Advanced Review

Human kin detection

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Natural selection has favored the evolution of behaviors that benefit not only one's genes, but also their copies in genetically related individuals. These behaviors include optimal outbreeding (choosing a mate that is neither too closely related, nor too distant), nepotism (helping kin), and spite (hurting non-kin at a personal cost), and all require some form of kin detection or kin recognition. Yet, kinship cannot be assessed directly; human kin detection relies on heuristic cues that take into account individuals' context (whether they were reared by our mother, or grew up in our home, or were given birth by our spouse), appearance (whether they smell or look like us), and ability to arouse certain feelings (whether we feel emotionally close to them). The uncertainties of kin detection, along with its dependence on social information, create ample opportunities for the evolution of deception and self-deception. For example, babies carry no unequivocal stamp of their biological father, but across cultures they are passionately claimed to resemble their mother's spouse; to the same effect, 'neutral' observers are greatly influenced by belief in relatedness when judging resemblance between strangers. Still, paternity uncertainty profoundly shapes human relationships, reducing not only the investment contributed by paternal versus maternal kin, but also prosocial behavior between individuals who are related through one or more males rather than females alone. Because of its relevance to racial discrimination and political preferences, the evolutionary pressure to prefer kin to non-kin has a manifold influence on society at large.

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INTRODUCTION

A statue of Lady Justice is prominently featured in many courthouses. She typically weighs the metaphorical evidence blindfolded, symbolizing the view that treating people fairly means considering their actions without regard to who they are—be they family, friends, or strangers. However, in daily life we hardly act like Lady Justice: we treat people with whom we have a good relationship more equitably than others and tend to favor our relatives over unrelated individuals.[1] In fact, kin detection has been a formidable force in shaping the evolution of our sexual and social behavior.

WHY WE DETECT KIN

Whether consciously or unconsciously, kin detection affects our choice of who to mate with (optimal outbreeding), who to help without expecting a return (altruism), and who to harm without achieving a benefit (spite).

Inbreeding Avoidance and Optimal Outbreeding

Of most genes we inherit one copy (*allele*) from our mother and one from our father. If the two alleles differ (*heterozygosity*) and one is defective, the other may be able to compensate and offer protection from genetic disease. If the two alleles are identical (*homozygosity*), genetic disease is therefore more likely. The dangers of homozygosity can be reduced by eschewing inbreeding, which normally means avoiding sex with kin (which are more likely than non-kin to carry the same alleles).

Indeed, consanguinity is associated with more frequent miscarriages and higher infant morbidity and mortality.[2] One of the first to discuss the effects of consanguineous marriages was Charles Darwin, who had married his first cousin and became later preoccupied with the health of their children. It appears these worries were justified, considering that, of his 10 children, 3 died in childhood and at least another 3 turned out to be infertile.[3]

Fathers usually help raise offspring, but their contribution is not guaranteed. Only mothers' resources are used during pregnancy and breastfeeding; in addition, due to fertility windows that are short and limited in their lifetimes, women have fewer opportunities to reproduce than men. Thus, the costs of inbreeding are higher in women than in men. Consistently, women have been found to be more averse to potential partners with whom they have resided during childhood[4-6] or who look like opposite-sex parents or siblings.[7,8] They are also more inclined than men to treat close friends as kin,[9] which includes avoiding them as sexual partners.

Despite the arguments and evidence for inbreeding avoidance, forming a couple with a genetically related individual can have its advantages. These couples might, for example, benefit from (1) typical early marriage, (2) socioeconomic services and goods, such as the concentration of inherited property, and (3) passing to offspring genes, or gene combinations, that are locally adaptive.[10] In fact, couples consisting of third- and fourth-level cousins have been found to be reproductively more successful not only than more closely related couples, but also than more distantly related ones.[11] In other words, inbreeding should not be avoided beyond the limits of 'optimal outbreeding'.[12]

Altruism and Spite

An individual (actor) can behave toward another person (recipient) in four meaningfully different ways,[13] that respectively involve (1) mutual benefit (a gain to both the actor and the recipient), (2) selfishness (a gain to the actor and a loss to the recipient), (3) altruism (a loss to the actor and a gain to the recipient), and (4) spite (a loss to both the actor and the recipient). The first two behaviors are beneficial to the actor and it is easy to see why they might have evolved. The latter two, however, are harmful to the actor and, before Hamilton,[14] have posed a tough challenge to evolution theory.

This challenge has been met by reinterpreting the concept of *fitness*. In practice, fitness equals the number of healthy offspring one produces (where 'healthy' means that they will produce offspring of their own). Alternatively, fitness can be seen as the transmission of genes to subsequent generations. Therefore, because relatives share some genes with us by common descent, we can increase our fitness not only by producing healthy offspring ourselves, but also by helping our relatives produce them (*inclusive fitness*[14]). The idea is that a gene causing its carrier to behave altruistically toward others will be able to spread if (and only if) it leaves more replica genes in the next generation than a gene lacking such effect. Effectively, this means that altruism can evolve if, and only if, (a) it is directed to people who are likely to share the benefactor's altruism gene, *and* (b) the advantage conferred to copies of the gene outweighs the disadvantage to the benefactor's own copy.

If the carrier of a given gene (e.g., a gene for altruism; Box 1) shares an ancestor with another person, then the more recent this ancestor is, the more likely it is that this other person also carries that gene. More precisely, altruism can evolve if $br>c$, where b=reproductive benefit gained by the beneficiary of the altruism, r=relatedness by descent (i.e., beyond that shared with non-kin) between the benefactor and the beneficiary, and c=cost to the benefactor's own reproduction (*Hamilton's rule*[14]). Note that, in this formula, relatedness by descent is equivalent to the probability that the two individuals share a gene for altruism. Contrary to common misconception, the proportion of other shared genes *per se* (overall genetic similarity) does not bear on the evolution of altruism,[15,16] although, to the extent that it leads to phenotypic similarity, it can serve as one heuristic cue to relatedness by descent. Note that Hamilton's rule effectively reduces altruism to nepotism (favoritism toward relatives).

BOX 1
THE SEARCH FOR ALTRUISM GENES

The hormones oxytocin and vasopressin have long been associated with maternal and pair bonding, and later, more broadly, with altruism.[17] Recently, it has been suggested[17] that two genes that mediate blood oxytocin levels (OXTR and CD38) might be among the famous altruism genes postulated by Hamilton.[14] Although altruism is present to some extent in all of us, even in psychopaths,[18] not everybody is equally altruistic; likewise, not everybody has the same versions of the OXTR and CD38 genes. These behavioral and genetic variations may reflect differences in survival strategy. In fact, the OXTR variant associated with lower blood oxytocin and diminished altruism is linked to superior mental-rotation ability, suggesting a trade-off between altruistic tendencies and visuospatial ability.[17] This trade-off is reminiscent of the one in autism-spectrum disorders in which social skills (such as empathy, that is likely to mediate some altruistic behaviors) tend to be poor compared to visuospatial abilities, whereas the converse is observed in psychosis-spectrum disorders.[19] A legitimate question is whether evolutionary strategies that incorporate stronger or weaker altruistic behavior might implicate, respectively, enhanced or reduced kin-detection skills. On the one hand, whereas sex, age, and parental status all have large effects on survival strategies, none of them affect the ability to detect genetic relatedness from faces.[20,21] On the other hand, being laterborn rather than firstborn does sharpen one's sensitivity to facial similarities, potentially improving sibling identification (see section *Maternal Perinatal Association*). This suggests that differences in kin-detection abilities, rather than being genetically fixed, might be flexibly and adaptively contingent on those environmental conditions that entail fitness variations.

Imagine the emergence of the first altruism gene. The probability of sharing this gene with one's identical twin is 1; with one's offspring is 1/2, equal to the probability that they have inherited one's own ('altruistic') rather than the other parent's ('non-altruistic') copy of the gene. On average, the probability is 1/2 for full siblings; 1/4 for half siblings, uncles or aunts, nephews or nieces, grandparents, or grandchildren; 1/8 for first cousins or great-grandchildren. Third cousins (1/128) have nearly the same probability of sharing the altruism gene as any pair of random individuals.[22] Thus, an altruism gene could theoretically spread even at the expense of the benefactor's life, provided, for example, that the sacrifice saved more than two siblings or four half siblings or eight first cousins. Naturally, due to the fallibility of kinship cues, deception, or self-deception, genetic relatedness can always be misjudged, curtailing the fitness of the altruism gene. Hence, in nature, more selfishness should be expected than genetic relatedness alone forecasts.[22]

Spite could be predicted from Hamilton's rule whenever r is negative, that is, whenever the recipient of spite is less related to the actor than average.[23] That negative relatedness can be identified is suggested by the finding that faces that deviate from the average in a direction opposite to one's own face are judged less attractive and less trustworthy.[24] Wartime infanticide, which normally targets non-kin, might be regarded as a form of spite; it costs the killer time and energy without any personal benefit. Some forms of terrorism may also fall in the same class.

Wilson[25] has suggested that spite could evolve whenever a spiteful action benefits a related third party more than it costs the actor and the recipient. Typically, related individuals can benefit from harm to unrelated ones when this reduces competition for resources. Although Hamiltonian and Wilsonian spite have been regarded as distinct concepts, it has been argued that they are one and the same, differing only in that Hamilton focuses on spite's negative effects on non-kin, whereas Wilson focuses on its positive effects on kin.[26] The main point is that the only form of spite that can evolve is the one that amounts to altruism toward kin. The crucial difference between behaviors is therefore not whether they are altruistic or spiteful, but whether they propel genes into the next generation by increasing reproduction or reducing competition.

Consistent with Hamilton's rule, altruism among humans increases with genetic relatedness between benefactor and beneficiary (as confirmed by archival analyses of last wills[27]), and is for example greater among full, than among half, siblings.[28,29] Differences in genetic relatedness can affect altruism even when they are much subtler than those between full and half siblings; a peculiar case is that of grandmothers and their biological grandchildren.

Grandmothers' reputation for being widely supportive of their grandchildren has recently been tarnished by two lines of evidence: (1) in modern populations, grandmothers tend to favor granddaughters at the expense of grandsons, although the effect is not always statistically significant[30,31]; (2) in preindustrialized populations, the presence of a paternal grandmother increases the survival of granddaughters but, shockingly, reduces that of grandsons.[32] This counterintuitive finding was predicted on the basis of the idea that a mutation on a sex chromosome, say Y, would confer it a transmission advantage (via a decrease in sibling competition) if it harms offspring of the sex that does not carry that chromosome, in this case females. However, because the X chromosome contains far more functional genes than the Y chromosome, mutations on the X (selected to harm boys) would predominate over mutations on the Y (selected to harm girls).

What makes this case interesting is that X-chromosome relatedness between grandmothers and grandchildren varies by line of descent and sex of grandchild. The reason is that a father's X chromosome is transmitted to all of his daughters but none of his sons, favoring X-linked mutations that cause fathers to invest more in their daughters than in their sons. Given that a father always inherits his X chromosome from his mother, the paternal grandmother will show the same investment tendency toward her grandchildren, but, unlike her son, without the counterbalancing effect of a Y chromosome. If they have grandchildren of both sexes, then, paternal grandmothers reduce sibling competition for their granddaughters by directly or indirectly harming their own grandsons.[33-35] This example gives an interesting twist to the interpretation of the term 'nepotism', which derives from the Italian word used not only for nephew or niece, but also for grandchild.

HOW WE DETECT KIN—CONTEXTUAL CUES

Inbreeding avoidance and nepotism (which covers both altruism and spite) require kin detection. Genetic relatedness cannot be assessed directly, hence relatives can only be identified probabilistically. Interestingly, this is the case even for the most certain of genetic relationships, that between mother and child: one well-studied case concerns a woman who was found not to be the biological mother of two of her three sons.[36] Presumably, her eggs had originated from two separate genomes, belonging to nonidentical twin sisters who had fused in the womb; an occurrence that might be much more frequent than one would like to think, given that twin conceptions rarely result in twin births.[37]

Verbal communication, including gossip and rumors, can be a direct source of information on kinship (we know who our relatives are because we are told), but can also be deceptive. Besides, kin detection evolved at least in part before our language ability emerged, and non-verbal cues play a critical role in it. These cues fall into at least two broad classes. The first is *contextual*: people identify as relatives all individuals encountered in a situation or location where others are likely to be kin (e.g., those who are associated with one's mother or with one's home).[38] The second is *phenotypic*: people identify as relatives all individuals who match an internal kin template (e.g., those who display the family traits or odors). The second mechanism may rely on the first. For example, a template could be based on the traits of those with whom one grew up and subsequently applied to those one did not grow up with. Any cue may work as a kinship signal, provided it is statistically associated with relatedness: one outstanding example is emotional closeness (feelings of concern and caring).

Maternal Perinatal Association

For the whole of human evolutionary history, mothers and newborns have remained in close association after birth, providing a basis for reliable detection of the mother by the child and of the child by the mother. Having repeatedly witnessed a child being nursed, or cared for, by a person identified as one's own mother,[38] thus, is a strong cue that this child is a sibling. The importance of maternal perinatal association is revealed by the findings that people (1) are more inclined to help others if they have witnessed them being taken care of by their own mother and (2) feel less attracted to them, are less likely to choose them as mates, and are more disgusted by the idea of having sex with them (as shown by both survey evidence[38] and physiological evidence[39]). In the same line, women with younger brothers are less attracted to men whose faces contain relatedness cues than women with no brothers, or only older ones.[40]

Coresidence Duration

Children may not necessarily have observed a sibling being taken care of by their mother. More crucially, whereas older siblings can witness their mother nurse a younger sibling, the converse is impossible. This implies that individuals who have older siblings are forced to use alternative strategies to identify them as such. Consistent with this prediction, laterborns turn out to be better than firstborns at recognizing family cues in faces.[41] However, if (and only if) the cue of maternal perinatal association is unavailable, kinship is inferred not from facial resemblance but from the more robust signal of childhood coresidence duration.[38]

Evidence that coresidence duration is used as a kinship cue includes the findings that (1) prolonged separation from an opposite-sex sibling during childhood increases the propensity to have sexual intercourse with this sibling,[42] (2) growing up with a person of the opposite sex reduces the propensity to have sexual intercourse with this person (the revised[42] *Westermarck effect*[43]), and (3) growing up with an opposite-sex sibling increases rejection of others' incest as morally wrong.[4,5]

Coresidence duration predicts altruism and sexual aversion even when individuals know that their sibling is genetically unrelated to them, as in the case of adoptions—showing that the output of this kin-detection system is unaffected by contrasting beliefs.[38] Particularly informative in this regard are complementary studies performed in Taiwan and Israel. In Taiwan, there used to be a form of marriage in which bride and groom were raised together at the groom's home, and finalized their union as young adults. Suggestive of a Westermarck effect, couples married in this way produced fewer offspring, had more extramarital affairs, and were 20 times more likely to get divorced or separated than couples raised apart, other things being equal.[44]

Matching evidence was collected in an Israeli kibbutz. Children on a kibbutz spend most of their time with genetically unrelated peers rather than with their own family. Parents do not prohibit relationships between the children when they become adults and may even favor them. Yet, the study found that coresidence increased not only altruism but also sexual aversion between peers and—mediated by this personal aversion—a general moral condemnation of sex among peers.[45]

Indications exist that even a much wider sense of coresidence may work as a kinship cue. It has been argued,[46] for example, that country people are more inclined than city people to help strangers,[47] although not family members,[48] because the probability that, unbeknownst to all, a stranger is kin is greater in the countryside than in the city.

HOW WE DETECT KIN—PHENOTYPIC CUES

If we came across a stranger who looked exactly like us, we would at least wonder whether we might not be twins, or at least siblings, separated at birth. Various studies have indeed suggested that visual similarity is used as a kinship cue. Relative to some other mammals (e.g., dogs and rats), our vision seems very strong and our olfaction very weak. Still, whether consciously or not, we do recognize the smell of various family members, and this ability plays a unique role in kin detection.

Phenotypic traits are partly heritable; thus, phenotypic similarity can function as a cue to genetic similarity and genetic similarity can, in turn, function as a cue to kinship. It has been argued, though, that phenotype-based kin detection does not necessarily imply the existence of phenotype-based kin-detection mechanisms, because it could emerge as a mere side effect of mechanisms dedicated to the detection of conspecifics, group members, or particular individuals. Group-member detection, for instance, could depend on templates based on socially rather than genetically related individuals, but still be useful in detecting kin as well.[49]

Olfactory Similarity

Newborns recognize the smell of their mothers, parents the smell of their children (but not of their stepchildren), siblings the smell of their full (but not half or step) siblings, and strangers the similarity between the smells of people who are related to one another.[50] Several brain areas known to process social information—such as the fusiform, cingulate, and insular cortices—are involved, as suggested by evidence from chemosensory event-related potentials (CSERPs), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI).[51,52]

That odors affect kin detection in a consequential way is tentatively suggested by the preliminary findings that fathers feel emotionally closer to, and mothers punish less, children whose odors they can recognize.[53] Mutual olfactory aversion has been observed in father–daughter and brother–sister relationships, but not in other relationships with incest potential, such as the one between mother and son.[52]

A particularly noteworthy determinant of one's personal odor is the major histocompatibility complex (MHC), in humans also called human leukocyte antigen (HLA). The MHC is a set of cell-surface molecules ('antigens') that display a unique sample of each cell's protein content to the immune system.[54] If the content is 'histocompatible' (meaning 'tissue-compatible'), the cell is left alone. If not, pathogen invasion or viral protein production may be to blame and, to halt the spread of infection, the cell is killed. The greater the MHC diversity in an individual, the greater the variety of antigens, and hence, the more information the immune system has about potentially infected cells.

MHC molecules have been argued to affect body odor either directly in sweat, saliva, urine, or blood,[55] or indirectly by modifying the composition of the population of micro-organisms on our skin; what we take to be body odor could in fact be these organisms' metabolites.[10] If indeed expressed through body odor, MHC variations could help discriminate kin from non-kin. Supporting evidence comes from a well-known study[56] that reported that women near ovulation, presumably to ensure MHC diversity in their offspring, prefer the smell of T-shirts worn by men whose MHC differs the most from their own, and are thus the least likely to be kin.

Although some studies have replicated this intriguing result, others have not.[10] As mentioned earlier, however, humans engage in optimal, rather than maximal, outbreeding. Likewise, helping to explain inconsistencies between different studies, women have recently been found to optimize, rather than maximize, MHC diversity.[57] Interestingly, it transpired that women's preference was only affected by the paternally inherited portion of their MHC and not by the maternally inherited one.[57] Paternal MHC recognition may thus specifically aid paternal kin detection—precisely the kind that is hard to achieve with any other major kin-detection cue.

Odors of MHC-similar individuals provoke stronger brain responses than odors of MHC-dissimilar ones, pointing to a self-referent mechanism for detecting genetic similarity.[51-58] When coming from same-sex persons, MHC-similar odors are elaborated differently in men and women; it has been suggested that they may favor communal behavior (hence, kin affiliation) in women and competitive behavior in men.[58] In an interesting parallel, a sniff of oxytocin (a hormone that, among its numerous effects, modulates some instances of animal olfactory behavior[59]) has been shown to improve the detection of kin relationships in women and of competitive relationships in men.[60]

Visual Similarity

Because many traits, such as craniofacial features, are highly heritable,[61] genetic similarity between individuals tends to be expressed as phenotypic similarity (Figure 1). Evidence that similarities in adult or adolescent faces can be used as a kinship cue include the findings that, from photos, (1) pairs of parent/child,[21] as well as pairs of siblings and grandparent/grandchild,[62] are perceived as depicting people who belong to the same family more often than chance, and (2) pairs of aunt–uncle/nephew and cousins more often than unrelated pairs.[62] On the other hand, family resemblance does not appear to be prominently featured in the faces of very young children, which, as we will discuss later, could have an adaptive function.

FIGURE 1. These images, obtained by splicing together photographs of relatives, show how striking family resemblances can be. On the left: sister/brother (Karine, 29 and Dany, 25). On the right: grandmother/granddaughter (Ginette, 61 and Ismaëlle, 12). (Genetic portraits by Ulric Collette, http://genetic.ulriccollette.com. Reprinted with permission).

Facial similarity of others to oneself influences one's attitudes even when it is too slight to be noticed. For example, subtle cues of self-resemblance (obtained by digital manipulation of photographs; Figure 2) increase perceived trustworthiness, and decreases perceived sexual appeal, of opposite-sex strangers.[63,64] Self-resemblance enhances attractiveness more for same-sex than for opposite-sex faces, which is consistent with the expectation that, for the latter, non-sexual attraction is likely to be at least partly cancelled out by sexual aversion.[65] In women, preference for self-resemblant (especially female) faces increases with progesterone levels within the menstrual cycle, hinting at a mechanism for increasing affiliative behavior toward kin during pregnancy—when progesterone is high.[66] Both men and women find self-resemblant children more attractive and would be more willing to adopt them, whether self-resemblance is objective[67,68] or subjective.[69] Finally, the presence of self-resemblant faces in a group promotes cooperation for the public good in a game where participants can choose how much to invest and are punished for being selfish,[70] although it does not increase the tendency to assume that others will cooperate rather than cheat in a game where participants are forced to invest, and benefit only when interactants are cooperators.[71]

The resemblance of others to oneself is likely assessed by comparing their features to a kin template, a process called *phenotype matching*. The template used for phenotype matching may draw either on one's own appearance or on that of close kin. However, despite that the absence of mirrors in ancestral times may have made it hard to obtain an accurate image of oneself, there is evidence that similarity to oneself outweighs similarity to individuals that are strongly presumed to be kin, such as a co-twin—even an identical one.[72] Unlike a template based on reputed kin, a template that incorporates information on oneself could in principle also help identify one's biological father (who might not be the social one) and paternal relatives, and discriminate full siblings from maternal half siblings (an impossible feat if one relies on contextual cues alone).

FIGURE 2. An example of the type of digital manipulation typically used in self-resemblance experiments. The man's face on the left has been merged in a 35:65 proportion with the female model's face on the right. The resulting face, in the middle, is then presented to the man. Self-resemblance is slight enough to go unnoticed, but powerful enough to drive the man's responses. (Male portrait by C. F. Wesenberg, Creative Commons License)

Relatives tend to be more similar than strangers not only in facial traits but also in attitude, values, and personality.[73] Thus, it makes sense that noticing such similarities in strangers may evoke a feeling of kinship. For example, we are more willing to help, and to implicitly associate with words like 'brother' and 'sister', a person described as attitudinally similar to ourselves than one described as dissimilar.[74] Even superficial resemblances between individuals, like a shared last name (a loose but legitimate proxy for common ancestry), have been shown to favor altruism between them.[75]

HOW WE DETECT KIN—EMOTIONAL CUES

Several forms of nepotistic behavior appear to be preferentially driven by cues that would seem only vaguely diagnostic of actual kinship. For example, the tendency to vigilate over others' romantic affairs does increase with genetic relatedness, but this relationship has been reported to be entirely mediated by physical similarity and emotional closeness. These highly imperfect, heuristic cues did supersede coresidence duration and even actual genetic relatedness.[76] A study on siblings[29] found that the impact of perceived physical similarity to a sibling on altruism toward that sibling was not direct (as one might expect if resemblance were used as a straightforward proxy for relatedness); instead, it was mediated by perceived psychological similarity, whose effect on altruism was in turn mediated by emotional closeness. In short, physical similarity worked by enhancing emotional closeness. A father's objective physical similarity to his child has been shown to predict emotional closeness to the child[77]; it is thus entirely possible that the known correlation between paternal resemblance and investment (see section *Uncertainties and Biases*) could also be mediated by emotional closeness.

Because the long-term proximity typical of relatives facilitates bonding, emotional closeness does increase with genetic relatedness and can work as a kinship cue.[78] It has actually been argued that, rather than a tendency to help kin, humans have evolved a tendency to help people they felt emotionally close to and whom they felt obligated to help (which, more often than not, happened to be kin).[79] This theory is consistent with the observation that certain non-kin (most prominently spouses and friends) are helped as much as kin, or more. Still, emotional closeness does not entirely mediate the association between helping behavior and genetic relatedness,[79] suggesting that there is more to nepotism than warm feelings. In fact, in one study[29] people reported they would be more willing to save, at their own peril, the life of a full sibling (or a half sibling with whom they had cohabited—the longer, the better) than that of a step sibling (or a half sibling with whom they had never cohabited). This hierarchy was independent of emotional closeness. Still, step siblings were more likely to be saved if they were emotionally close than if they were not, whereas among full siblings emotional closeness did not matter.

Reflecting the evolutionary relevance of emotional closeness in kin relationships, the psychology of friendship can echo that of kinship. Yet, the likelihood that the kinship module is activated by non-kin differs between sexes. Women's prosocial and sexual responses to friends closely mimick their responses to kin, whereas men treat friends very differently from kin.[9] A female bias toward overinclusive kin detection may have been adaptive not only by warding off incest, whose cost is much greater for women than for men, but also by helping women to establish social networks with non-kin under conditions of ancestral patrilocality, in which wives resided with their husband's family or tribe.[9]

HOW WE DETECT KIN—UNCERTAINTIES AND BIASES

The dependence of kin detection on heuristic information and thus its limited reliability, together with the diverse and sometimes diverging interests of interacting individuals, creates an ideal environment for the evolution of deception and self-deception. A striking illustration of this point is the problem of paternity uncertainty. Because of possible cuckolding, men run a small (as shown by worldwide nonpaternity estimates[80]) but non-negligible risk of investing in a child that is not their own. How averse men are to this type of investment is graphically illustrated by the fact that a stepchild's risk of being killed ranges from 40 to 100 times that of a child living with both biological parents.[81]

Yet, remarkably, up to at least 1 year of age children tend to look anonymous—they can be matched to their fathers only *very* slightly better than chance[82,83]; in a recent study, nearly half of father/newborn pairs were not identified above chance.[84] If fathers marked their babies—for example, by making them unambiguously similar to themselves—paternity uncertainty would of course be virtually nil and paternal investment less risky. However, fathers can also produce illegitimate children with other men's spouses, and if they carried the marks of their biological fathers these babies would be promptly identified and disinvested upon (a euphemism that covers maltreatment and infanticide). Because, population-wise, the probability that a father is presented with an adulterine child equals the probability that this father slips his own out-of-wedlock child into another family, the benefits of marking offspring are offset by its costs.[85,86]

It has been proposed[87] that, when the nonpaternity probability in a population is larger than 1 in 10, babies might actually benefit from concealing their fathers' identity. A subsequent mathematical model[86] has shown that, if parental investment decreases with increasing nonpaternity probability (which is the case in both animals and humans[88,89]), offspring marking will *never* evolve—regardless of how low the nonpaternity probability in the population is.

Although in such a scenario parents and babies all benefit from child anonymity, child anonymity reduces paternity confidence and nobody benefits from the paternal disinvestment that could result from that.[90] A smart solution to this evolutionary conundrum would be for men to (1) produce anonymous-looking babies, (2) be very sensitive to any cues that they might not have fathered their presumed babies, and (3) lacking such cues, care for the babies as though they *had* fathered them. This argument[86] is consistent with the empirical findings the (1) babies do not reliably look like their biological fathers,[82,83] (2) men greatly value sexual faithfulness in their spouses[91] and invest more in children that look like them,[92-94] and (3) unless they have specific reasons to mistrust their spouses (the median nonpaternity rate is about 30% in men who doubt their paternity but less than 2% in men who do not[80]), men typically do treat their alleged children as though they were their own—despite objective uncertainty and without first requiring a DNA test.

In agreement with an effort to increase paternity confidence, mothers tend to ascribe more paternal than maternal resemblance to their babies,[82,95,96] although infants do not resemble their fathers more than their mothers according to independent observers that are blind to their kin relationships.[82,83] This blindness is an important methodological detail, because, when judging family resemblances, people are powerfully influenced by alleged relatedness.[97] Unrelated parent/child pairs that are believed to be related are seen as more resemblant than related pairs that are believed to be unrelated (a result obtained in Italy[97] and independently replicated in Japan[98]). Consistent with the hypothesis that they have evolved to encourage paternal investment, biases in judging relatedness are strongest in men who are fathers, among which overestimation of resemblance in photos of parent/child pairs is significantly larger than in both women and men who are not fathers.[21]

Every male in the relatedness line between two people introduces one degree of uncertainty in their genetic link. Consistently, even investment by grandparents is affected by paternity uncertainty, with maternal grandmothers investing the most in their daughter's children and paternal grandfathers investing the least in their alleged son's alleged children[99-101] (although a study carried out in China suggests that this effect could be overruled by cultural or economic factors[102]). Hypothetical altruism among cousins follows the same pattern, with mother's sister's children being helped the most and father's brother's children being helped the least.[103] An impressively drastic solution to the problem of paternity uncertainty has been embraced in societies with very low paternity confidence, where men direct material resources to their sisters' offspring (to whom they are certainly related) rather than to their own alleged children.[104]

CONCLUSION

Lady Justice stands for a moral value we much treasure in our society: equitable treatment for all without regard to people's status, be they family, friends, or strangers. Yet, virtually nobody abides by this moral value in his or her personal life. Rather than setting other people's status aside, we put it center stage. Our inheritance, for example, we leave to our children and rarely to equally or more deserving strangers. Cues to kinship play a crucial role not only in how we choose our mates, but also in how egoistic, altruistic, or spiteful we are toward others. We have shown that, at the level of the genes, all our behaviors can be considered egoistic. This implies that, at the level of individuals, spite could only have evolved as a form of altruism and altruism could only have evolved as a form of nepotism. This nepotism we extend to society at large. Ingroup members are more likely to be kin than outgroup members, and we are famously more inclined to assist the ingroup than the outgroup and to assault the outgroup than the ingroup.

It has been suggested[105] that the xenophobic behavior of some, but not all, individuals of the Argentine ant may help understand the mechanism that drives this type of discrimination. The more genetically homogeneous the colony in which an ant was raised, the more violent its later reaction to unfamiliar conspecifics. It could be argued that the flexibility of the ant's kin template decreases with increasing similarity among the members of its home colony. Remarkably, the attitudes of American voters appear to mirror the ants' conduct: endorsers of more conservative political ideas, associated with nationalism and reduced sympathy for immigrants, are typically found in rural areas with homogeneous populations as opposed to cities with heterogeneous ones (Figure 3).

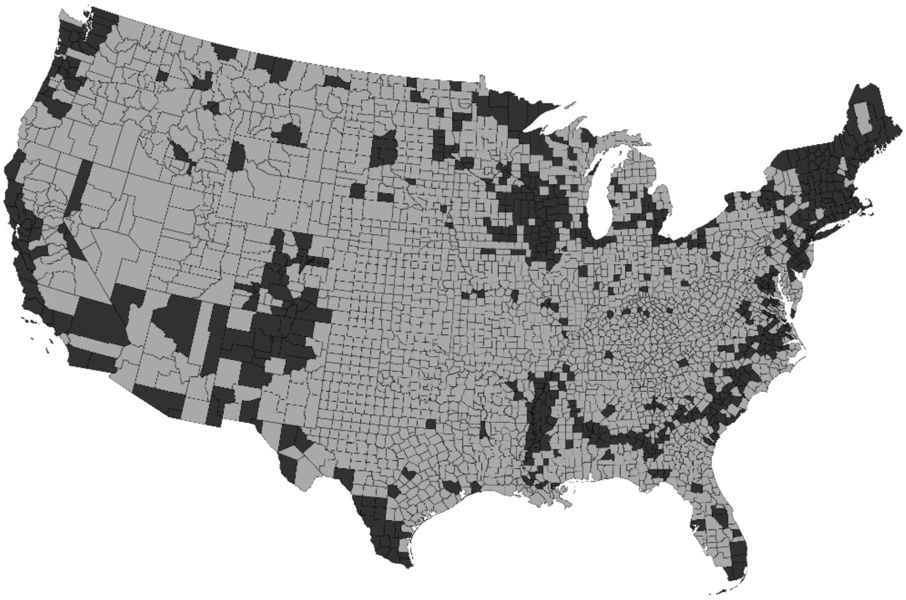

FIGURE 3. A map of the 2012 presidential-election results in the contiguous United States. Light areas indicate counties where the conservative candidate won; dark areas counties where the liberal candidate won. Although the map is dominated by light gray, the final winner was the liberal and not the conservative candidate, because the light counties tend to be rural and the dark ones urban—and thus more populated. Results of earlier presidential races show a similar pattern. (Adapted from a figure by Mark Newman, University of Michigan, Creative Commons License)

The shaping of political preferences by genetic factors has recently received much attention.[106] Among the genes most likely to affect such preferences are those that regulate human kin detection and the behaviors that depend on it: outbreeding, altruism, and spite. Hence, research on the genetic substratum of kin detection may hold promise for understanding much more than the substratum itself—with profound bearings on social sciences and everyday life.

REFERENCES

1. Holmes WG. The development and function of nepotism: why kinship matters in social relationships. In: Blass EM, ed. *Handbook of Behavioral Neurobiology*. Developmental Psychobiology, vol. 13. New York: Plenum; 2001, 281–316.

2. Thornhill NW. *The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives*. Chicago: University of Chicago Press; 1993.

3. Berra TM, Alvarez G, Ceballos FC. Was the Darwin/Wedgwood dynasty adversely affected by consanguinity? *BioScience* 2010, 60:376–383. doi:10.1525/bio.2010.60.5.7.

4. Fessler DM, Navarrete C. Third-party attitudes toward sibling incest. *Evol Hum Behav* 2004, 25:277–294. doi:10.1016/j.evolhumbehav.2004. 05.004.

5. Lieberman D, Tooby J, Cosmides L. Does morality have a biological basis? An empirical test of the factors governing moral sentiments relating to incest. *Proc Biol Sci* 2003, 270:819–826. doi:10.1098/rspb.2002.2290.

6. Walter A, Buyske S. The Westermarck effect and early childhood co-socialization: sex differences in inbreeding-avoidance. *Br J Dev Psychol* 2003, 21:353–365.

7. Marcinkowska UM, RantalaMJ. Sexual imprinting on facial traits of opposite-sex parents in humans. *Evol Psychol* 2012, 10:621–630.

8. Marcinkowska UM, Moore FR, Rantala MJ. An experimental test of the Westermarck effect: sex differences in inbreeding avoidance. *Behav Ecol* 2013, 24:842–845.

9. Ackerman JM, Kenrick DT, Schaller M. Is friendship akin to kinship? *Evol Hum Behav* 2007, 28:365–374. doi:10.1016/j.evolhumbehav.2007.04.004.

10. Havlicek J, Roberts SC. MHC-correlated mate choice in humans: a review. *Psychoneuroendocrinology* 2009, 34:497–512. doi:10.1016/j.psyneuen. 2008.10.007.

11. Helgason A, Pálsson S, Gudbjartsson DF, Kristjánsson T, Stefánsson K. An association between the kinship and fertility of human couples. *Science* 2008, 319:813–816. doi:10.1126/science.1150232.

12. Bateson P. Sexual imprinting and optimal outbreeding. *Nature* 1978, 273:659–660.

13. Gardner A, West SA. Spite. *Curr Biol* 2006, 16:R662–R664.

14. Hamilton WD. The genetical evolution of social behaviour. I, II. *J Theor Biol* 1964, 7:1–52.

15. Dawkins R. Twelve misunderstandings of kin selection. *Z Tierpsychol* 1979, 51:184–200.

16. Park JH. Persistent misunderstandings of inclusive fitness and kin selection: their ubiquitous appearance in social psychology textbooks. *Evol Psychol* 2007, 5:860–873.

17. Thompson GJ, Hurd PL, Crespi BJ. Genes underlying altruism. *Biol Lett* 2013, 9:20130395. doi:10.1098/rsbl.2013.0395.

18. Krupp DB, Sewall LA, Lalumière ML, Sheriff C, Harris GT. Nepotistic patterns of violent psychopathy: evidence for adaptation? *Front Psychol* 2012, 3:305. doi:10.3389/fpsyg.2012.00305.

19. Crespi B, Badcock C. Psychosis and autism as diametrical disorders of the social brain. *Behav Brain Sci* 2008, 31:241-261; discussion 261-320. 10.1017/S0140525X08004214

20. Nesse RM, Silverman A, Bortz A. Sex differences in ability to recognize family resemblance. *Ethol Sociobiol* 1990, 11:11–21.

21. Bressan P, Dal Pos S. Fathers see stronger family resemblances than non-fathers in unrelated children's faces. *Arch Sex Behav* 2012, 41:1423–1430. doi:10.1007/s10508-012-9983-x.

22. Dawkins R. *The Selfish Gene*. New York: Oxford University Press; 2006.

23. Hamilton WD. Selfish and spiteful behaviour in an evolutionary model. *Nature* 1970, 228:1218–1220.

24. Krupp DB, DeBruine LM, Jones BC, Lalumière ML. Kin recognition: Evidence that humans can perceive both positive and negative relatedness. *J Evol Biol* 2012, 25:1472–1478. doi:10.1111/j. 1420-9101.2012.02553.x.

25. Wilson EO. *Sociobiology: The New Synthesis*. Cambridge: Harvard Press; 1975.

26. Lehmann L, Bargum K, Reuter M. An evolutionary analysis of the relationship between spite and altruism. *J Evol Biol* 2006, 19:1507–1516. doi:10.1111/j. 1420-9101.2006.01128.x.

27. Smith MS, Kish BJ, Crawford CB. Inheritance of wealth as human kin investment. *Ethol Sociobiol* 1987, 8:171–182.

28. Pollet TV. Genetic relatedness and sibling relationship characteristics in a modern society. *Evol Hum Behav* 2007, 28:176–185.

29. Bressan P, Colarelli SM, Cavalieri MB. Biologically costly altruism depends on emotional closeness among step but not half or full siblings. *Evol Psychol* 2009, 7:118–132.

30. Chrastil ER, Getz WM, Euler HA, Starks PT. Paternity uncertainty overrides sex chromosome selection for preferential grandparenting. *Evol Hum Behav* 2006, 27:206–223.

31. Tanskanen AO, Rotkirch A, Danielsbacka M. Do grandparents favor granddaughters? Biased grandparental investment in UK. *Evol Hum Behav* 2011, 32:407–415.

32. Fox M, Sear R, Beise J, Ragsdale G, Voland E, Knapp LA. Grandma plays favourites: X-chromosome relatedness and sex-specific childhood mortality. *Proc Biol Sci* 2010, 277:567–573. doi:10.1098/rspb.2009.1660.

33. Rice WR, Gavrilets S, Friberg U. The evolution of sex-specific grandparental harm. *Proc Biol Sci* 2010, 277:2727–2735. doi:10.1098/rspb.2010.0409.

34. Fox M, Johow J, Knapp LA. The selfish grandma gene: the roles of the X-chromosome and paternity uncertainty in the evolution of grandmothering behavior and longevity. *Int J Evol Biol* 2011, 2011:165919. doi:10.4061/2011/165919.

35. Johow J, Fox M, Knapp LA, Voland E. The presence of a paternal grandmother lengthens interbirth interval following the birth of a granddaughter in Krummhörn (18th and 19th centuries). *Evol Hum Behav* 2011, 32:315–325.

36. Yu N, Kruskall MS, Yunis JJ, Knoll JH, Uhl L, Alosco S, Ohashi M, Clavijo O, Husain Z, Yunis EJ, et al. Disputed maternity leading to identification of tetragametic chimerism. *N Engl J Med* 2002, 346:1545–1552. doi:10.1056/NEJMoa013452.

37. Boklage CE. The frequency and survival probability of natural twin conceptions. In: Keith L, Papiernik E, Keith D, Luke B, eds. *Multiple Pregnancy: Epidemiology, Gestation and Perinatal Outcome*. New York: Parthenon Publishers; 1995, 41–50.

38. Lieberman D, Tooby J, Cosmides L. The architecture of human kin detection. *Nature* 2007, 445:727–731. doi:10.1038/nature05510.

39. De Smet D, Van Speybroeck L, Verplaetse J. The Westermarck effect revisited: a psychophysiological study of sibling incest aversion in young female adults. *Evol Hum Behav* 2014, 35:34–42.

40. DeBruine LM, Jones BC, Watkins CD, Roberts SC, Little AC, Smith FG, Quist MC. Opposite-sex siblings decrease attraction, but not prosocial attributions, to self-resembling opposite-sex faces. *Proc Natl Acad Sci U S A* 2011, 108:11710–11714.

41. Kaminski G, Ravary F, Graff C, Gentaz E. Firstborns' disadvantage in kinship detection. *Psychol Sci* 2010, 21:1746–1750. doi:10.1177/0956797610388045.

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

43. Westermarck E. *The History of Human Marriage*. London: Macmillan; 1921.

44. Wolf AP. Childhood association and sexual attraction: a further test of the Westermarck hypothesis. *Am Anthrop* 1970, 72:503–515.

45. Lieberman D, Lobel T. Kinship on the Kibbutz: coresidence duration predicts altruism, personal sexual aversions and moral attitudes among communally reared peers. *Evol Hum Behav* 2012, 33:26–34. doi:10.1016/j.evolhumbehav.2011.05.002.

46. Park JH, Schaller M, Van Vugt M. Psychology of human kin recognition: heuristic cues, erroneous inferences, and their implications. *Rev Gen Psychol* 2008, 12:215–235. doi:10.1037/1089-2680.12.3.215.

47. Steblay NM. Helping behavior in rural and urban environments: a meta-analysis. *Psychol Bull* 1987, 102:346.

48. Amato PR. Urban-rural differences in helping friends and family members. *Soc Psychol Q* 1993, 56:249–262.

49. Grafen A. Do animals really recognize kin? *Anim Behav* 1990, 39:42–54.

50. Porter RH, Cernoch JM, Balogh RD. Odor signatures and kin recognition. *Physiol Behav* 1985, 34:445–448.

51. Pause BM. Processing of body odor signals by the human brain. *Chemosens Percept* 2012, 5:55–63. doi:10.1007/s12078-011-9108-2.

52. Weisfeld GE, Czilli T, Phillips KA, Gall JA, Lichtman CM. Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *J Exp Child Psychol* 2003, 85:279–295.

53. Dubas JS, Heijkoop M, Aken MAG. A preliminary investigation of parent–progeny olfactory recognition and parental investment. *Hum Nat* 2009, 20:80–92. doi:10.1007/s12110-009-9058-4.

54. Thorsby E. A short history of HLA. *Tissue Antigens* 2009, 74:101–116. doi:10.1111/j. 1399-0039.2009.01291.x.

55. Wobst B, Zavazava N, Luszyk D, Lange K, Ussat S, Eggert F, Ferstl R, Müller-Ruchholtz W. Molecular forms of soluble HLA in body fluids: potential determants of body odor cues. *Genetica* 1998, 104:275–283.

56. Wedekind C, Seebeck T, Bettens F, Paepke AJ. MHC-dependent mate preferences in humans. *Proc Biol Sci* 1995, 260:245–249. doi:10.1098/rspb. 1995.0087.

57. Jacob S, McClintock MK, Zelano B, Ober C. Paternally inherited HLA alleles are associated with women's choice of male odor. *Nat Genet* 2002, 30:175–179. doi:10.1038/ng830.

58. Pause BM, Krauel K, Schrader C, Sojka B, Westphal E, Müller-Ruchholtz W, Ferstl R. The human brain is a detector of chemosensorily transmitted HLA-class I-similarity in same- and opposite-sex relations. *Proc Biol Sci* 2006, 273:471–478. doi:10.1098/rspb.2005.3342.

59. Levy F, Keller M, Poindron P. Olfactory regulation of maternal behavior in mammals. *Horm Behav* 2004, 46:284–302.

60. Fischer-Shofty M, Levkovitz Y, Shamay-Tsoory SG. Oxytocin facilitates accurate perception of competition in men and kinship in women. *Soc Cogn Affect Neurosci* 2013, 8:313–317. doi:10.1093/scan/nsr100.

61. Kim HJ, Im SW, Jargal G, Lee S, Yi JH, Park JY, Sung J, Cho SI, Kim JY, Kim JI, et al. Heritabilities of facial measurements and their latent factors in Korean families. *Genomics Inform* 2013, 11:83–92.

doi:10.5808/GI.2013.11.2.83.

62. Kaminski G, Dridi S, Graff C, Gentaz E. Human ability to detect kinship in strangers' faces: effects of the degree of relatedness. *Proc Biol Sci* 2009, 276:3193–3200. doi:10.1098/rspb.2009.0677.

63. DeBruine LM. Trustworthy but not lust-worthy: context-specific effects of facial resemblance. *Proc Biol Sci* 2005, 272:919–922. doi:10.1098/rspb.2004.3003.

64. DeBruine L, Jones B, Little A, Perrett D. Social perception of facial resemblance in humans. *Arch Sex Behav* 2008, 37:64–77.

65. DeBruine LM. Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proc Biol Sci* 2004, 271:2085–2090. doi:10.1098/rspb.2004.2824.

66. DeBruine LM, Jones BC, Perrett DI. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Horm Behav* 2005, 47:379–383. doi:10.1016/j.yhbeh.2004.11.006.

67. DeBruine LM. Resemblance to self increases the appeal of child faces to both men and women. *Evol Hum Behav* 2004, 25:142–154. doi:10.1016/j.evolhumbehav.2004.03.003.

68. Bressan P, Bertamini M, Nalli A, Zanutto A. Men do not have a stronger preference than women for self-resemblant child faces. *Arch Sex Behav* 2009, 38:657–664. doi:10.1007/s10508-008-9350-0.

69. Volk AA, Quinsey VL. Parental investment and resemblance: replications, refinements, and revisions. *Evol Psychol* 2007, 5:1–14.

70. Krupp DB, DeBruine LM, Barclay P. A cue of kinship promotes cooperation for the public good. *Evol Hum Behav* 2008, 29:49–55. doi:10.1016/j.evolhumbehav.2007.08.002.

71. Giang T, Sorci G, Bell R, Buchner A. Does facial resemblance enhance cooperation? *PLoS One* 2012, 7:e47809. doi:10.1371/journal.pone.0047809.

72. Bressan P, Zucchi G. Human kin recognition is self- rather than family-referential. *Biol Lett* 2009, 5:336–338. doi:10.1098/rsbl.2008.0789.

73. Olson JM, Vernon PA, Harris JA, Jang KL. The heritability of attitudes: a study of twins. *J Pers Soc Psychol* 2001, 80:845–860. doi:10.1037//0022-3514.80.6.845.

74. Park JH, SchallerM. Does attitude similarity serve as a heuristic cue for kinship? Evidence of an implicit cognitive association. *Evol Hum Behav* 2005, 26:158–170.

75. Oates K, Wilson M. Nominal kinship cues facilitate altruism. *Proc Biol Sci* 2002, 269:105–109. doi:10.1098/rspb.2001.1875.

76. Faulkner J, Schaller M. Nepotistic nosiness: inclusive fitness and vigilance of kin members' romantic relationships. *Evol Hum Behav* 2007, 28:430–438.

77. Alvergne A, Faurie C, Raymond M. Are parents' perceptions of offspring facial resemblance consistent with actual resemblance? Effects on parental investment. *Evol Hum Behav* 2010, 31:7–15. doi:10.1016/j.evolhumbehav.2009.09.002.

78. Neyer FJ, Lang FR. Blood is thicker than water: kinship orientation across adulthood. *J Pers Soc Psychol* 2003, 84:310–321.

79. Korchmaros JD, Kenny DA. An evolutionary and close-relationship model of helping. *J Soc Pers Relat* 2006, 23:21–43.

80. Anderson KG. How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Curr Anthropol* 2006, 47:513–520.

81. Daly M, Wilson M. *Homicide*. New York: Aldine deGruyter; 1988.

82. McLain DK, Setters D, MoultonMP, Pratt AE. Ascription of resemblance of newborns by parents and

nonrelatives. *Evol Hum Behav* 2000, 21:11–23.

83. Bressan P, Grassi M. Parental resemblance in 1-year-olds and the Gaussian curve. *Evol Hum Behav* 2004, 25:133–141. doi:10.1016/j. evolhumbehav.2004.03.001.

84. Kaminski G, Méary D, Mermillod M, Gentaz E. Perceptual factors affecting the ability to assess facial resemblance between parents and newborns in humans. *Perception* 2010, 39:807–818.

85. Brédart S, French RM. Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld and Hill (1995). *Evol Hum Behav* 1999, 20:129–135.

86. Bressan P. Why babies look like their daddies: paternity uncertainty and the evolution of self-deception in evaluating family resemblance. *Acta Ethol* 2002, 4:113–118. doi:10.1007/s10211-001-0053-y.

87. Pagel M. Desperately concealing father: a theory of parent-infant resemblance. *Anim Behav* 1997, 53:973–981.

88. Clutton-Brock TH. *The Evolution of Parental Care*. Princeton University Press; 1991.

89. Gaulin SJ, Schlegel A. Paternal confidence and paternal investment: a cross cultural test of a sociobiological hypothesis. *Ethol Sociobiol* 1980, 1:301–309.

90. Geary DC. Evolution and proximate expression of human paternal investment. *Psychol Bull* 2000, 126:55. doi:10.1037//0033-2909.126.1.55.

91. Buss DM, Schmitt DP. Sexual strategies theory: an evolutionary perspective on human mating. *Psychol Rev* 1993, 100:204–232.

92. Alvergne A, Faurie C, Raymond M. Father-offspring resemblance predicts paternal investment in humans. *Anim Behav* 2009, 78:61–69.

93. Apicella CL, Marlowe FW. Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evol Hum Behav* 2004, 25:371–378. doi:10.1016/j.evolhumbehav.2004.06.003.

94. Platek SM. An evolutionary model of the effects of human paternal resemblance on paternal investment. *Evol Cogn* 2003, 9:189–197.

95. Daly M, Wilson MI. Whom are newborn babies said to resemble? *Ethol Sociobiol* 1982, 3:69–78.

96. Regalski JM, Gaulin SJ. Whom are Mexican infants said to resemble? Monitoring and fostering paternal confidence in the Yucatan. *Ethol Sociobiol* 1993, 14:97–113.

97. Bressan P, Dal Martello MF. Talis pater, talis filius: perceived resemblance and the belief in genetic relatedness. *Psychol Sci* 2002, 13:213–218. doi:10.1111/1467-9280.00440.

98. Oda R, Matsumoto-Oda A, Kurashima O. Effects of belief in genetic relatedness on resemblance judgments by Japanese raters. *Evol Hum Behav* 2005, 26:441–450. doi:10.1016/ j.evolhumbehav.2005.04.002.

99. Euler HA, Weitzel B. Discriminative grandparental solicitude as reproductive strategy. *Hum Nat* 1996, 7:39–59. doi:10.1007/BF02733489.

100. Bishop DI, Meyer BC, Schmidt TM, Gray BR. Differential investment behavior between grandparents and grandchildren: the role of paternity uncertainty. *Evol Psychol* 2009, 7:66–77.

101. Laham SM, Gonsalkorale K, von Hippel W. Darwinian grandparenting: preferential investment in more certain kin. *Pers Soc Psychol Bull* 2005, 31:63–72. doi:10.1177/0146167204271318.

102. Kaptijn R, Thomese F, Liefbroer AC, Silverstein M. Testing evolutionary theories of discriminative grandparental investment. *J Biosoc Sci* 2013, 45:289–310. doi:10.1017/S0021932012000612.

103. Jeon J, Buss DM. Altruism towards cousins. *Proc Biol Sci* 2007, 274:1181–1187. doi:10.1098/ rspb.2006.0366.

104. Kurland JA. Paternity, mother's brother, and human sociality. In: Chagnon NA, Irons W, eds. *Evolutionary*

Biology and Human Social Behavior. North Scituate: Duxbury Press; 1979, 145–180.

105. Krupp DB, DeBruine LM, Jones BC. Cooperation and conflict in the light of kin recognition systems. In: Salmon C, Shackelford TK, eds. *The Oxford Handbook of Evolutionary Family Psychology*. New York: Oxford University Press; 2011, 345–362.

106. Hatemi PK, McDermott R. The genetics of politics: discovery, challenges, and progress. *Trends Genet* 2012, 28:525–533. doi:10.1016/j.tig.2012.07.004.