelated to the participants were described as engaging in incest, the degree of relatedness between these two individuals was positively associated with the level of aversion it elicited in the participant. In **Study II** we wanted to see whether also factors other than the degree of relatedness, such as shared co-residence—which here can be thought of as indicating biological relatedness—and type of family relationship were associated with the strength of aversion elicited by unrelated third-party descriptions. The third aim was to address the question of whether between-individual and within-individual variables, such as sex and fertility, expected to moderate the fitness consequences of inbreeding also moderates incest aversion. Thus, in **Studies I, II, IVb, IVc, and V,** we addressed the question whether women are more averse to incest than men and in **Study III** we investigated whether within-individual variations in fertility over the menstrual cycle affect aversion to participant descriptions. To address the specificity of an eventual effect of fertility, we also investigated whether the variation in fertility over the menstrual cycle affects also third-party descriptions (the costs of which is not affected by variations in a participants own fertility). The fourth aim was to better understand the psychological mechanism by which factors affecting the costs of inbreeding to an individual participant extend to evaluations of third-party incest. In **Study IV** we addressed the question of whether such a link is mediated by a self-reflective (Egocentric empathy) process. Additionally, as a fifth aim, in **Study V** we wanted to address whether the availability of kin-recognition cues that indicate relatedness to an adult are used by children to moderate kin-selective behaviors, such as incest aversion and altruism. In other words, the aim for the studies included in the present thesis was to answer three types of questions: "*Why* do we not have sex with our family members?"; "*How* does this aversion come to manifest itself at the individual level?"; and the question "Why and how do we judge *others* who engage in incest?".

In our attempt to answer these questions, we formulated hypotheses based on the theoretical and empirical background reviewed above. (See Table 1 for research questions, hypotheses, and aims for each study). We then set out to gather empirical data to test these hypotheses in five different data-collections.

Table 1

General Research Questions and Specific Hypotheses for Studies I-V

Study	Research Question	Hypotheses
I	Inclusive-Fitness Model	1. Incest aversion reflects the fitness costs in participant incest
		2. Incest aversion reflects the fitness costs in third-party incest
II	Third-Party Aversion	1. Incest aversion reflects the fitness costs in third-party incest
III	Ovulatory Shift	1. Incest aversion reflects fertility variations in women
		2. Fertility has a stronger effect on participant than third-party incest
IV	Egocentric Empathy	1. Incest aversion to third-party incest is mediated by self-reflection
V	Children's Kinship Cues	1. Availability of kinship-cues predicts subjective certainty in relatedness to parents
		2. Availability of kinship-cues predicts incest aversion to parents

Participant incest: Incest that involves the individual himself. Third-Party incest: Incest that does not involve the individual himself, but two other individuals.

Table 2

Summary of Study Methodology and Participant Characteristics

Study	Time of Data-Collection	Sampling Frame	*N*	Mean Age	*SD*	M%/F%
I	April 2011	Convenience sample of university students	663*	26.0	6.9	28%/72%
II	September-November 2009	Convenience sample of university students	434	25.5	6.8	29%/71%
III	April 2011	Convenience sample of university students	206*	24.5	5.0	0%/100%
IV			1661	27.2	8.1	30%/70%
a*	April 2011	Convenience sample of university students	646*	25.9	6.9	28%/72%
b	May-September 2013	On-line convenience sample	585	30.2	10.9	35%/65%
c	May-September 2013	On-line convenience sample	430	24.9	6.2	25%/75%
V	April-May 2012	Convenience sample of students	702	26.1	6.4	21%/79%

*Analyses conducted on participants from the same data-collection. Differences in sample size, age distribution, and sex ratio are due to inclusion and exclusion criteria and missing data.

3 Materials and Methods

3.1 Participants

Combining all studies we obtained information from 2797 individuals with a mean age of 26.8 years. These observations were gathered in five different data-collections. Twenty-seven percent of the participants were men and 73% were women. In all studies convenience sampling was employed. Because a process formed by natural selection over a long period of time should not necessarily differ a lot between different university students and non-university students within the same population, it was argued that none of the studies necessitated a population-based sample. Participants were therefore recruited from universities and polytechnic schools in Finland and on-line through social media (See Table 2 for participant characteristics for the specific studies).

3.2 Procedures

In all studies participants were presented with various fictive descriptions of incest between two individuals. These fictive descriptions could vary along several dimensions and describe different types of incest. There were three *levels* of the descriptions: The descriptions could involve the participant him- or herself and another individual (participant description) or not involve the participant him- or herself, but two other individuals (third-party description). Third-party descriptions could further describe incest between two individuals who both were related to the participant (related third-party descriptions) or between two individuals who both were unrelated to the participant (unrelated third-party descriptions). Within each level (participant descriptions, related third-party descriptions, and unrelated third-party descriptions) we also varied other factors of interest, such as the *degree of relatedness* between those described as involved in incest (e.g., full-siblings, half-siblings, or cousins; or biological or socio-legal relationship), the *type of family relationship* (e.g., siblings or parent-child), and presence of *kin-recognition cues* (i.e., shared co-residence or not). As a final factor, descriptions also varied in *similarity* to actual relationships reported by the participant.

Self-similar descriptions reflected an own actual relationship reported by the participant, and self-dissimilar descriptions did not reflect an own actual relationship reported by the participant. (See Table 3 for the description types used in Studies I to V). In all studies, incest aversion was operationalized as the self-reported levels of disgust the descriptions elicited in the participants.

Apart from the survey in Study IIIb, which was administered in Polish and English, all surveys were administered in Swedish.

Table 3

Levels of and Factors Varied within the Incest Descriptions used in Studies I-V

Study	Levels of Incest Descriptions	Factors Varied within Level(s) of Incest Descriptions
I*	Participant	Degree of relatedness (Full-sibling Vs. Half-Sibling Vs. and Cousins)
	Related Third-Party	
	Unrelated Third-Party	
II	Unrelated Third-Party	Type of Family Relationship (Siblings Vs. Parent-Child: Biological Vs. Socio-legal)
		Availability of Kinship Cues (Shared Co-residence Vs. No Shared Co-residence)
III*	Participant	
	Related Third-Party	
	Unrelated Third-Party	
IV	Unrelated Third-Party	Self-Similarity (Self-similar vs. Self-Dissimilar)
V	Unrelated Third-Party	

*Analyses conducted on participants from the same data-collection.

3.2.1 Study I

In this quasi-experimental study we tested whether the strength of incest aversion followed predictions derived from inclusive-fitness theory. The participants were in a first step asked to report the number of same-sex siblings, opposite-sex siblings, opposite-sex half siblings, and opposite-sex cousins. If a participant reported having more than one relative in any of these categories, then one of these individuals was randomly selected for subsequent questioning. This was done by asking the respondent to think about their "[third] oldest same-sex sibling]" or their "[second] oldest opposite-sex sibling", where the ordinal identifier was randomly chosen between 1 [oldest] and the actual number of relatives reported for each kinship category of interest. If a respondent reported having zero relatives in any of the kinship categories, they were not asked any further questions including kin of this type. In order to facilitate information gathering, the respondent was asked to provide the name of each of these randomly selected relatives. The names were not saved in the data file and this procedure therefore did not endanger anonymity. Each participant was presented with three different levels of incest descriptions: participant descriptions, related third-party descriptions, and unrelated third-party descriptions.

The focal person in the various description levels was either the participant (participant descriptions) or a same-sex sibling (related third-party descriptions) or a same-sex individual (unrelated third-party descriptions). For each level of incest description, there was up to three different degrees of relatedness between those described as participating in incest (focal person vs. full sibling, half sibling or cousin). The number of participant- and related third-party incest descriptions was determined by the actual relationships reported by each participant. For all participants unrelated third-party incest descriptions included all possible relationships. To control for order effects of description level we used a Latin Square procedure and to control for order effects of degree of relatedness we pseudo randomized the order of descriptions within each level, setting a randomized order for each version of the experiment. Thus, the eventual order effects were counterbalanced across the whole study. In all, three different versions of the web-administered experiment were created for each sex yielding a total of six experiment versions. Participants were asked to choose a version according to their month of birth, distributing the participants evenly across the different versions.

For each incest description the participants were asked to self-report their level of disgust on a Likert-type scale with the anchors 0 (*not at all disgusting*) and 9 (*extremely disgusting*).

3.2.2 Study II

In this experimental study where we investigated sensitivity to third-party incest, participants were asked to read descriptions of two to the participant unrelated individuals engaging in incest. We manipulated whether these persons were biologically or socio-legally related (2); had shared co-residence or not (x 2); were father-daughter, mother-son, or brother-sister (x 3), and were engaging in reproductive sexual activity (i.e., vaginal intercourse) or not (x 2). Due to a limitation in the manipulation of whether the persons described as engaging in incest were engaging in reproductive sexual activity or not, this factor was excluded from analyses. This yielded a mixed-design with the between-subjects factor sex (male vs. female respondent) and three within-subject factors with the dependent measure disgust, which was self-reported using a Likert-type scale with the anchors 1 (*not at all disgusted*) and 5 (*very disgusted*).

3.2.3 Study III

In this study using a natural-groups design, we investigated the specificity of the ovulatory shift in female incest aversion. We used observations given by female participants for participant-, related third-party-, and unrelated third party descriptions from the data-collection described of Study I.

As a proxy-measure of fertility status, we measured menstrual-cycle position using drop-down menus through which participants provided the dates of the onsets of their most recent menses and the expected onset of the next menses.

After this we estimated current menstrual-cycle position by counting forward from the onset of the prior menses. A dichotomous variable was based on Wilcox and colleagues (2001) benchmark values of the likelihood of conception for each day during the menstrual cycle. We coded women who responded to the survey during a time frame in which the mean fertility is 6% as fertile and women outside this time frame as non-fertile. Outside the fertile time frame the mean fertility is 1%.

3.2.4 Study IV

In this study we explored whether judgments of third-party incest are done through self-reflective processes (i.e., egocentric empathy) using three different approaches.

Study IVa. As a natural-groups approach, we coded each unrelated third-party description in the data-collection described in Study I as either self-similar (i.e., corresponding to an own actual relationship) or self-dissimilar (i.e., not corresponding to an own actual relationship).

Study IVb. In this correlational study, participants with an other-sex sibling were as a first step asked to read a short description of a person of the same sex as the participant telling a friend about his/her relationship to his/her other-sex sibling. In this part, the relationship was described as warm and friendly. After this and before a second part of this description participants were asked to rate the degree the described relationship was comparable to the relationship between themselves and their other-sex sibling and to which degree they had been thinking about their other-sex siblings while reading the description on Likert-type scales ranging from 0 (*not at all*) to 9 (*extremely much*). After this participants were asked to read a second part of the description. In this part the focal person told their friend that they had thought about having sex with their other-sex sibling and that they had felt very sexually aroused at this thought, and that at one time they had also been watching their other-sex sibling taking a bath. After this part of the description participants were asked to rate how disgusting they perceived the incestuous sexual interest to be on a Likert-type scale ranging from 0 (*not at all* *disgusting*) to 9 (*extremely disgusting*). (See Figure 4 for a schematic overview of the methodological procedure).

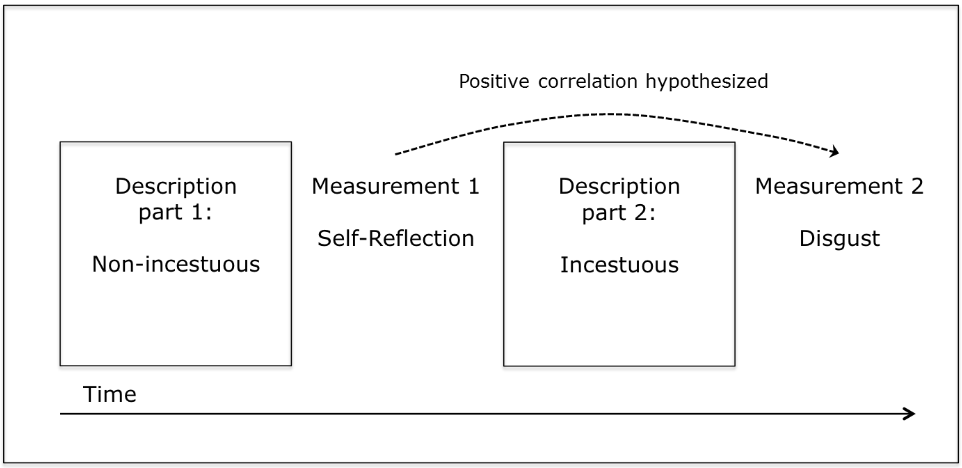


Figure 4. Schematic overview of the procedure in Study IVb, in which participants were asked to read a description of a sibling pair in two steps (Part 1 and 2). In Part 1 the description did not have any incestuous content. After reading Part 1 and before reading Part 2, we measured participants' self-reflection. Part 2 contained incestuous sexual interest between the siblings. After Part 2 participants were asked to rate how disgusted they felt. We hypothesized a positive correlation between Measurement 1 and Measurement 2.

Study IVc. In this experiment, we created self-similar and self-dissimilar unrelated third-party descriptions based on features (age, height, and hair color) regarding the participants' own other-sex sibling obtained earlier in the survey. In order to mask the manipulation we obtained information about features (birth month, sexual orientation and how often they met this sibling) that we did not use in the manipulation and also asked the participants to report the same features about themselves. We also embedded the incest description among questions regarding how common the participants thought other types of moral transgressions to be and how likely they were to commit such transgressions. Participants were chosen to the conditions based on their birth month. In the self-similar condition, the information provided by the respondent was automatically copied over to the description using a function available in the software used. In the self-dissimilar condition the information provided by the respondent was altered before it was included in the description. For instance, if a male participant reported that the other-sex sibling was younger than himself or herself, the self-similar condition included the following wording “a man and his *younger* sister” while in the self-dissimilar condition the wording was altered to “a man and his *older* sister”. The unrelated third-party description was preceded by a prompt asking the participants to try to create mental images of the described situation and try to imagine the ambience and the feelings experienced by the persons described. After reading the description, participants were asked to report the degree to which they felt disgusted by the story on a Likert-type scale with the anchors 0 (not at all) to 9 (extremely much). (See Figure 5 for a schematic overview of the methodological procedure).

To test whether the groups were comparable in their attitudes towards incest prior to the manipulation, one of the moral transgressions was consensual incest between two adults and the participants were asked to decide how people engaging in incest should be punished on a scale with the options no prison/0-6 months/6 months-1 year/1-2 years/2-5 years/6-10 years/11-19 years/20 years or more. Finally, although we tried to mask the manipulation and thus the hypothesis, we thought it possible for participants to see through this manipulation. To deal with this possibility, we included a question at the end of the survey, where we asked the participants to choose which hypothesis, out of seven possibilities, that was put to the test in the study. All participants who answered that they thought that the tested hypothesis was that “the reaction to a description of others engaging in incestuous sex depends on whether one simultaneously imagines one’s own sibling or not” were excluded from further analyses.

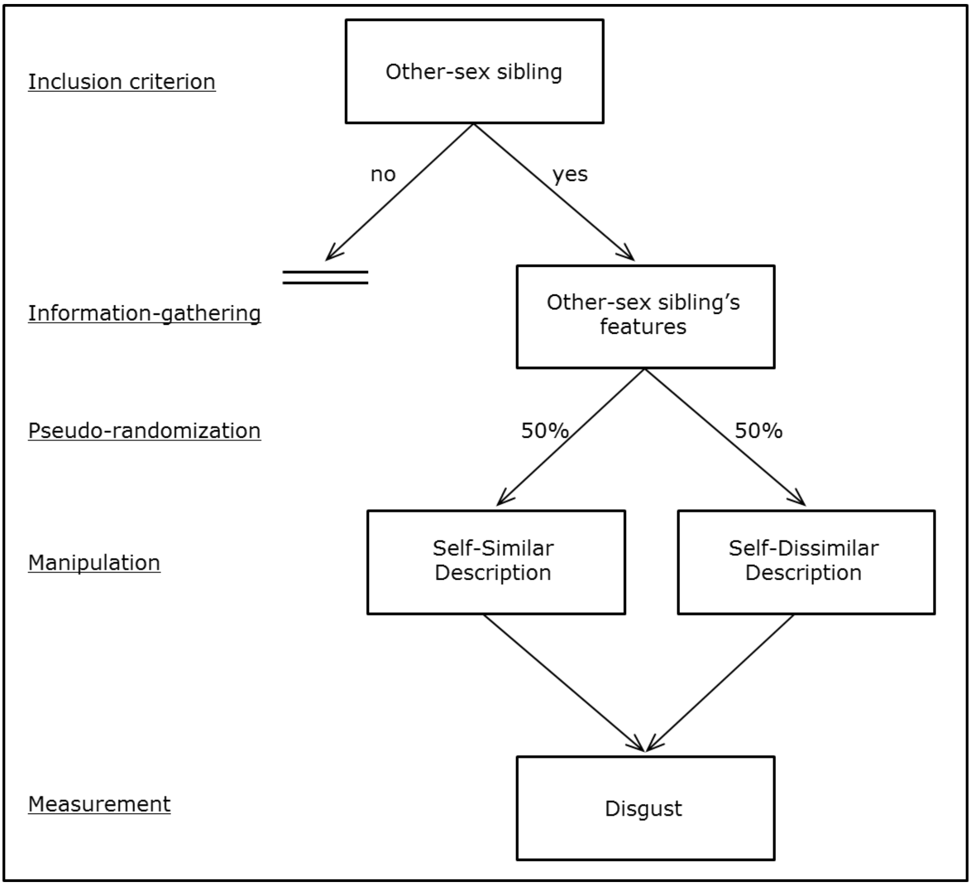


Figure 5. Schematic overview of the methodological procedure in Study IVc. We included only participants who reported having an other-sex sibling. In a next step we gathered information about features of participants' other-sex siblings. Some of these features were used to create two experimental conditions, to which participants were pseudo-randomized. In the experimental conditions participants were asked to read unrelated third-party incest descriptions that could be either self-similar or self-dissimilar. After reading these descriptions participants were asked to self-report the level of disgust they felt.

3.2.5 Study V

In this study we explored how the availability of kinship cues during childhood affects incest aversion to parents in adulthood. To do this we first asked participants to retrospectively report the presence of 32 different cues possibly providing information about relatedness to their parents. These items included, for example, received support, time spent together, and phenotypic and behavioral similarity. After this we factorized the responses to create scale values for each participant. Using this scale values as predictors and subjective certainty in relatedness and incest aversion as dependent variables, we then assessed the validity of these cues as a proximate mechanism in the development of incest aversion.

3.3 Statistical Analyses

Because we repeated measures within participants in Studies I, II, III study IVa, and V, we analyzed the data using Generalized Estimation Equations (GEE) in SPSS. Repeated observations from individual participants are generally clustered (i.e., positively correlated) and this should be taken into account when analyzing data (Agresti, 2007). GEE fits a generalized linear model to observations with an unknown correlation structure (Gardiner, Luo, & Roman, 2009). Similarly to a generalized linear model, the GEE gives population-averaged effects rather than the effects of changing one or more factor for a given individual (Hardin & Hilbe, 2003).

In the correlative study, Study IVb, we used correlations and in the experimental study, Study IVc, we used an independent samples *t*-test that we corroborated with a Mann-Whitney U-test.

In Study V, where we explored the association between the availability of kinship cues in childhood and kin-directed behavior in adulthood, we first factorized the availability of kinship cues in childhood using an Exploratory Factor Analysis. The obtained factor solution was then corroborated using a Confirmatory Factor Analysis in AMOS Graphics 7.0. From this factor solution we created scale measures of kinship cues that we used as a predictor in regression analyses with subjective certainty, altruism, and incest aversion as the dependent variable.

As an additional analysis conducted for the present thesis, we conducted a meta-analysis of the effect of sex on incest aversion. To do this we obtained effect size and precision estimates of the effect of sex on incest aversion from each data-collection and used Comprehensive Meta-Analysis 2.0 to calculate the combined effect. As there was some variation across the included studies regarding sampling, methodology, and operationalizations (see Tables 1, 2, and 3), we used a random-effects model. A random effects model assumes that the computed combined effect is the mean of effect sizes in different populations, rather than the mean of different estimations of an effect size in the same population (Borenstein, Hedges, J. P. T. Higgins, & Rothstein, 2009).

4 Results

4.1 Inclusive-Fitness Theory Predicts Strength of Incest Aversion

In Study I our aim was to test whether the strength of incest aversion followed predictions derived from inclusive-fitness theory.

4.1.1 The Effect of Description Level on Incest Aversion

We first tested our expectation that participant incest descriptions and related third-party incest descriptions would elicit stronger aversive reactions than unrelated third-party incest descriptions, and furthermore, that participant descriptions would be found more aversive than related third-party descriptions. We found an effect of type of incest description on levels of elicited disgust. However, there was no difference between participant incest descriptions and related third-party incest descriptions. (See Figure 6 for means and standard errors.) Next, we recalculated these analyses separately for men and women. We found the same pattern in both women and men.

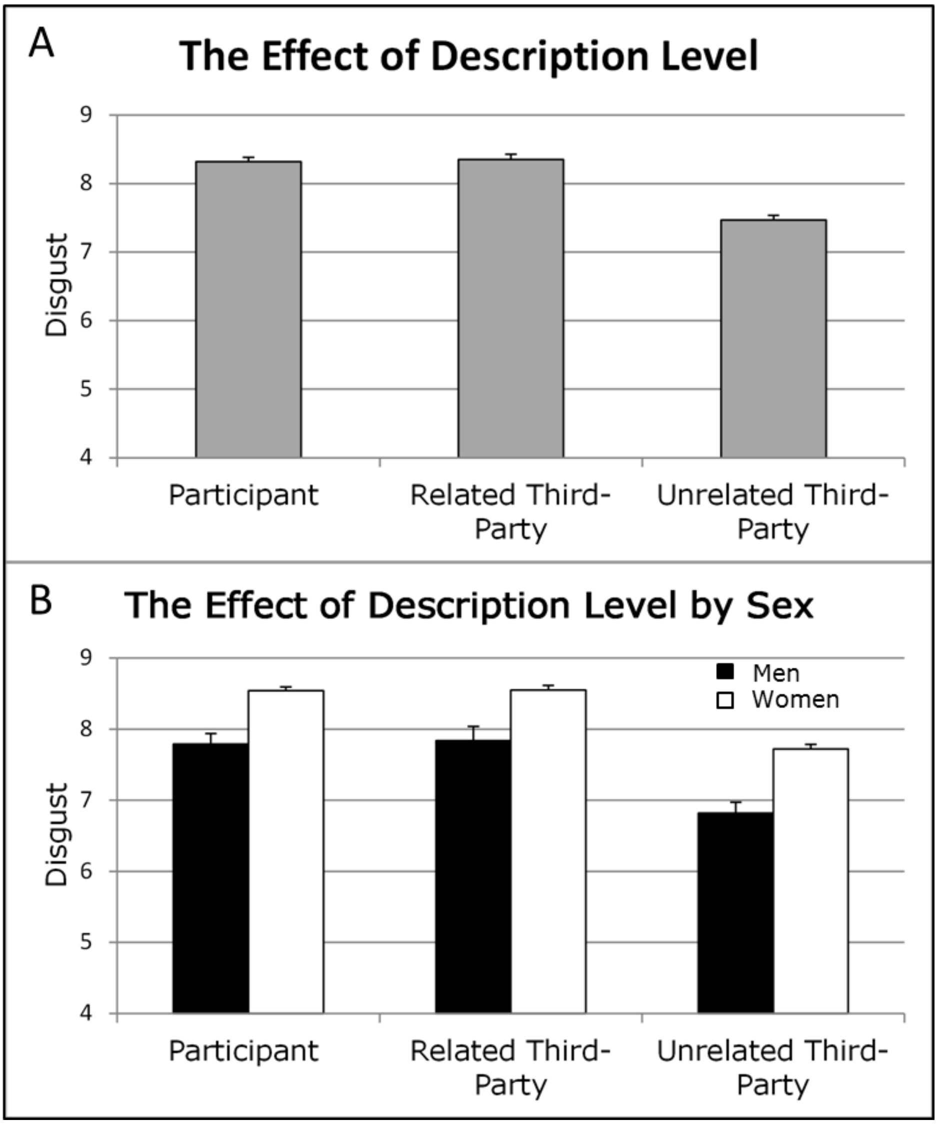


Figure 6. The effect of description level (participant, in which participants themselves were presented as having sex with their actual opposite-sex relatives; related third-party, in which participants' actual same-sex sibling was presented as having sex with the participants' opposite-sex relatives; and unrelated third-party, in which a same-sex individual unrelated to the participant was presented as having sex with their opposite-sex relatives) on disgust. Higher values indicate more disgust. The upper panel A consider men and women simultaneously and the below panel B men and women separately. There was an effect both in men (*p* >.001) and women (*p* >.001) and across both sexes (*p* >.001).

4.1.2 The Effect of Relatedness on Incest Aversion

We next tested our expectation that the degree of relatedness between those described as participating in the inbreeding descriptions would moderate disgust reactions such that the higher the relatedness the more disgust the descriptions would elicit. We found an effect of relatedness between those described as participating in inbreeding (r = .50, r = .25, and r = .125) on levels of elicited disgust, so that the higher the degree of relatedness the stronger the inbreeding aversion. Again, we recalculated this analysis separately for men and women. We found the same pattern for women. For men, however, we found no difference in disgust to inbreeding between cousins and half-siblings. (See Figure 6).

Taken together, we found that human inbreeding aversion is sensitive to the fitness costs a person would suffer from various types of inbreeding irrespective of whether the person him- or herself is involved in the inbreeding. These results suggest that inbreeding aversion follows predictions derived from inclusive-fitness theory.

4.2 Sensitivity to Fitness Cost in Third-Party Inbreeding

As a final step in Study I we expected to find an effect of relatedness between those described as participating not only in participant descriptions, but also in third-party incest descriptions. We found that in all description levels, including related and unrelated third-party descriptions there was an effect of degree of relatedness. In all description levels, the less related the described individuals were, the less disgust did the description elicit in the participant. The only exception to this was that we did not find any difference between r = .5 and r = .25 in participant descriptions. (See Figure 8).

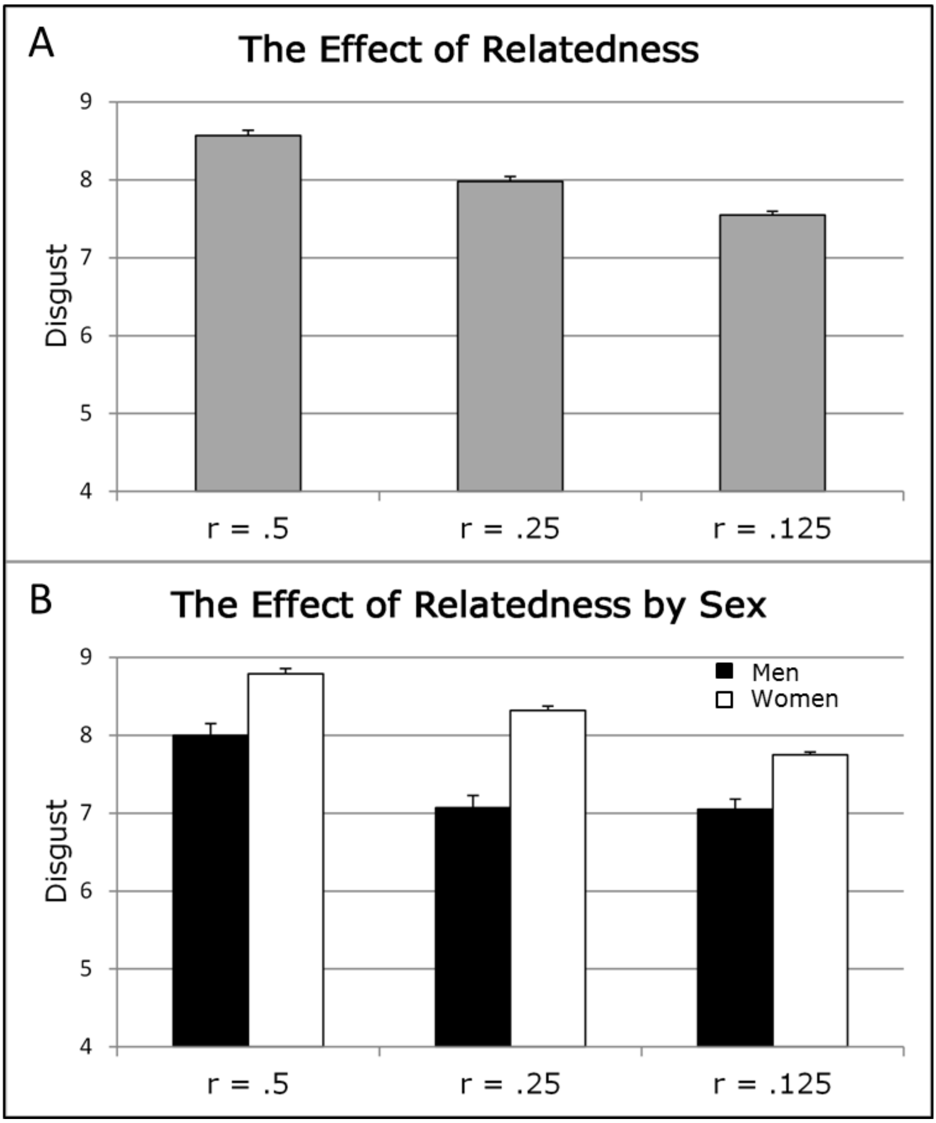


Figure 6. The effect of degree of relatedness (*r* = .50 [full siblings], *r* = .25 [half siblings], and *r* = .125 [cousins]) between those described as participating in incest descriptions on self-reported disgust with higher values indicating stronger disgust reactions. Higher values indicate more disgust. The upper panel A considers men and women simultaneously and the below panel B considers men and women separately. There was an effect both in men (*p* >.001) and women (*p* >.001) and across both sexes (*p* >.001).

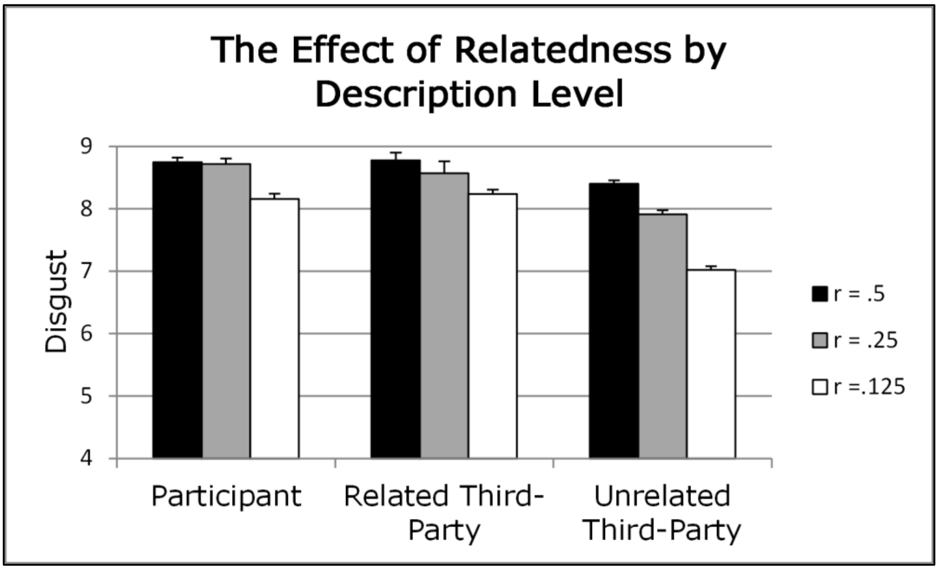


Figure 8. The effect of relatedness (*r*) between those described as participating in incest within each incest description; (participant incest descriptions, in which participants were presented as having sex with their actual opposite-sex relatives; related third-party incest descriptions, in which participants' actual same-sex sibling was presented as having sex with the participants' opposite-sex relatives; unrelated third-party incest descriptions, in which a same-sex individual unrelated to the participant was presented as having sex with their opposite-sex relatives). Higher values indicate more disgust. Error bars represent the standard error of the point estimates. The interaction was significant ($p <. 001$).

This result suggests that not only are humans sensitive to the fitness costs they would suffer from engaging in inbreeding, they are also sensitive to the fitness costs *others* suffer from engaging in inbreeding. To explore this further, in Study II, we analyzed how biological relatedness (biologically related vs. socio-legally related), co-residence (co-residence vs. no co-residence), and type of family relationship (parent-child vs. sibling) moderated incest aversion in unrelated third-party descriptions. We found support for our hypotheses that human incest aversion is sensitive to fitness cost variations in third-party incest and to the availability of kinship cues between these individuals. The results confirmed our predictions that biologically related incest would elicit more disgust than socio-legal incest (See Figure 9), that incest between individuals described as having co-resided would elicit more disgust than incest between individuals described as not having co-resided (See Figure 10), and that parent-child incest would elicit more disgust than sibling incest (See Figure 11).

Taken together, we found that biological relatedness, a solid cue of relatedness (co-residence), and the type of family relationship all modulated the strength of aversion to unrelated third-party incest. These results suggest that human incest aversion is sensitive to fitness cost variations in situations where there is no direct cost to the person him- or herself.

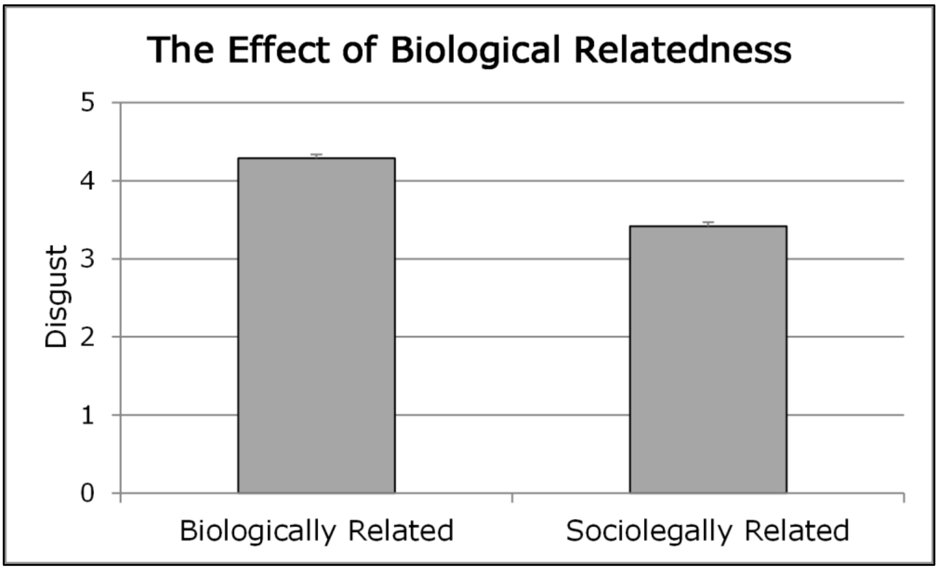


Figure 9. Incest between individuals described as biological related elicited more disgust than incest between individuals described as socio-legally related (p < .001). Higher values indicate more disgust. Error bars represent the standard error of the point estimates.

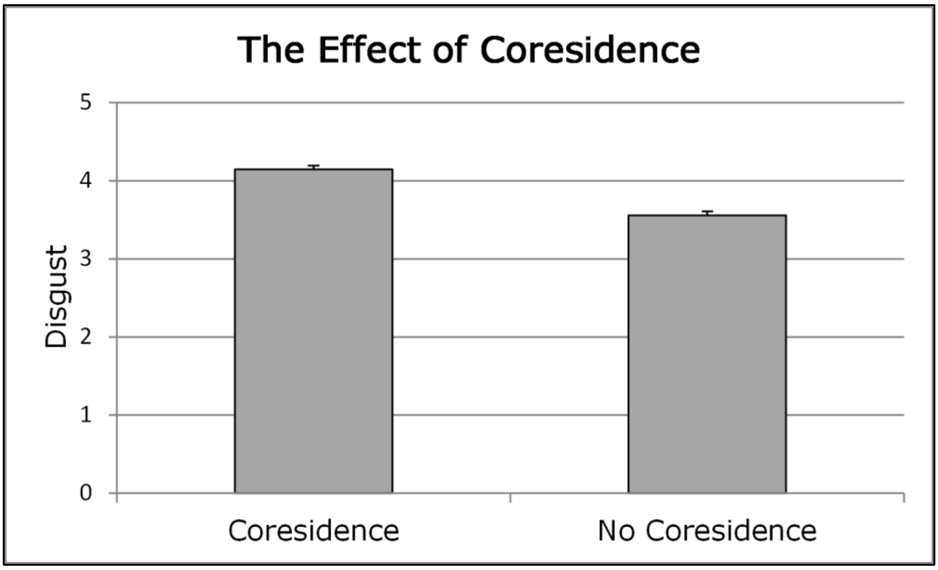


Figure 10. Incest between individuals described as having co-resided elicited more disgust than incest between individuals described as not having co-resided ($p < .001$). Higher values indicate more disgust. Error bars represent the standard error of the point estimates.

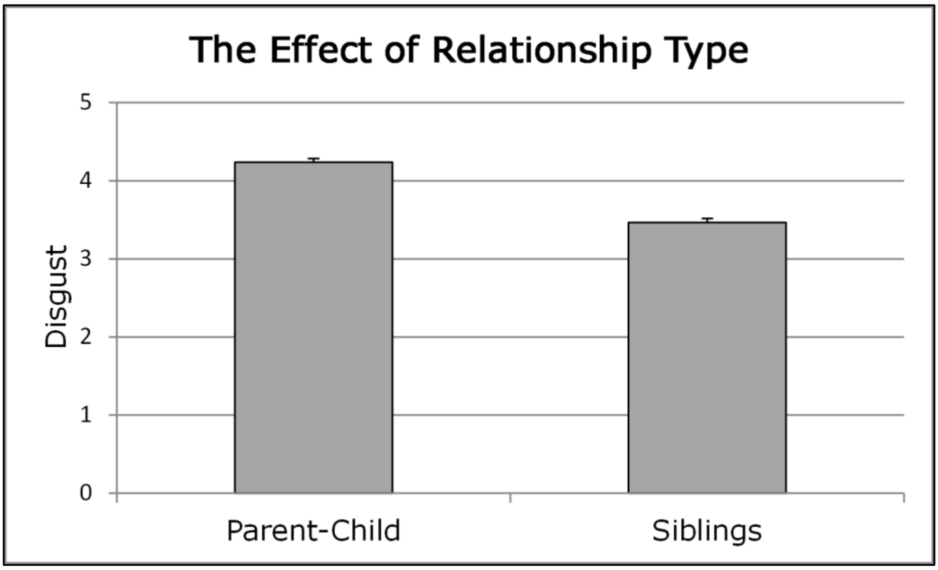
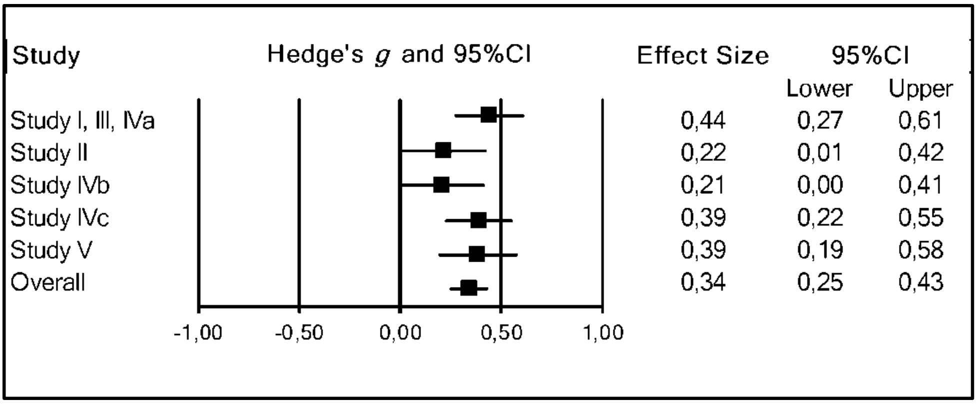


Figure 11. Incest between individuals described as parent and child elicited more disgust than incest between individuals described as siblings ($p < .001$). Higher values indicate more disgust. Error bars represent the standard error of the point estimates.

4.3 Sex Moderates the Strength of Incest Aversion

To analyze the effect of sex on incest aversion, we obtained an effect size estimate of the effect of sex on incest aversion and the precision of this estimate for each of the separate data-collections. We found that, across these data-collections, women were more averse to incest than men, yielding a small to medium combined effect size. (See Figure 12 for details.)



Study	Effect Size	95%CI Lower	95%CI Upper
Study I, III, IVa	0,44	0,27	0,61
Study II	0,22	0,01	0,42
Study IVb	0,21	0,00	0,41
Study IVc	0,39	0,22	0,55
Study V	0,39	0,19	0,58
Overall	0,34	0,25	0,43

Figure 12. The forest-plot diagram shows the dispersion and precision of the estimated effect sizes of the effect of sex on incest aversion for each of the data-collections and the computed effect size of the effect of sex on incest aversion across these data-collections. Positive values indicate stronger incest aversion for women and negative values indicate stronger incest aversion for men.

4.4 The Strength of Incest Aversion during the Menstrual Cycle

To test how within-individual variations in the potential cost inbreeding would have on incest aversion, we in Study III analyzed the effects of variations in fertility across the menstrual cycle on incest aversion in women. As expected women were overall more disgusted by incest when fertile compared to when not fertile. As a second step we also explored how the effect of fertility was moderated by description level. We found an effect of fertility status on disgust elicited by participant, but not by related or unrelated third-party descriptions. (See Figure 13).

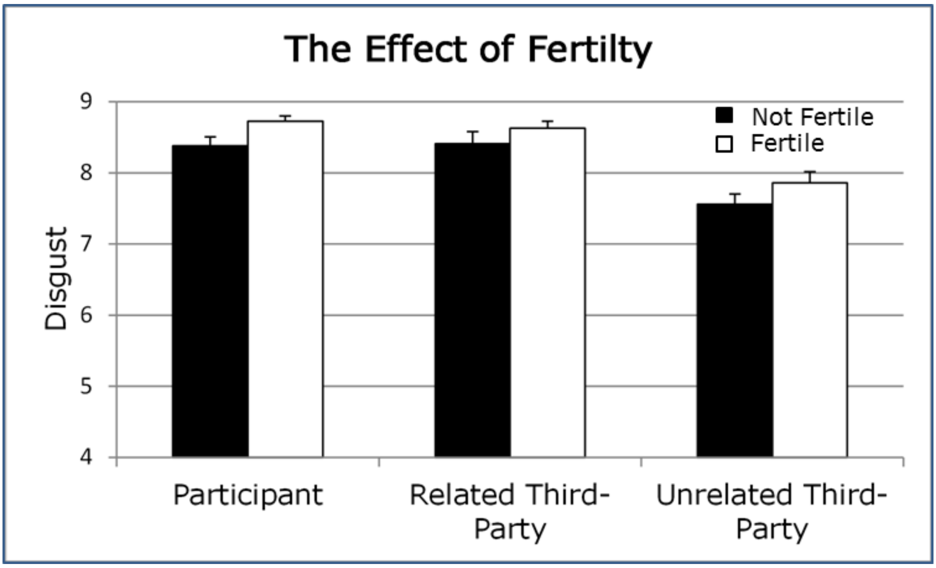


Figure 13. The effect of fertility on incest aversion in women within description levels. Higher levels indicate more disgust. Error bars represent standard error of he point estimates. There was an interaction between fertility and description level (p<.001).

These results suggest that the effect of fertility is stronger in self-regulatory situations than in situations where the aversion is extended to encompass situations in which one’s own fertility does not affect the fitness costs to those involved in incest. As we observed non-significant effects of fertility status also in third-party descriptions and the direction of these effects was in the same direction for all description types, we proceeded by comparing the magnitude of these effects. There was a difference in the magnitude between Participant- and Unrelated Third-Party Descriptions. There was however no difference between Participant- and Related Third-Party Descriptions or between Related- and Unrelated Third Party Descriptions.

4.5 Egocentric Empathy in Evaluating Third-Party Incest

In Study IVa, we tested whether self-similar unrelated third-party incest descriptions evoked higher levels of disgust than self-dissimilar unrelated third-party descriptions, arguing that an empathic process would be more accessible in self-similar descriptions. In line with this prediction, we found disgust to be higher as a reaction to self-similar than to self-dissimilar descriptions. This suggests that when judging unrelated third-party descriptions, there was an effect of having a similar relationship oneself. This result is in line with the egocentric empathy theory, as this theory assumes that the easier mental representations of a given incest situation can be related to oneself participating in a similar situation, the more easily an as-if reaction can be transferred to others.

In Study IVb, we tested the correlation between self-reflection and incest aversion, by, in a first step, asking participants to read a description of a sibling pair and after reading this measuring how participants considered the relationship of this sibling pair to be similar to participant's own actual relationship with their sibling and the degree to which participants thought about their own sibling. In a second step, participants were asked to read a continuation of the description. This continuation included sexual interest between the siblings. After reading this, participants were asked to report how disgusted the description made them feel. We argued that should participants employ an egocentric process in their evaluations of unrelated third-party incest descriptions, the degree of self-reflection employed in the first measure would be positively correlated with the degree of disgust in the second measure. In line with this expectation, we found a positive correlation, suggesting that the more the participants self-reflected the more disgusted they found the incestuous part of the story. (See Table 4 for details.)

This result suggests that the more an individual compares a situation to an actual own situation, the more disgust does unrelated third-party incest elicit in this individual. However, due to the correlative nature of this study a spurious connection between these variables cannot be ruled out. It is possible, for instance, that family values affect both the degree to which one thinks about one's sibling, and the degree to which one finds incest disgusting.

Table 4

Correlation Matrix for the Degree to which Participants Found the Unrelated Third-Party Description Similar to Their own Actual Relationship, Thought about Their own Actual Relationships while Reading the Description, and the Degree to which they Judged the Descriptions Behaviors as Disgusting

	1.		2.		3.	
	r	(*n*)	*r*	(*n*)	*r*	(*n*)
1. Comparability with own relationship	1	(356)				
2. Thought about own relationship	.583***	(359)	1	(359)		
3. Unrelated Third-Party Disgust	.124**	(356)	.121**	(356)	1	(356)

† $p < .1$ * $p < .05$, ** $p < .01$, *** $p < .001$, one-tailed.

In Study IVc, we manipulated the information used in unrelated third-party descriptions, so that third-party descriptions could be either self-similar (i.e., using features from the participant's real relationship) or self-dissimilar (i.e., not using features from the participant's real relationship). Prior to examining the effect of this manipulation, we checked whether participants in the two conditions differed in their attitudes towards incest prior to the manipulation. They did not. We thus concluded that the groups were comparable regarding attitudes to incest. After the manipulation, the group reading the self-similar scenario reported feeling more disgusted than the group reading the self-dissimilar scenario. This suggests that including features from the participant's real relationship in the description significantly increased their incest aversion compared to when such features were not included. This result is in line with the egocentric empathy theory. As we maintained high experimental control and the experimental groups were comparable, this result indicates that the observed effects in Studies IVa and IVb are likely due to the possibility to make self-references. Over these three studies, we found support of an egocentric empathy process accounting for some of the variation in judging third-party incest.

4.6 Children's Kinship Cues Predict Kin-Directed Behavior

In Study V, we measured how the availability cues providing information about relatedness to parents predicted subjective certainty in relatedness and incest aversion towards parents. In a first step we factorized 32 items measuring availability of kinship cues. We randomly chose 50% of the responses to an Exploratory Factor Analysis and found three factors that were conceptualized as parental support, phenotypic similarity, and behavioral similarity. This factor structure was confirmed in a Confirmatory Factor Analysis using the other 50% of responses. In the Confirmatory Factor Analysis we only included the items with the highest factor loadings for each factor. We also found that the same factor structure was applicable to observations regarding both female and male parents. After this we selected the four items with highest factor loadings for each factor to create scale values. (See Figure 14 for factor loadings).

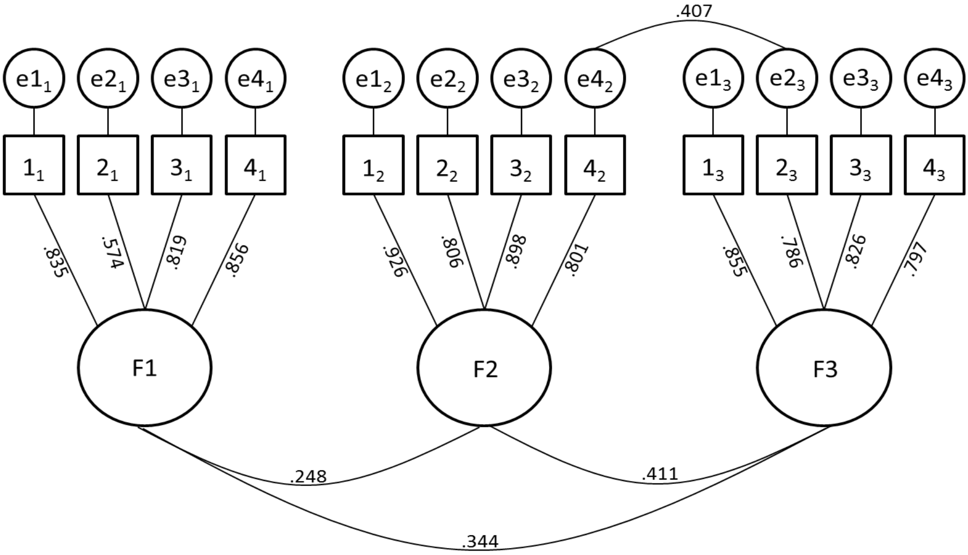


Figure 14. Item loadings on the factors phenotypic similarity (F1), parental support (F2), and behavioral similarity (F3). (1_1)”How much did your parent talk to you when you were a child?”, (2_1)”How aware was your parents of where you spent your time and what you did with your friends when you were a child?”, (3_1)”Did your parent praise you when you did something well when you were a child?”, (4_1)”How much physical closeness did your parent offer you as a child?”, (1_2)“How much have your parent’s relatives said you and your parent resemble each other regarding looks?”, (2_2)“How much do you resemble your parent regarding looks?”, (3_2)”How much have non-relatives said you and your parent resemble each other regarding looks?”,(4_2) ”How much have your other parent's relatives said that you and your parent resemble each other regarding looks?”, (1_3)”How much have your parent's relatives said you and your parent resemble each other regarding behavior?”, (2_3)”How much have your other parent's relatives said that you and your parent resemble each other regarding behavior?”, (3_3)”How much have non-relatives said that you and your parent resemble each other regarding behavior?”, (4_3)”How much has your other parent said that you and your parent resemble each other regarding behavior?”. Items 4_2 and 2_3 were allowed to co-vary.

We then investigated the predictive value of the scales. Using the scale variables as predictors in multiple regression analyses, we found support for the expectation that available kinship cues during childhood predict subjective certainty in relatedness and altruism to parents and incest aversion to mothers. They did, however, not predict incest aversion to fathers. (See Table 5 for details).

Table 5

Regression Analyses with the Dependent Variables Subjective Certainty in Relatedness, Cooperation, and Incest Aversion towards Mothers and Fathers with the Predictor Variables Parental Support, Phenotypic Similarity, and Behavioral Similarity

Predictor Variables	Criterion Variables					
	Mother			Father		
	Subjective Certainty[a]	Cooperation[b]	Incest Aversion[a]	Subjective Certainty[a]	Cooperation[b]	Incest Aversion[a]
	B(SE)	*B(SE)*	*B(SE)*	*B(SE)*	*B(SE)*	*B(SE)*
Parental Support	.07(.12)	.48(.05)***	.13(.04)*	.18(.06)**	.50(.04)***	.05(.05)
Phenotypic Similarity	.35(.09)***	.09(.03)**	.01(.04)	.25(.06)***	.03(.04)	.05(.05)
Behavioral Similarity	-.19(.10)*	.14(.04)***	.07(.05)	-.08(.36)	.15(.04)***	-.02(.01)
Variance	R^2 = .07[c]	R^2 = .22[d]	R^2 = .02[c]	R^2 = .09[c]	R^2 = .29[d]	R^2 = .01[c]
Model Fit	χ^2=16.16***	*F*=60.51***	χ^2=10.14*	χ^2=30.87***	*F*=85.03***	χ^2 = 2.77

[a] Binary logistic regression model; [b] Linear regression model; [c] Nagelkerke's R^2; [d] Adjusted R^2

† p < .01, * p <.05, ** p <.01, *** p <.001

5 Discussion

Based on observations from a total of 2797 individuals we in five studies empirically addressed questions regarding why and how incest aversion operates in humans. To do this we created four web-administered surveys and two web-administered experiments. In these we used different types of descriptions of situations involving incest, adapting the format of these descriptions so as to be able to test our hypotheses. The hypotheses we set out to test were derived from evolutionary theory. With some minor exceptions, we found support for our hypotheses regarding both the ultimate question of *why* close kin are avoided as mating partners and the proximate mechanisms governing the manifestation of incest aversion on an individual level. Moreover, we also addressed how we judge others engaging in incest. To our best knowledge, each of these studies provides novel information regarding human incest aversion. However, before addressing the results in more detail and before discussing the implications of these results, there are a few methodological limitations that need to be addressed.

5.1 Limitations

One limitation across the studies included in the present thesis concerns the sample. In all studies we relied on convenience sampling, and in all but one of these cases we gathered participants from university settings. Although university students and non-university students share their evolutionary background, there may be differences in how they understand the descriptions and in how they chose to report their emotions. Some studies suggest that compared to others, university students could be more likely to base moral judgments on reason and less likely to base moral judgments on emotion (Greene et al., 2008; Pizarro & Bloom, 2003; however see also Helkama, Uutela, & Pohjanheimo, 2003). This could potentially mean that, rather than being true to their emotions, our participants have reported what they have reason to think is a good or accurate response. This, in turn, means that to the degree that our studies include questions where there are belief systems or norms that would lead to the same response pattern as emotion-based responses we cannot separate reason-based and emotion-based responding. It should be noted, however, that in most of the cases, such as in analyses of between-individual differences, biased responding due to belief systems and norms is unlikely to have affected our results. Moreover, in the cases we feared it possible that belief systems or norms could affect the robustness of our studies we made attempts to decrease this possibility. One example is the experimental study, in which we excluded all participants who were aware of the purpose of our study.

Another concern regarding the sample is its ethnical and cultural homogeneity. Although all students in Finland are not of Finnish heritage and although one study included English and Polish speakers, there is reason to believe most participants were Swedish-speaking Finns. This, in turn, raises two limitations. First of all, the pool of Swedish-speaking students in Finland is small and it is possible that some participants have partaken in more than one of these studies. This would mean that the true amount of participants, on whose responses we based our conclusions, is smaller than the number of participants indicates. This could further decrease generalizability. Another limitation is that the homogeneity of the sample pool may limit the generalizability of the obtained results to other ethnic groups and cultures. In attempting to answer questions regarding a phenomenon's evolutionary history or adaptive value, cross-cultural information can be important. Cross-cultural studies are the only studies that efficiently reduce culturally induced variation, and therefore more closely examine culturally universal structures. Because we did not specifically attempt to gather participants with different backgrounds and/or gather participants subscribing to different belief systems, our results should, again, be generalized with some caution. Nevertheless, the ethnical and cultural homogeneity of our sample only poses risks to the degree it truly affects the questions studied and affects them in the predicted direction. This means that for the sample homogeneity to undermine our results, Finns should not only differ from others in how they feel regarding incest, for example, across the menstrual cycle, but also differ in such a way that Finns are *more* affected by fertility variations across the menstrual cycle than are others. Although this cannot be ruled out, it unlikely poses a serious threat to our results.

The correlative nature of several of the studies also introduces limitations. The natural groups and quasi-experimental approaches employed in Studies I, III, and IVa cannot rule out the possibility that the observed effect was caused by something else than the information provided in the various descriptions. For instance, it is possible that the degree of relatedness between those described in the descriptions (Study I) and self-similarity (Study IVa) are spurious and reflect some other underlying factor that is associated to both the predictor variables and the dependent variables. One such possibility is family values. It is possible that the more important you find your family, the more likely you are to think about your family members, and also, the more aversive you find incest. In two studies (II and IVc) we employed a true experimental method and found support for our predictions without the possibility of the aforementioned type of confound. This, by extension, increases our belief in the interpretation of the correlative evidence.

Another threat to our interpretation stems from the use of fictive descriptions as a prompt of incest aversion. These fictive stimuli of incest have limited ecological validity when trying to explain the aversion that is assumed to be part of avoiding sex with close kin in real life. Recognizing this limitation, we nevertheless opted for a method that did not involve real-life situations. It would be ethically and practically unfeasible to ask participants to react to actual incest, as this means that such incestuous events would have to be displayed. Our reason for prompting incest aversion with written descriptions was based on previous studies in which reactions to various scenarios have been measured in similar vignette-type approaches have produced interpretable results. Such vignettes have been used in a wide array of research, including medicine (e.g., Kamal, Iwaarden, & Dijkstra, 2014), legal psychology (e.g., Finnilä-Tuohimaa, Santtila, Sainio, Niemi, & Sandnabba, 2009), and evolutionary psychology (e.g., Kushnick, 2013) and generally been shown to have sufficient validity. It is, however, likely that this increases error variation that, in turn, can reduce the power to detect effects. Thus, we conclude it unlikely that these measurements yield predicted effects a more ecologically valid measurement would not have yielded.

Another related question is whether aversion and actual behavior correspond. Some studies on mate choice have shown that self-reported preferences do not reflect actual behavior very well (Eastwick & Finkel, 2008). Observations of preferences being defied in some circumstances are not surprising. In the same way as thirst can supersede initial disgust reactions to dirty water it is possible that a reduced range of mate choice can supersede initial preferences in the mating domain as well. It is apparent in the literature (e.g., Sariola & Uutela, 1996) that in some cases family members have sexual contact, although this is quite rare. Aversion is probably not the only predictor of sexual contact within the family. A strong aversion may, however, influence the degree to which other factors, such as substance abuse or anti-social traits, can influence the propensity to engage in incest. Exactly how well incest aversion predicts actual incestuous behavior is unknown. Studies employing behavioral propensity measures or case-control (incest vs. no-incest) studies in which aversion is thought of as a predictor of actual sexual behavior could be informative. Future studies should also investigate the possible interaction between aversion and other possible risk factors, such as alcohol abuse or psychopathic traits.

Finally, we operationalized incest aversion in all studies as the degree of disgust participants reported after reading these descriptions. Although this choice rests firmly on earlier evidence regarding the incompatibility of arousal and disgust and on evidence of disgust operating as an emotional reaction to incest, we do not wish to claim that incest aversion is *all* about disgust. Incest aversion may also be related to, for example, moral indignation. Moral indignation is, however, closely linked to a rational perspective on behavior (e.g., Gleichgerrcht & Young, 2013; Greene et al., 2008; Koenigs et al., 2007; Valdesolo & Desteno, 2006; Young et al., 2007) and thus more likely to follow social norms than is the emotion disgust. Although the accuracy of self-reporting disgust has been questioned (e.g., de Jong, van Overveld, & Peters, 2011), studies (Royzman et al., 2008, De Smet et al., 2014) show that physiological correlates of disgust also are sensitive to incest. With this we conclude that self-reported disgust is a feasible measure of incest aversion.

With these considerations in mind, we, with a sufficient degree of confidence in our results, can turn to a discussion of their relation to earlier evidence and to their implications.

5.2 Interpretation of the Results

Our results provide new and important information both regarding the ultimate and the proximate mechanisms involved in the development of human incest aversion. In other words, the studies included in this thesis contribute new information both regarding the selection pressures that crafted human sexual behavior so as to typically exclude close kin as mating partners and regarding how this tendency is accomplished on an individual level.

5.2.1 Incest Aversion Reflects Inclusive-Fitness

It has been known that inbreeding brings about a decrease in fitness in humans as in many other species. As it is known that inbreeding decreases genomic heterozygosity, the evolutionary explanation of inbreeding avoidance goes as far back as the advantage of sexual reproduction over self-replication. The literature indeed provides evidence of a strong and persistent selection pressure against incest. Moreover, inclusive-fitness theory suggests that alleles can increase the probability of their own transmission to future generation by directing investment to our kin, and thereby aiding their reproduction. An allele can gain as much by avoiding or counteracting behavior that is detrimental to its transmission. Thus, an allele that only decreases the propensity of its carrier to engage in incest would be less effectively transmitted over generations than an allele that also contributes to decreasing incest between other individuals to which its carrier is related. However, to our best knowledge, no empirical data have earlier been put forward in support of human incest aversion reflecting an inclusive-fitness perspective. Indeed, our results suggest that the psychological construct of incest aversion may be derived from kin-selection processes. Our studies show that not only do fitness costs predict the aversion associated with an individual him- or herself engaging in incest, they also show that the aversion associated with *others* engaging in incest can be predict by the inclusive fitness cost this situation brings the individual. We found that the fitness costs to the participant were associated with the strength of incest aversion in both participant and third-party descriptions. To the degree this aversion influences behavior that successfully counteracts inbreeding between relatives it is possible that its adaptive function stems from kin-selection. Before adopting these results as strong evidence for a kin-selection process underlying incest aversion in humans, we should turn our eye to possible alternative explanations of our results.

One possible alternative explanation of these results would be the claim that social norms predict the same pattern. Indeed, norms and law could indeed have stronger prescriptions against incest between siblings than between cousins. However, we are not aware of any prescriptions that would separate between full- and half-siblings in the observed manner. On the contrary, social norms tend to dictate that these categories have the same value. Therefore, our results do not fit very well with the view that incest is avoided since it is not approved by society.

In all, our results provide some preliminary evidence of incest aversion following predictions derived from inclusive-fitness theory. The perhaps most serious limitation to this evidence is the imprecision of the measurement. From inclusive-fitness theory clear predictions can be made about the magnitude of the differences in fitness costs from various incest situations. As our data are ordinal we cannot verify these predictions with much precision. With this limitation in mind, we hope future research corroborates our novel empirical finding that kin-selection may have shaped incest aversion.

5.2.2 Sex and Fertility in Incest Aversion

According to parental-investment theory, women are expected to have more to gain from avoiding sub-optimal breeding. Indeed, research clearly supports this hypothesized sex difference (e.g., Bjorklund & Kipp, 1996; Buss, 1989; Buss, Larsen, Westen, & Semmelroth, 1992; Feingold, 1992; Kenrick & Keefe, 1992; Kenrick, Sadalla, Groth, & Trost, 1990). Previous studies on incest aversion have also supported this claim. Thus, our finding that women are more averse to incest than men is not a very novel finding. That said we provide solid evidence for an effect of sex on incest aversion across five studies, each with different measures, efficiently summed in a meta-analysis. In the meta-analysis, we found a small to medium effect size. However, it is possible that this effect size could be somewhat larger as any study where a ceiling effect diminishes variation will also contribute to a decrease in the effect size calculated in the meta-analysis. This limitation does not pose a risk to our conclusion that women are more averse to incest than men. It only limits us in making claims about exactly how much more stronger women's incest aversion is. Again, a different type of measurement would be needed in order to make more precise claims about the degree of difference between men and women when it comes to incest aversion. A strength in our results is that they are derived from different measures, suggesting that the effect of sex on incest aversion is unlikely an artefact of a single measure, but rather a true effect that can be observed with a number of different measures.

It should be noted, however, that women may certainly be subjected to other norms than men, especially regarding sexual behavior. The prediction derived from this fact would also be directionally equivalent to the one derived from evolutionary theory. Therefore it is difficult to in this case efficiently separate between these two models in this case.

Nevertheless, we also found that variations in fertility were associated with the strength of incest aversion. Women are less likely to suffer fitness costs if engaging in incest when they are unlikely to get pregnant than they are when they are more likely to get pregnant, and the strength of incest aversion reflects this across the menstrual cycle. Again, this particular finding is perhaps not very novel. Prior research has shown this effect regarding other sub-optimal sexual behavior. However, our method allowed us to investigate in more detail to extension of this effect. The theory suggests that this effect should be mainly self-regulatory as individual fluctuations in fertility bear no effect on the fitness costs *others* will suffer from inbreeding. In line with this line of thought, we found that the effect of fertility was stronger in participant descriptions than in third-party descriptions. This result suggests that the effect of fertility is quite specific and does not extend to increase aversive reactions to incest between others without a substantial reduction. Apart from adding novel and interesting data regarding the specificity of the effect of fertility in women, these results are difficult to subsume in non-evolutionary models. Fertility in women is concealed—many times even from the women themselves—and there seem to be no norms dictating behavioral differences based on fertility as a function of the menstrual cycle (although there are norms regarding behavior during the menses). Furthermore, any norms dictating such differences, should they exist, would also have to lead to the prediction that this effect is reduced when it comes to extending this effect beyond self-regulation.

5.2.3 Sexual Attraction and Aversion

The rational for the studies was that aversion and the strength of incest aversion is an instrument crafted by evolutionary forces to diminish unfavorable inbreeding. It should be noted that aversion, as such, does not rule out attraction. It is conceivable that a sexual attraction to family members also is present but that this latent attraction is generally not expressed. This idea was famously proposed by Freud (1918), who suggested the existence of a subconscious attraction towards family members. Separating the empirical question from the ontological question of whether a non-observable sexual attraction to family members can be meaningfully interpreted as existing, this idea can be taken to mean either of two things: either 1) initial overt sexual attraction to a family member is replaced by aversion at some developmental stage, after which attraction is absent or 2) a dormant attraction is continuously suppressed by aversion. The first of these possibilities would imply a behavioral or psychological change so that children may be attracted to their family members in an early developmental stage, but in a later developmental stage attraction is replaced by aversion. It is, for example, possible that an aversion is activated only after the onset of puberty, after which there is a risk of conception. While some studies show that children display a wide range of behavior that can be interpreted as a display of sexual attraction to their family members (Friedrich, Fischer, Broughton, Houston, & Shafran, 1998), recently acquired data suggest that already before the age of 12, the likelihood of genital sexual play with family members is markedly lower than the likelihood of such sexual contact or sexual play with non-family members (Antfolk, unpublished data). It thus seems that although some childhood experiences of a sexual nature may involve family members, a preference for individuals not belonging to the family is apparent already in pre-pubertal children.

The second of these possibilities—the possibility that a dormant attraction is suppressed by aversion—implies that aversion and attraction share at least some of their physiological correlates for active suppression to be possible. There is some evidence suggesting these two systems interact. Disgust and sexual attraction involve largely the same neural structures: the occipital lobe, the amygdala, the hippocampus, and the thalamus are involved in processing both disgusting and sexually arousing stimuli (Stark et al., 2005). Moreover, in men (Lange, Wincze, Zwick, Feldman, & Hughes, 1891) and in women (Meston, 2000) physiological sexual arousal is inhibited by activation of the sympathetic nervous system, and several negative emotions, including disgust, have been found to correlate with activation of the sympathetic branch of the autonomic nervous system (Ekman, Levenson, & Friesen, 1983). Disgust has also been found to inhibit sexual arousal (Koukounas & McCabe, 2001; Malamuth & Check, 1980; Rempel & Baumgartner, 2003) and has been implicated in sexual dysfunctions (Borg, de Jong, & Schultz, 2010; de Jong, van Overveld, & Borg, 2013; van Overveld et al., 2013). Conversely, arousal has also been found to down-regulate disgust (Borg & Jong, 2012). Moreover, a preliminary analysis of recently acquired data shows that in the incest domain, disgust is strongly and negatively correlated with arousal (Antfolk, unpublished data). In sum, there is evidence of both an overlap between the physiological correlates between disgust and sexual arousal and a mutual inhibitory effect of psychological disgust and arousal. While this confirms a necessary condition for a continuous suppression, it does not show that arousal is activated when aversion is not present. It would also be necessary to show that an attraction appears when disgust is attenuated. For example, individuals with a low propensity to feel disgusted should be relatively likely to feel sexual attraction to family members.

Another less Freudian possibility is that attraction is absent and this absence is reinforced by aversion as a safe-guard against inbreeding. Should this be the case, a removal of the disgust response would not result in a display of incestuous attraction. Instead such a removal would result in cold disinterest. It is important to note that it may be adaptively advantageous for humans to possess a dormant potential for sexual attraction to family members. If a usually dormant attraction can be activated in situations where opportunity costs are significantly decreased, a capacity to inbreed would outweigh the costs of severely reduced reproduction. To my best knowledge, there are currently no available data against which these theories can be tested. These questions should be addressed in future studies.

5.2.4 What about the others?

In Studies I and II we also found human incest aversion to be sensitive to fitness costs (and a proxy of fitness costs indicated by availability of kinship cues) that others, to whom the participants are *not* related, would suffer if engaging in inbreeding. This indeed is an observed effect that needs additional explanations in order to fit well with evolutionary theory. First of all, there seem to be no advantage to an allele underlying such an aversion unless there is an increased likelihood that these individuals also share this particular allele. In fact, if they are unlikely to share this allele, there may be a relative disadvantage of counteracting this behavior. Before dodging the bullet by saying that one should not expect evolution to be perfect, parsimonious explanations that fit these observations should be addressed (and tested). One such explanation can be derived from Aoki's (2004) study, where, given that prohibitions are not assumed costly, cultural transmission of norms against third-party incest can evolve beyond its inclusive-fitness function. The proximate mechanism by which this extension is carried out could be the type of as-if process based on sympathizing with the third-person situation (Fessler & Navarrete, 2004; Haig, 2011; Westermarck, 1906). One testable prediction of this explanation is that individuals who self-reflect and find sex with own kin disgusting also endorse moral rules prohibiting (i.e., react with third-party disgust) to incest. In line with this prediction, we, in a series of three studies (Studies IVa-IVc), found that the more likely an individual was to self-reflect, the harsher they also reacted to others engaging in incest. Moreover, in Study III, we observed non-significant increases in disgust reactions to both related and unrelated third-party incest descriptions as a function of fertility status. Because the individual likelihood of conception does not affect the costs of third-party incest, these observations cannot be explained as consequences of fertility status on opportunity costs to the individual. It is, however, possible that fertile women felt more disgusted at the thought themselves engaging in incest. Self-reflection of third-party descriptions would then result in an increased disgust response. This emotional response may then have up-regulated disgust reactions to third-party incest descriptions as well.

Although our results are in line with the egocentric empathy explanation and the evolutionary argument underlying it, the results are also consistent with several non-evolutionary theories within social psychology. However, these theories mainly describe the important social role empathy has, and does that without attempting to describe *why* this is the case. To truly test the adaptive value of the egocentric empathy theory and the computational model of third-party moralizing, other types of studies are needed. For example, studies would need to show that punishment can be avoided by affecting social norms, and that this avoidance can be shown to have (or have had) a survival value.

In all, although our results provide some information about the underlying process employed in reacting to *others* engaging in incest, it provides little evidence of this process itself having an adaptive value. We conclude that more studies are needed to address this issue.

5.2.5 The Development of Incest Aversion on the Individual Level

To avoid inbreeding with close kin we first need to efficiently separate our relatives from non-relatives. Some heuristic cues by which other individuals can be identified as kin or non-kin have been described in earlier studies. As mentioned earlier, there is a large body of evidence showing that children who grow up in the same household tend to perceive each other as kin. Furthermore, it has been shown that this cue is secondary for older children who can see their own mother nursing a younger child. There is also evidence of phenotypic similarity between two individuals increasing their certainty in relatedness. As awareness of one's own phenotypic features may have been limited during most parts of our evolutionary background, one theory suggests that the effect of phenotypic similarity is mainly *other-referent*, that is, that it relies on similarity between the individual to be identified and a template generated from already identified relatives and their phenotypic features. Both the maternal perinatal association and the other-referent phenotypic similarity data rest on the assumption that, as a first developmental step, some given individual can reliably be identified as kin. Based on the human family environment it is possible that this first identification is a child's identification of its parents. In Study V we studied a number of possible kinship cues that may be used by children in the identification of their parents. We also, in the same study, with some limitations, confirmed that these cues predicted kin-directed behavior, including incest aversion. Although these results may provide an interesting avenue into the exploration of the developmental processes involved in kin-identification, the results suffer from two limitations embedded in the study. First, the observations are based on retrospective self-report data that are susceptible to error, including a reversal of the causal order; participants certain in their relatedness or with a strong incest aversion to their parents could possibly—and erroneously—report a higher availability of kinship cues in their childhood. Second, apart from the measure of altruism, both the measure of certainty in relatedness and the measure of incest aversion suffered a restriction in range limiting interpretable variation, and thus limiting the power to find effects. This limitation is however likely to underestimate the effect of kinship cues on certainty in relatedness and incest aversion to parents. With these limitations in mind, we hope that these preliminary results will be tested in longitudinal studies where other types of measurements are used.

To fully understand the development of incest aversion future research will need to answer several questions. Evidently, humans are not born with a fully developed aversion; nor does such an aversion appear instantaneously at a certain age. Research should therefore address the question whether there are any necessary developmental experiences, without which an aversion does not emerge. Moreover, there may be sensitive periods with regard to the effect of any particular kinship-cue. Finally, to truly understanding the developmental processes of incest aversion on the individual level still need to uncover the start-off point, a primary kinship-cue, based on which subsequent kin-identification depends.

5.3 What Else is there to Human Inbreeding Avoidance?

Although the studies included in the present thesis provide important information about both the selection pressures crafting incest aversion and the development of incest aversion on the individual level, there are certainly many areas that still need to be addressed. Apart from addressing the limitations already mentioned here, it should be noted that there is certainly more to human inbreeding avoidance than just incest aversion. For example, dispersion of siblings could be achieved through exogamy rules, a possibility that, to our best knowledge, remains untested. Another interesting question is how population viscosity (the average relatedness between members of a population) affects inbreeding and incest aversion. Because inbreeding purges recessive alleles, inbreeding depression from mating with close-kin may be decreased in populations with low viscosity, where mating between highly related individuals is more common. In such populations, incest aversion could also be lower. Moreover, a strict aversion in populations with low viscosity can be costly. This is because avoiding sex with close kin, when the population is constituted mainly of kin, could severely attenuate an individual's reproduction. Although such theories have been presented, little effort has been made to test these theories empirically. Also, another important question that has not received sufficient attention is how variations in opportunity costs affect the strength of incest aversion. For example, individuals with low access to optimal mating partners have relatively less to lose from engaging in incest. For an individual with no other sexual access there is no personal cost of inbreeding and constraints are solely the inclusive fitness costs through the partner. In line with this prediction, recently acquired data suggest that men not currently living together with a female partner report markedly lower incest aversion than men currently living together with a female partner, and among men not living with a female partner mate value is positively correlated with incest aversion (Antfolk, unpublished data). Furthermore, it is possible that the societal costs (repercussion from other individuals) may be a function of the mate value of those engaging in incest. For example, other men might feel an increased anger towards a man, who, through incest, removes a high value female from the pool of potential mates. From this perspective clear predictions can be made on how individual mate value, mating success, and the prevalence of more optimal mates in the everyday surrounding could affect the strength of incest aversion. Yet, studies aimed to directly test these predications are lacking from the current literature.

Although norms tabooing incest exist in most cultures, there is some cultural variation in norms regarding, for instance, which behaviors constitute incest and how it is punished. Such norms may play a role in the shaping of attitudes regarding incest. Indeed, norms are likely to affect the degree to which certain behaviors are avoided. If a certain behavior implies costly punishment (and thereby direct fitness consequences) in culture A but not in culture B, it is not unreasonable to expect that this norm has an effect on behavior so that it is more prevalent in culture B than in culture A. Perhaps even more interesting is the question whether such norms are internalized to the degree that they affect emotions: Could it be that also aversion, or more specifically, the emotional disgust reaction, reflects societal norms? One way to empirically answer this question would be to test whether individuals from two different cultures, one in which mating and marriage between first-cousins is tabooed and one in which mating and marriage between first-cousins is not tabooed, differ in their emotional response to the thought of having sex with a first-degree cousins. Studies addressing such questions would provide useful information about whether incest taboos are merely a consequence of incest aversion, or whether incest taboos might have a causal effect on aversion.

Another interesting question is whether incest aversion is similar in same-sex and opposite-sex dyads. In the case of same-sex sexual behavior, there are no fitness consequences of incest. It is thus conceivable that incest aversion is lower in homosexual individuals than in heterosexual individuals. According Symons' (Symons, 1979) theory of homosexuality the only difference between homosexual and heterosexual individuals is the sex of the desired object. This theory would then predict and equally strong aversion to same-sex and opposite-sex incest. Data regarding incest aversion could thus be used to test this theory against other theories of homosexuality.

Finally, studies suggest that some inbreeding may occur. For instance, about 0.5% of Finnish fifteen-year-old girls report having been sexually abused by an individual that they believe to be their biological father. A girl cannot, however, be completely certain that the perpetrator really is her biological father, and neither can he be that she is his biological daughter. Moreover, the rate of misattributed paternity is actually higher (Anderson, Kaplan, & Lancaster, 2006; 2007) than the rate of incestuous sexual abuse. This fact allows for one interesting possibility: The already low number of actual biological incest may actually be much lower than data from these types of victimization studies show. Moreover, it is possible that a decreased availability of kinship cues between the fathers and their daughters mediate this risk. Studies that would test this and do so with robust methodology would provide important information regarding the degree to which inbreeding is actually avoided in the human population while also providing information regarding the factors that could predict intra-familial sexual abuse.

5.4 Implications of the Results

Biology matters and it matters in more than just one way. First of all, our results corroborate earlier studies suggesting that the function and strength of human incest aversion is shaped by evolution. This means that understanding our evolutionary biology is important in understanding human incest aversion. It could also mean that there are pre-dispositions in the human psyche that are not easily changed by norms. Also, although societies can go through rapid cultural changes, biological evolution is not an equally fast process. This means that what was once adaptive may in the current environment be harmful. For instance, a decreased tendency to avoid sexual contact with non-biological family members may be biologically adaptive. Such a tendency could, however, have direct and harmful consequences such as social exclusion. Moreover, no moral guidelines can be directly drawn from these observed facts. To give one example, a man may not suffer any evolutionary disadvantage from having sex with a stepdaughter. This does not mean that norms against this behavior are ineffective; nor does it mean that such norms are fallacious.

The improved understanding of the evolutionary background of human incest aversion has important implication in, at least, two settings: Family policy and forensic investigations of alleged intra-familial child sex abuse.

Regarding family policy a number of important biological factors regarding the intrinsic motivations to avoid detrimental behavior and direct positive behavior to different individuals are known. For example, it seems to be the case over a number of studies that compared to socio-legal family members, biologically related individuals are more prepared to invest in and avoid detrimental behavior towards each other. This is not always incorporated into governmental policies. For example, Finland has longstanding traditions in preparing biological parents-to-be through education. All parents who are expecting a biological child are given free consultation regarding the needs of the child and consultation about how to succeed in their new family situation. However, most non-biological parents are not given similar education, even if it is possible that they would benefit even more from such consultation. Another aspect of family policy, where biology often is overlooked, is instances where decisions regarding custody are made. Removing children from their biological parents and placing them with a foster family should be made on a cost-benefit basis. However, a valid cost-benefit analysis is difficult to make if the benefits of biological relatedness is completely disregarded. For example, victimization studies suggest that incestuous child sexual abuse is as much as fifteen times higher for girls living with a non-biological father than for girls living with their biological father (Sariola & Uutela, 1996). Both the absence of a biological father and the absence of a biological mother increase the risk of sexual abuse (Laaksonen et al., 2011). Similar effects are reported when it comes to physical abuse and neglect (Daly & Wilson, 1985, 1996; Turner, Finkelhor, & Ormrod, 2007; Wilson, Daly, & Weghorst, 1980). This means that placement to a non-biological family may involve risks not always accounted for in these decision processes.

In investigations of alleged intra-familial child sexual abuse, the empirical evidence suggests that evolutionary theory could be used as a thinking tool. For example, we know that non-biological family members are more likely perpetrators than are biological family members. We also know that it is likely that the risk within biological families is mediated by the availability of kinship cues. Fathers who lack such cues regarding their child may have a higher propensity to engage in such abuse. Obtaining data regarding the availability of such cues and information regarding the subjective certainty of relatedness the father has in his child may guide the information-gathering process in a fruitful way. For example, the effects of kinship-cues on the risk of intra-familial abuse can be used to update the base probability of abuse having occurred. More empirical data from studies with high ecological validity are needed in order to obtain fully understand the role of kinship cues as a risk factor. It is already clear, however, that the evolutionary perspective should not be neglected in these types of investigation.

5.5 Conclusions

We may not have completely answered the questions “Why do brothers not have sex with theirs sisters?” and “How come children do not find their parents sexually attractive?”. There is indeed much more to human inbreeding avoidance and human incest aversion than we have managed to address in the studies included in the present thesis. Nevertheless, we have succeeded in providing novel information regarding some key aspects of human incest aversion, both regarding its natural history, its development on the individual level, and the somewhat curious case of how we do when we react to *others* engaging in incest. We hope that more studies aimed at unravelling the nature of incest aversion will be conducted, and we hope that the results we have obtained in our studies provide useful information to those interested in addressing what to so many may seem to be nonsensical questions with obvious answers.

References

Ackerman, J., Kenrick, D., & Schaller, M. (2007). Is friendship akin to kinship? *Evolution and Human Behavior*, *28*(5), 365-374.

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

Agresti, A. (2007). *An Introduction to Categorical Data Analysis*. Hoboken: John Wiley & Sons.

Alvergne, A., Faurie, C., & Raymond, M. (2007). Differential facial resemblance of young children to their parents: Who do children look like more? *Evolution and Human Behavior*, *28*(2), 135-144.

Alvergne, A., Faurie, C., & Raymond, M. (2009). Father–offspring resemblance predicts paternal investment in humans. *Animal Behaviour*, *78*(1), 61-69.

Alvergne, A., Faurie, C., & Raymond, M. (2010). Are parents' perceptions of offspring facial resemblance consistent with actual resemblance? Effects on parental investment. *Evolution and Human Behavior*, *31*(1), 7-15.

Anderson, K, Kaplan, H, & Lancaster, J. (2007). Confidence of paternity, divorce, and investment in children by Albuquerque men. *Evolution and Human Behavior*, *28*(1), 1-10.

Anderson, KG, Kaplan, Hillard, & Lancaster, J. B. (2006). Demographic correlates of paternity confidence and pregnancy outcomes among Albuquerque men. *American journal of Physical Anthropology*, *131*, 560-571.

Aoki, K. (2004). Avoidance and prohibition of brother–sister sex in humans. *Population Ecology*, *47*(1), 13-19.

Bailey, D. H., Durante, K. M., & Geary, D. C. (2011). Men's perception of women's attractiveness is calibrated to relative mate value and dominance of the women' s partner. *Evolution and Human Behavior*, *32*(2), 138-146.

Bar-yam, N. B., & Darby, L. (1997). Fathers and breastfeeding: A review of the literature. *Journal Of Human Lactation*, *13*, 45-50.

Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, *16*, 395-424.

Bateson, P. (1978). Sexual imprinting and optimal outbreeding. *Nature*, *295*, 259-260.

Bell, G. (1982). *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. Berkeley: University of California Press.

Bereczkei, T., & Casanaky, A. (1996). Mate choice, marital success, and reproduction in a modern society. *Ethology and Sociobiology*, *17*, 17-35.

Bevc, I., & Silverman, I. (1993). Early proximity and intimacy between siblings and incestuous behavior: A test of the Westermarck Hypothesis. *Ethology and Sociobiology*, *14*(3), 171–181.

Bevc, I., & Silverman, I. (2000). Early separation and sibling incest. A test of the revised Westermarck theory. *Evolution and human behavior : official journal of the Human Behavior and Evolution Society*, *21*(3), 151-161.

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

Bjorklund, D. F., & Kipp, K. (1996). Parental investment theory and gender differences in the evolution of inhibition mechanisms. *Psychological Bulletin*, *120*(2), 163-188.

Borenstein, M., Hedges, L., Higgins, J. P. T., & Rothstein, H. R. (2009). *Introduction to Meta-Analysis*. Chichester: John Wiley & Sons.

Borg, C., & Jong, P. J. (2012). Feelings of disgust and disgust-induced avoidance weaken following induced sexual arousal in women. *PloS one*, *7*(9).

Borg, C., de Jong, P. J., & Schultz, W. W. (2010). Vaginismus and dyspareunia: Automatic vs. deliberate disgust responsivity. *Journal of Sexual Medicine*, *7*(6), 2149-2157.

Boven, L. V., Dunning, D., & Loewenstein, G. (2000). Egocentric empathy gaps between owners and buyers: Misperceptions of the endowment effect. *Journal of Personality and Social Psychology*, *79*(1), 66-76.

Bretman, A., Wedell, N., & Tregenza, T. (2004). Molecular evidence of post-copulatory inbreeding avoidance in the field cricket. *Proceedings of the Royal Society B: Biological Sciences*, (271), 159-164.

Burleson, M. H., Trevathan, W. R., & Gregory, W. L. (2002). Sexual behavior in lesbian and heterosexual women: Relations with menstrual cycle phase and partner availability. *Psychoneuroendocrinology*, *27*(4), 489-503.

Buss, D.M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and brain sciences*, *12*(01), 1–14. Cambridge Univ Press.

Buss, David M, Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, *3*(4), 251-255.

Cernoch, J. M., & Porter, R. H. (1985). Recognition of maternal axillary odors by infants. *Child Development*, *56*, 1593-1598.

Charlesworth, B., & Charlesworth, D. (1999). The genetic basis of inbreeding depression. *Genetics Research*, *74*, 329-340.

Charlesworth, D., & Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology, Evolution and Systematics*, *18*, 237-268.

Daly, M., & Wilson, M. I. (1985). Child abuse and other risks of not living with both parents. *Ethology and Sociobiology*, *6*(4), 197-210.

Daly, M., & Wilson, M. I. (1996). Violence Against Stepchildren. *Current Directions in Psychological Science*, *5*(3), 77-81.

Darwin, C. (1859). *On the Origin of Species*. *Main*. London: Murray.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: Murray.

Dawkins, R. (1976). *The Selfish Gene*. Oxford: Oxford University Press.

Dawkins, R. (1979). Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie*, *51*, 184-200.

Dawkins, R. (1983). Opportunity costs of inbreeding. *Behavioral and Brain Sciences*, *6*, 105-106.

DeBruine, L. M. (2004). Resemblance to self increases the appeal of child faces to both men and women. *Evolution and Human Behavior*, *25*(3), 142-154.

DeBruine, L. M. (2005). Trustworthy but not lust-worthy: Context-specific effects of facial resemblance. *Proceedings. Biological sciences / The Royal Society*, *272*(1566), 919-22.

DeBruine, L. M., Jones, B. C., Watkins, C. D., Roberts, S. C., Little, A. C., Smith, F.

G., & Quist, M. C. (2011). Opposite-sex siblings decrease attraction, but not prosocial attributions, to self-resembling opposite-sex faces. *Proceedings of the National Academy of Science, 108*(28), 11710-11714.

Denic, S., Agarwal, M. M., & Nagelkerke, N. (2012). Growth of consanguineous populations: Effect of family and group size. *Asian Pacific Journal of Tropical Disease*, *2*, S227-S232.

Dubas, J. S., Heijkoop, M., & van Aken, M. A. G. (2009). A Preliminary investigation of parent – progeny olfactory recognition and parental investment. *Human Nature*, *20*, 80-92.

Durante, K. M., Li, N. P., & Haselton, M. G. (2008). Changes in women's choice of dress across the ovulatory cycle: Naturalistic and laboratory task-based evidence. *Personality and Social Psychology Bulletin*, *34*, 1451-1460.

Durham, W. H. (1991). *Coevolution: Genes, Culture, and Human Diversity*. Stanford: Stanford University Press.

Eastwick, P. W., & Finkel, E. J. (2008). Sex differences in mate preferences revisited: Do people know what they initially desire in a romantic partner. *Journal of Personality and Social Psychology*, *94*(2), 245-264.

Edlund, J. E., & Sagarin, B. J. (2010). Mate value and mate preferences: An investigation into decisions made with and without constraints. *Personality and Individual Differences*, *49*(8), 835-839.

Ekman, P., Levenson, R. W., & Friesen, W. V. (1983). Autonomic nervous system activity distinguishes among emotions. *Science*, *221*, 1208-1210.

Emlen, S. T. (1997). The evolutionary study of human family systems. *Social Science Information, 36,* 563-589.

Eskine, K. J., Kacinik, N. A., & Prinz, J. J. (2011). A bad taste in the mouth: Gustatory disgust influences moral judgment. *Psychological Science*, *22*(3), 295-299.

Fehring, R. J., Schneider, M., & Raviele, K. (2006). Variability in the phases of the menstrual cycle. *Journal of Obstetric, Gynecologic, and Neonatal Nursing*, *35*(3), 376-384.

Feingold, A. (1992). Gender differences in mate selection preferences: A test of the parental investment theory. *Psychological Bulletin*, *112*(1), 125-139.

Fessler, D. M. T., & Navarrete, C. D. (2004). Third-party attitudes toward sibling incest: Evidence for Westermarck's hypotheses. *Evolution and Human Behavior*, *25*, 277 - 294.

Fessler, D., & Navarrete, D. (2003). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior*, *24*, 406 - 417.

Finnilä-Tuohimaa, K., Santtila, P, Sainio, M., Niemi, P., & Sandnabba, K. (2009). Expert judgment in cases of alleged child sexual abuse: Clinicians sensitivity to suggestive influences, pre-existing beliefs and base rate estimates. *Scandinavian Journal of Psychology*, *50*, 129-142.

Frankham, R. (1995). Conversation genetics. *Annual Review of Genetics*, *29*, 305-307.

Freud, S. (1918). *Totem and Taboo*. New York: Moffart Yard & Co.

Friedrich, W. N., Fischer, J., Broughton, D., Houston, M., & Shafran, C. R. (1998). Normative sexual behavior in children: A contemporary sample. *Pediatrics*, *101*(4), 1-8.

Gangestad, S. W., & Tornhill, R. (1998). Menstrual cycle variation in women's preference for the scent of symmetrical men. *Proceedings. Biological sciences / The Royal Society*, *265*, 927-933.

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, J. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science*, *15*, 203-207.

Gardiner, J. C., Luo, Z., & Roman, L. A. (2009). Fixed effects, random effects and GEE: What are the differences? *Statistics in Medicine*, *28*, 221-239. doi:10.1002/sim

Gardner, A., & West, S A. (2004). Spite and the scale of competition. *Journal of Evolutionary Biology*, *17*(6), 1195-1203.

Gleichgerrcht, E., & Young, L. (2013). Low levels of empathic concern predict utilitarian moral judgment. *PLoS ONE*, *8*(4).

Grafen, A. (1985). A geometric view of relatedness. *Oxford Surveys in evolutionary Biology*, (2), 28-90.

Greene, J. D., Morelli, S. A., Lowenberg, K., Nystrom, L. E., & Cohen, J. D. (2008). Cogntive load selectively interferes with utilitarian moral judgment. *Cognition*, *107*, 1144-1154.

Greene, J. D., Sommerville, R. B., & Nystrom, L. E. (2001). An fMRI Investigation of Emotional Engagement in Moral Judgment. *Science*, *293*, 2105-2108.

Griffin, A. S., & West, Stuart A. (2002). Kin selection: Fact and fiction. *Trends in Ecology & Evolution*, *17*(1), 15-21.

Haig, D. (1999). Asymmetric relations: Internal conflicts and the horror of incest. *Evolution and Human Behavior*, *20*, 83-98. doi:10.1055/s-0028-1090152

Haig, D. (2009). Transfers and transitions: Parent – offspring conflict, genomic imprinting, and the evolution of human life history. *Proceedings of the National Academy of Science*, *107*, 1731-1735.

Haig, D. (2011). Sympathy with Adam Smith and reflexions on self. *Journal of Economic Behavior and Organization*, *77*(1), 4-13.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Evolution*, 1-16.

Hamilton, W. D. (1990). Sexual reproduction as an adaptation to resist parasites. *Proceedings of the National Academy of Science*, *87*, 3566-3573.

Hardin, J., & Hilbe, J. (2003). *Generalized Estimating Equations*. London: Chapman & Hall.

Haselton, M. G., & Miller, G. E. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence. *Human Nature*, *17*(1), 50-73.

Haselton, M. G., Mortezaie, M., Pillsworth, E. G., Bleske-Rechek, A., & Frederick, D. A. (2007). Ovulatory shifts in human female ornamentation: Near ovulation, women dress to impress. *Hormones and behavior*, *51*(1), 40-5.

Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters*, *1*, 256-259. doi:10.1098/rsbl.2005.0332

Helgason, A., Pálsson, S., Gudbjartsson, D. F., Kristjánsson, T., & Stefánsson, K. (2008). An association between the kinship and fertility of human couples. *Science*, *319*(5864), 813-6.

Helkama, K., Uutela, Antti, & Pohjanheimo, E. (2003). Moral reasoning and values in medical school: A longitudinal study in Finland. *Scandinavian Journal of Educational Research*, *47*(4), 37-41.

Higgins, E. T. (1980). Role taking and social judgment: Alternative developmental perspectives and processes. In J. H. Flavell & L. Ross (Eds.), *Social Cognitive Development: Frontiers and possible futures* (pp. 119-153). New York: Cambridge University Press.

Ickes, W. J. (1997). *Misunderstandings in human relations*. *Delta*. New York: Guilford Press.

de Jong, P. J., van Overveld, M., & Borg, C. (2013). No Giving in to arousal or staying stuck in disgust? Disgust-based mechanisms in sex and sexual dysfunction. *The Journal of Sex Research*, *50*(3-4), 247-262.

de Jong, P. J., van Overveld, M., & Peters, M. L. (2011). Sympathetic and parasympathetic responses to a core disgust video clip as a function of disgust propensity and disgust sensitivity. *Biological psychology*, *88*(2-3), 174-9.

Judge, D. S., & Hrdy, S. B. (1992). Allocation of accumulated resources among close kin: Inheritance in Sacramento, California, 1890-198. *Ethology and Sociobiology*, *13*, 495-522.

Kamal, R. M., Iwaarden, S. V., & Dijkstra, B. A. G. (2014). Decision rules for GHB (gamma-hydroxybutyric acid) detoxification : A vignette study. *Drug and Alcohol Dependence*, *135*, 146-151.

Kaplan, Hillard, Hill, K., Lancaster, Jane, & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156-185.

Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits, and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality*, *58*(1), 97-116.

Kenrick, D., & Keefe, R. (1992). Age Preferences in Mates reflect sex differences in mating strategies. *Behavioral & Brain Sciences*, *15*, 75-91.

Koenigs, M., Young, L., Adolphs, R., Tranel, D., Cushman, F., Hauser, M., & Damasio, A. (2007). Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature*, *446*, 908-911.

Kokko, H., & Ots, I. (2006). When not to avoid inbreeding. *Evolution*, *60*(3), 467-475.

Koukounas, E., & McCabe, M. P. (2001). Sexual and emotional variables influencing sexual response to erotica: a psychophysiological investigation. *Archives of Sexual Behavior*, *30*(4), 393-408.

Krupp, D. B., DeBruine, L. M., & Jones, B. C. (2011). Cooperation and Conflict in the Light of Kin Recognition Systems. In C. Salmon & T. K. Schackelford (Eds.), *The Oxford Handbook of Evolutionary Family Psychology* (pp. 345-362). New York: Oxford University Press.

Krupp, D. B., DeBruine, L. M., Jones, B. C., & Lalumière, M. L. (2012). Kin recognition: Evidence that humans can perceive both positive and negative relatedness. *Journal of Evolutionary Biology*, *25*, 1472-1478.

Kuma, K., Iwabe, N., & Miyata, T. (1995). Functional constraints against variations on molecules from the tissue-level-slowly evolving brain-specific genes demonstrated by protein-kinase and immunoglobin supergene families. *Molecular Biology and Evolution*, *12*(1), 123-130.

Kushnick, G. (2013). Access to resources shapes Maternal decision making: Evidence from a factorial vignette experiment. *PLoS ONE*, *8*(9), 1-9.

Laaksonen, T., Sariola, Heikki, Johansson, A., Jern, P., Varjonen, M., Pahlen, B. V. D., Sandnabba, N. K., et al. (2011).

Changes in the prevalence of child sexual abuse, its risk factors, and their associations as a function of age cohort in a Finnish population sample. *Child Abuse & Neglect*, *35*(7), 480-490.

Lange, J. D., Wincze, J. P., Zwick, W., Feldman, S., & Hughes, K. (1891). Effects of demand for performance, self-monitoring of arousal, and increased sympathetic nervous system activity in male erectile response. *Archives of Sexual Behavior*, *10*(5), 444-464.

Lieberman, D. (2009). Rethinking the Taiwanese minor marriage data: evidence the mind uses multiple kinship cues to regulate inbreeding avoidance. *Evolution and Human Behavior*, *30*(3), 153-160.

Lieberman, D., Pillsworth, E. G., & Haselton, M. G. (2011). Kin affiliation across the ovulatory cycle: Females avoid fathers when fertile. *Psychological Science*, *22*, 13-18.

Lieberman, D., Tooby, J., & Cosmides, L. (2003). Does morality have a biological basis? An empirical test of the factors governing moral sentiments relating to incest. *Proceedings. Biological sciences / The Royal Society*, *270*(1517), 819-26.

Lieberman, D., Tooby, J., & Cosmides, L. (2007). The architecture of human kin detection. *Nature*, *445*(7129), 727-31.

Malamuth, N. M., & Check, J. V. (1980a). Sexual arousal to rape and consenting depictions: The importance of the woman's arousal. *Journal of Abnormal Psychology*, *89*(6), 763.

Malamuth, N. M., & Check, J. V. (1980b). Sexual arousal to rape and consenting depictions: The importance of the woman's arousal. *Journal of Abnormal Psychology*, *89*(6), 763. American Psychological Association.

Manson, J. H., & Perry, S. E. (1993). Inbreeding avoidance in Rhesus Macaques: Whose choice? *American journal of Physical Anthropology*, *90*, 335-344.

Marcinkowska, U. M., & Rantala, M. J. (2012). Sexual Imprinting on facial traits of opposite-sex parents in humans. *Evolutionary Psychology*, *10*(3), 621-630.

Marcinkowska, U. M., Moore, F. R., & Rantala, M. J. (2013). An experimental test of the Westermarck effect: Sex differences in inbreeding avoidance. *Access*, *24*(4), 842-845. 8

Matteo, S., & Rissman, E. F. (1984). Increased sexual activity during the midcycle portion of the human menstrual cycle. *Hormones and Behavior*, *18*, 249-255.

Maynard Smith, J. (1989). *Evolutionary Genetics*. Oxford: Oxford University Press.

Mayr, E. (1961). Cause and effect in biology. *Science*, *134*(3489), 1501-1506.

McCabe, J. (1983). FBD marriage: Further Support for the Westermarck Hypothesis of the incest taboo? *American Anthropologist*, 50-69.

Meston, C. M. (2000). Sympathethic nervous system activity and female sexual arousal. *American Journal of Cardiology*, *86*, 30F-34F.

Mihm, M., Gangooly, S., & Muttukrishna, S. (2011). The normal menstrual cycle in women. *Animal reproduction science*, *124*(3-4), 229-36.

Mitteldorf, J., & Wilson, D. S. (2000). Population viscosity and the evolution of altruism. *Journal of Theoretical Biology*, *204*(4), 481-496.

Moore, J., & Ali, R. (1984). Are dispersal and inbreeding avoidance related? *Animal Behaviour*, *32*, 94-112.

Morton, N. E., Crow, J. F., & Muller, H. J. (1956). An estimate of the mutational damage in man from data on consanguineous marriages. *PNAS*, *42*, 855-863.

Nakagawa, S., & Waas, J. R. (2004). "O sibling, where art thou?" – A review of avian sibling recognition with respect to the mammalian literature. *Biological Reviews*, *79*, 101-119.

van Overveld, M., de Jong, P. J., Peters, M. L., van Lankveld, J., Melles, R., & ter Kuile, M. M. (2013). The Sexual Disgust Questionnaire: A psychometric study and a first exploration in patients with sexual dysfunctions. *Journal of Sexual Medicine*, *10*(2), 396-407.

Park, J. H., & Schaller, M. (2005). Does attitude similarity serve as a heuristic cue for kinship? Evidence of an implicit cognitive association. *Evolution and Human Behavior*, *26*(2), 158-170.

Penn, D. J., & Frommen, J. G. (2010). Kin Recognition: An Overview of Conceptual Issues, Mechanisms and Evolutionary Theory. In P. Kappeler (Ed.), *Animal Behaviour: Evolution and Mechanisms* (pp. 55-85). Heidelberg: Springer.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, D. M., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, *399*, 741-742.

Petralia, S. M., & Gallup Jr, G. G. (2002). Effects of a sexual assault scenario on handgrip strength across the menstrual cycle. *Evolution and Human Behavior*, *23*, 3 - 10.

Pizarro, D. A., & Bloom, P. (2003). The intelligence of the moral intuitions: Comment on Haidt (2001). *Psychological Review, 110*(1), 193-196.

Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E., & Gallup Jr, Gordon G. (2003). How much paternal resemblance is enough? Sex differences in hypothetical investment decisions but not in the detection of resemblance. *Evolution and Human Behavior*, *24*, 81-87.

Pusey, Anne, & Wolf, M. (1996). Inbreeding avoidance in animals. *Trends in ecology & evolution, 11*(5), 201-206.

Pusey, AE. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour, 28*(2), 543-552.

Qirko, H. N. (2011). Fictive Kinship and Induced Altruism. In C. Salmon & T. K. Schackelford (Eds.), *The Oxford Handbook of Evolutionary Family Psychology* (pp. 310-328). New York: Oxford University Press.

Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution*, *43*(2), 258-275.

Ralls, K., Ballou, J. D., & Templeteon, A. (1988). Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology*, *2*(2), 185-192.

Rantala, M. J., & Marcinkowska, U. M. (2011). The role of sexual imprinting and the Westermarck effect in mate choice in humans. *Behavioral Ecology and Sociobiology*, *65*, 859-873.

Rempel, J. K., & Baumgartner, B. (2003). The relationship between attitudes towards menstruation and sexual attitudes, desires, and behavior in women. *Archives of Sexual Behavior*, *32*(2), 155-63.

Royzman, E. B., Leeman, R. F., & Sabini, J. (2008). "You make me sick": Moral dyspepsia as a reaction to third-party sibling incest. *Motivation and Emotion*, *32*(2), 100-108.

Sariola, H, & Uutela, A. (1996). The prevalence and context of incest abuse in Finland. *Child Abuse & Neglect*, *20*(9), 843-50.

Schaich Borg, J., Lieberman, D., & Kiehl, K. a. (2008). Infection, incest, and iniquity: investigating the neural correlates of disgust and morality. *Journal of cognitive neuroscience*, *20*(9), 1529-46.

Schnall, S., Haidt, J., Clore, G. L., Jordan, A. H., Clore, G. L., & Jordan, A. H. (2008). Disgust as embodied moral judgment. *Personality and Social Psychology Bulletin*, *34*, 1096-1108.

Shepher, J. (1971). Mate selection among second generation kibbutz adolescents and adults: Incest avoidance and negative imprinting. *Archives of Sexual Behavior*, *1*(4), 293-307.

Shepher, J. (1983). *Incest: A Biosocial View*. New York: Academic Press.

De Smet, D., Van Spreybroeck, L., & Verplaetse, J. (2014). The Westermarck effect revisited: A psychophysiological study of sibling incest aversion in young female adults. *Evolution and Human Behavior*, *35*(1), 34-42.

Spiro, M. F. (1958). *Children of the Kibbutz*. Cambridge: Harvard University Press.

Stark, R., Schienle, A., Girod, C., Walter, B., Kirsch, P., Blecker, C., Ott, U., et al. (2005). Erotic and disgust-inducing pictures: Differences in the hemodynamic responses of the brain. *Biological Psychology*, *70*(1), 19-29.

Starratt, V. G., & Shackelford, T. K. (2012). He said, she said: Men’s reports of mate value and mate retention behaviors in intimate relationships. *Personality and Individual Differences*, *53*(4), 459-462. Elsevier Ltd.

Symons, D. (1979a). *The Evolution of Human Sexuality*. New York: Oxford University Press.

Symons, D. (1979b). *The Evolution of Human Sexuality*. New York: Oxford University Press.

Szulkin, M., & Zelazowski, P. (2009). inbreeding avoidance under different null models of random mating in the great tit. *Journal of Animal Ecology*, *78*, 78-788.

Tal, I., & Lieberman, D. (2007). Kin detection and the development of sexual aversion: toward and integration of theories on family sexual abuse. In C. A. Salmon & T. K. Schackelford (Eds.), *Family Relationships - An Evolutionary Perspective* (pp. 205-229). New York: Oxford University Press.

Talmon, Y. (1964). Mate selection in collective settlements. *American Sociological Review*, *29*(4), 491-508.

Thornhill, N. W. (1991). An evolutionary analysis of rules regulating human inbreeding and marriage. *Behavioral and Brain Sciences*, *14*(2), 247-261.

Thornhill, N. W. (1993). *The Natural History of Inbreeding and Outbreeding*. Chicago: University of Chicago Press.

Thornhill, R., & Gangestad, S. W. (2008). *The Evolutionary Biology of Human Female Sexuality*. New York: Oxford University Press.

Tinbergen, N. (1963). On aims and methods of Ethology. *Zeitschrift für Tierpsychologie*, *20*, 410-433.

Tooby, J. (1982). Pathogens, Polymorphism, and the Evolution of Sex. *Journal of Theoretical Biology*, *97*, 557-576.

Trivers, R. (1972). Parental investment and sexual selection. *Natural Selection and Social Theory: Selected Papers of Robert Trivers*. New York: International University Press.

Turner, H. A., Finkelhor, D., & Ormrod, R. (2007). Family structure variations in patterns and predictors of child victimization. *American Journal of Orthopsychiatry*, *77*(2), 282-295.

Tybur, J. M., Lieberman, D., Kurzban, R., & Descioli, P. (2013). Disgust: Evolved function and structure. *Psychological Review, 120*(1), 65- 84.

Valdesolo, P., & Desteno, D. (2006). Manipulations of emotional context shape moral judgment. *Psychological Science*, *17*(6), 476-477.

Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory, 1*, 1-30.

Walter, A. (1997). The evolutionary psychology of mate selection in Morocco: A Multivariate Analysis. *Human Nature*, *8*(2), 113-137.

Warner, P., & Bancroft, J. (1988). Mood, sexuality, oral contraceptives and the menstrual cycle. *Journal of Psychosomatic Research*, *32*(4-5), 417-427.

Webster, G. D. (2004). Human kin investment as a function of genetic relatedness and lineage. *Evolutionary Psychology, 2*, 129-141.

Webster, G. D., Bryan, A., Crawford, C. B., Mccarthy, L., & Cohen, B. H. (2008). Lineage, sex, and wealth as moderators of kin investment evidence from inheritances. *Human Nature*, *19*, 189-210. doi:10.1007/s12110-008-9038-0

West, Stuart A., Murray, M. G., Machado, C. A., Griffin, A. S., & Herre, E. A. (2001). Testing Hamilton's rule with competition between relatives. *Nature*, *409*(6819), 510-513.

Westermarck, E. (1891). *The History of Human Marriage*. London: Macmillian.

Westermarck, E. (1906). *The Origin and Development of the Moral Ideas*. London: Macmillan.

Wheatley, T., & Haidt, J. (2005). Hypnotic Disgust Makes Moral Judgments More Severe. *Psychological Science*, *16*(10), 780-785.

Wilcox, A. J., Dunson, D. B., Weinberg, C. R., Trussell, J., & Day, D. (2001). Likelihood of conception with a single act of intercourse: Providing benchmark rates for assessment of post-coital contraceptives. *Contraception*, *63*, 211-215.

Wilcox, A. J., Weinberg, C. R., & Baird, D. D. (1995). Timing of sexual intercourse in relation to ovulation. *The New England Journal of Medicine*, *333*(23), 1517-1521.

Wilson, M. I., Daly, M., & Weghorst, S. J. (1980). Household composition and the risk of child abuse and neglect. *Journal of Biosocial Science*, *12*(3), 333-340.

Wolf, A P. (1966). Childhood association, sexual attraction, and the incest taboo: A Chinese case. *American Anthropologist*, *68*, 883-898. doi:10.1126/science.1204978

Wolf, A P. (1968). Adopt a daugther-in-law, marry a sister: A Chinese solutuin to the problem of the incest taboo. *American Anthropologist*, *70*, 864-874.

Wolf, A P. (1970). Childhood association and sexual attraction: A further test of the Westermarck Hypothesis. *American Anthropologist*, *72*, 503-512.

Wolf, A P. (1995). *Sexual attraction and childhood association: A Chinese brief for Edward Westeramrck*. Stanford: Stanford University Press.

Wolf, A. P., & Durham, W. H. (2004). *Inbreeding, Incest, and the Incest Taboo: The State of Knowledge at the Turn of the Century*. Stanford: Stanford University Press.

Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. *PNAS*, *104*(20), 8235-8240.

Zelazo, P. D., Helwig, C. C., & Lau, A. (1996). Intention, act, and outcome in behavioral prediction and moral judgment. *Child Development*, *3*, 2478-2492.

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