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# Coresidence Duration and Cues of Maternal Investment Regulate Sibling Altruism Across Cultures

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Genetic relatedness is a fundamental determinant of social behavior across species. Over the last few decades, researchers have been investigating the proximate psychological mechanisms that enable humans to assess their genetic relatedness to others. Much of this work has focused on identifying cues that predicted relatedness in ancestral environments and examining how they regulate kin-directed behaviors. Despite progress, many basic questions remain unanswered. Here we address three of these questions. First, we examine the replicability of the effect of two association-based cues to relatedness—maternal perinatal association (MPA) and coresidence duration—on sibling-directed altruism. MPA, the observation of a newborn being cared for by one's mother, strongly signals relatedness, but is only available to the older sibling in a sib-pair. Younger siblings, to whom the MPA cue is not available, appear to fall back on the duration of their coresidence with an older sibling. Second, we determine whether the effects of MPA and coresidence duration on sibling-directed altruism obtain across cultures. Last, we explore whether *paternal* perinatal association (PPA) informs sibship. Data from six studies conducted in California, Hawaii, Dominica, Belgium, and Argentina support past findings regarding the role of MPA and coresidence duration as cues to siblingship. By contrast, PPA had no effect on altruism. We report on levels of altruism toward full, half, and step siblings, and discuss the role alternate cues might play in discriminating among these types of siblings.

*Keywords:* altruism, kinship, Westermarck effect, maternal perinatal association (MPA), paternal perinatal association (PPA)

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Genetic relatedness is a fundamental variable that regulates many aspects of social behavior (Hamilton, 1964). Across diverse taxa, increased genetic relatedness is associated with higher levels of altruism, reduced aggression, and inbreeding avoidance (Fletcher & Michener, 1987; Hepper, 1991). Humans, too, conform to this pattern: Across cultures, humans tend to avoid mating with close kin (Wolf & Durham, 2004), preferentially direct resources and aid toward relatives (Burnstein, 2005; Burnstein, Crandall, & Kitayama, 1994), and act less violently toward biological relatives than toward genetically unrelated individuals (Daly & Wilson, 1988).

With respect to the proximate psychological mechanisms governing these behaviors, evidence accumulating from across the social and behavioral sciences suggests that humans rely on particular cues of kinship to identify genetic relatives and to regulate levels of altruism, aggression, and sexual motivation accordingly (Ackerman, Kenrick, & Schaller, 2007; DeBruine, 2002, 2005; Fessler & Navarrete, 2004; Lieberman, Tooby, & Cosmides, 2007; Park, Schaller, & Van Vugt, 2008). Researchers have investigated a range of potential cues, including facial resemblance (DeBruine, 2002, 2005), major histocompatibility complex (MHC)-mediated olfactory cues (for reviews, see Havlicek & Roberts, 2009; Winternitz & Abbate, 2015), and, of interest here, coresidence duration as well as observations of maternal investment in a newborn, a cue termed maternal perinatal association (MPA; Lieberman, 2009; Lieberman & Lobel, 2012; Lieberman et al., 2007; Shepher, 1971; Westermarck, 1891; Wolf, 1995).

Although coresidence duration and MPA appear to mediate sibling detection and regulate sibling-directed behaviors, many questions remain. For instance, how robust are the effects of MPA and coresidence duration on sibling-directed altruism? To date, these effects have not been replicated. Further, do MPA and coresidence duration regulate sibling-directed altruism in cultures around the world—even in nonindustrial populations which more closely resemble the ecologies in which human kin detection systems evolved? And does the mind use the association of a

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newborn and a *father* to assess paternal sibship? *Paternal* perinatal association (PPA) may inform sibship along with, but independently of, MPA; this would enable the discrimination of (younger) full sibs from (younger) half sibs, and permit a finer calibration of altruism based on genetic relatedness. Here we discuss the logic behind the evolution of kin detection systems and then report six cross-cultural tests to address the above questions regarding the effect of three proposed cues to kinship—coresidence duration, MPA, and PPA—on sibling-directed altruism.

## Why Detect Kin: Ultimate Explanations

There are two major evolutionary selection pressures that would have conferred a reproductive advantage on individuals capable of discriminating kin from nonkin and distinguishing among different degrees of genetic relatives. The first selection pressure is characterized by inclusive fitness theory (Hamilton, 1964). Hamilton noted that an organism—or more specifically, a gene residing in an organism—could increase its probability of replication both directly, by promoting the reproduction of the body in which it resides, and indirectly, by promoting the reproduction of individuals likely to carry copies of the same gene. Genetic relatives represent one such type of individual because those who share recent common ancestors have a greater probability of sharing identical gene variants.

Hamilton's inclusive fitness theory predicts that genes that cause an individual to selectively direct resources and aid toward relatives can out-replicate, under some conditions, genes that do not have such effects. Evidence supports this claim. Humans and other animals, specifically those species in which relatives tend to interact across the life span, preferentially help closer relatives over more distant relatives or nonrelatives, particularly in times of dire need (Burnstein, 2005; Burnstein et al., 1994; Chapais, Savard, & Gauthier, 2001; Emlen & Wrege, 1988; Hartung, 1981; Holmes & Sherman, 1982; Queller & Strassmann, 1998; Russell & Hatchwell, 2001; Silk, 2006; Smith, Kish, & Crawford, 1987).

A second selection pressure promoting the evolution of kin detection systems relates to inbreeding. Mating with a close genetic relative such as a sibling increases the probability that the offspring will inherit identical deleterious alleles, which decreases the viability of offspring and results in potentially lethal congenital conditions (Bittles & Neel, 1994). Furthermore, inbreeding maintains a similar internal biochemistry across generations, making it easier for pathogens transmitted from parent to offspring to adapt to and defeat the offspring's immune system (Lieberman & Antfolk, 2015; Tooby, 1982). Humans, much like other animals and sexually reproducing plants, tend to defend against these negative consequences of inbreeding by avoiding mating with closely related individuals (Pusey & Wolf, 1996).

In sum, the genetic benefits accrued by aiding relatives and by avoiding the negative effects of inbreeding would have selected for systems that enabled individuals to identify close genetic relatives and to adaptively regulate cooperative and mating effort toward them. But what is the structure of these systems? That is, how might natural selection have engineered the human neurocognitive circuitry to solve the problem of kin detection?

## How to Detect Kin: Proximate Explanations

### Linguistic Information

One possibility is that cultural, linguistically transmitted information serves as a primary input for children learning about family members and how to treat them. Despite the importance of verbally transmitted information in humans, it is unlikely that linguistic information serves as a primary cue to kinship, particularly for nuclear family members, for several reasons. First, linguistic terms can blur genetic boundaries. For example, in English, the term *aunt* can refer to a parent's sister (a genetic relative) or a parent's brother's wife (not a genetic relative). Additionally, kin terms (e.g., *brother*, *father*) are used metaphorically in religious and coalitional contexts. Given the selection pressures associated with inbreeding avoidance and cooperation, it would have been critical to distinguish actual kin from fictive kin, and without prior valid assumptions, linguistic terms would not have carved reliably between the two.

Another reason why linguistic terms might not be a primary source of information regarding relatedness is that genetic relatedness is perspective-dependent. Every individual sits at the center of a unique web of genetic relationships, and it is not clear who in the social environment would be motivated to teach an individual the nature of these relationships. Consider, for instance, a mother with two sons sired by the same man, and a third child, a daughter, sired by another man. The mother is equally related to all three children. According to inclusive fitness theory, that mother will be selected to care for the three children equally and to encourage the children to value each other as highly as they value themselves (Trivers, 1974). However, the children are not all equally related to each other. From a son's perspective, he is 100% related to himself (that is, his genetic coefficient of relatedness, r, to himself equals 1.0), his brother is a full biological sibling who shares both mom and dad (r to brother equals 0.5), but his sister is only a maternal half sibling (r to sister equals 0.25). Inclusive fitness theory predicts that, all else equal, the son will weight his own welfare twice as highly as the welfare of his full brother and four times as highly as that of his maternal half-sister—a very different set of weights from those favored by the mother. But how would he learn this strictly from cultural information conveyed linguistically? Who would instruct him to allocate his effort differently among himself, his brother, and his sister? Not his mother, because she is designed to have her children value one another's welfare as highly as their own welfare. Genetic relatedness is actor-specific, and so information generated by another actor and transmitted linguistically would not necessarily be a reliable cue to relatedness. As a result, a psychology capable of using other, more reliable cues to identify kin would out-reproduce a psychology relying solely on linguistic information.

Last, other species are able to discriminate kin from nonkin even in the absence of linguistic and cultural information. A recent review concluded that the ability to discriminate kin from nonkin "appears universal across the animal kingdom" (Hepper, 2011, p. 215), and characterizes mammals (e.g., hyenas, elephants, rhesus macaques, bottlenose dolphins), birds (e.g., peacocks, turkeys, ostriches), reptiles (e.g., rattlesnakes, some lizards), amphibians (e.g., fire salamanders, various toads), fish (e.g., Atlantic salmon and rainbow trout), and invertebrates (e.g., ants, bees and termites;

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Hepper, 2011). It is unlikely that evolution would have jettisoned prior kin detection mechanisms in favor of ones that were less reliable and more prone to error. More likely, humans use ecologically valid cues that correlated with genetic relatedness in ancestral environments.

## Ecological Cues

Evolutionary biologists have identified several classes of ecological cues that nonhuman animals use to detect kin: location/proximity, association, and phenotype matching (Holmes & Sherman, 1983). Across the animal kingdom, some kin detection mechanisms take advantage of the recurrent correlation between the spatial proximity of conspecifics and the genetic relatedness to those conspecifics. Kin detection mechanisms inferring relatedness from proximity are common, for instance, among many nesting birds, where parents treat any nestling as offspring. Here, as with any well-designed detection mechanism, the correlation between the cue (e.g., egg in my nest) and the true state of the world (actual genetic relatedness) is high but not perfect, providing for the possibility of detection errors as well as exploitation by other species. Brood parasites such as cuckoo birds, for example, dupe some avian species into tending eggs that are not their own (see Davies, 2000; Johnsgard, 1997; Rothstein, 1990).

Other kin detection systems take advantage of patterns of association to infer relatedness. For instance, observing which female other young flock to, suckle from, sleep near, or get cleaned by can serve as information regarding relatedness. With respect to detecting siblings, association-based mechanisms are revealed by cross-fostering experiments, in which newborns are removed from the nest or litter of their birth and raised with genetically unrelated siblings (Mateo & Holmes, 2004). In Belding's ground squirrels, for example, individuals reared together displayed equally low levels of aggression when subsequently paired together as adults, regardless of their actual genetic relatedness (Holmes & Sherman, 1982). Likewise, as we discuss below, in humans, genetically unrelated children raised together under "sibling-like" conditions—as in the case of coreared peers living in Israeli Kibbutzim (Shepher, 1983) and the adopted infant-brides of Taiwanese minor marriages (Wolf, 1995)—also develop kin-like attitudes toward one another, evidenced by reduced marital fertility (Wolf & Durham, 2004), lowered sexual attraction, and increased altruism (Lieberman & Lobel, 2012). Such kin-relevant behavior targeted toward coreared but genetically unrelated individuals suggests that association-based mechanisms might be at work.

A final type of kin detection mechanism is phenotype matching, which exploits naturally occurring associations between genetic relatedness and similarity in physical or behavioral characteristics among individuals. Phenotype matching involves assessing one or more traits of a conspecific, comparing those traits to a template, and determining whether a sufficient match exists between the two. The template may reflect aspects of the individual itself (self-referencing) or traits previously linked to kin (other-referencing; Hepper, 2011; Krupp, DeBruine, & Jones, 2011). Other-referencing, it should be noted, presumes the prior functioning of an alternative kin detection mechanism, such as association, to form the basis of the kin template—otherwise, how would one know which targets constitute the basis of the template?

Phenotype matching has the advantage of enabling individuals to identify previously unencountered individuals as relatives (Mateo, 2002). Belding's ground squirrels again provide an intriguing example. Cross-fostering experiments revealed not only indistinguishably low levels of adult aggression among individuals reared together, irrespective of actual relatedness, but also reduced levels of aggression in genetically related female siblings *reared apart*, compared to genetically unrelated females reared apart (Holmes & Sherman, 1982). This latter finding, in conjunction with additional experiments ruling out association during prenatal development (Hanken & Sherman, 1981), implicates the operation of a phenotype matching mechanism. Subsequent work suggests that gland-based odors are the proximate means by which such matching occurs (Mateo, 2006, 2009). Belding's ground squirrels thus rely upon both association-based and phenotype-matching mechanisms to recognize siblings, and demonstrate that within a single species natural selection can take advantage of multiple cues for detecting kin.

## Sibling Detection in Humans

Early research on kin detection in humans focused on siblings and on proximate mechanisms based upon association. Much of this work originated with Edward Westermarck, a Finnish social scientist, who noted the commonplace observation that siblings rarely select one another as sexual partners. Westermarck (1891) proposed that close physical association during childhood leads to the development of strong sexual aversions during adulthood. A wealth of anthropological evidence has since supported Westermarck's hypothesis that childhood coresidency causes mutual sexual aversion between adults. Marital and fertility records from Israeli kibbutzim (Shepher, 1971), Taiwanese minor marriages (Wolf, 1995), and Lebanese cousin marriages (McCabe, 1983) show that opposite sex children reared together subsequently display reduced marriage rates, higher divorce rates if married, and lower fertility, compared to opposite sex children reared apart. Furthermore, data from the Israeli kibbutzim and Taiwanese minor marriages indicate that close physical association throughout childhood leads to sexual aversions even between individuals who are not genetically related and who are encouraged to mate by cultural norms. Although Westermarck's hypothesis and the supporting studies have not gone without challenge (e.g., Leavitt, 1990; Shor & Simchai, 2009; for review, see Fessler & Navarrete, 2004), evidence suggests overall that these novel cultural institutions led unrelated children to miscategorize each other as kin when they fell into a social arrangement typically occupied by actual genetic siblings.

Although the studies mentioned above provide valuable evidence relevant to Westermarck's hypothesis, their measures are somewhat removed from actual individual psychologies. Rates of marriage, divorce, and fertility are distal measures of sexual avoidance and sexual disgust—the direct outputs of inbreeding avoidance mechanisms. Later research has bridged this gap by using survey methods that more directly assess individual motivations and behavior. Studies conducted on samples of American undergraduates have found that coresidence duration predicts moral opposition to incest (Fessler & Navarrete, 2004; Lieberman et al., 2003, 2007), as well as increased altruism and increased sexual aversion among opposite sex siblings (Lieberman et al., 2007).

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More recently, researchers used facial electromyography to obtain a direct psychophysiological measure of sexual disgust in a sample of Belgian undergraduate women (De Smet, Van Speybroeck, & Verplaetse, 2014). Results indicated that duration of coresidency with an older brother predicted a facial disgust response among women viewing photographs of a sexual (vs. neutral) nature and imagining performing those acts with her brother (vs. her sexual partner).

Ethnographic observations of foragers suggest that childhood coresidency, the cue proposed by Westermarck, would have been a good predictor of genetic siblingship in ancestral environments. In the last decade researchers have proposed another association-based cue that might serve to identify siblings: observations of a female investing in (e.g., breast-feeding) a newborn, a cue termed Maternal Perinatal Association (MPA; Lieberman et al., 2007). Because any infant regularly nurtured by one's mother is highly likely to be a sibling, MPA should be a stronger, more reliable cue than coresidency. However, MPA would have been available only to older siblings in a sibling pair, not younger ones. On this basis, Lieberman et al. (2007) predicted, and found, that the effect of coresidence duration hinges upon the presence of MPA: Coresidence duration predicts sexual aversions between opposite sex siblings and altruism toward both same and opposite sex siblings, but only when the MPA cue is absent. Typically, this means that for a younger sibling in a sib-pair, the longer the younger sibling lived with the older sibling throughout childhood, the greater the sexual aversion toward that older sibling (if of the opposite sex) and the greater the cooperative intent. However, when the MPA cue is present, coresidence duration *does not* predict altruism or sexual aversion. That is, for an older sibling in a sib-pair who is exposed to the MPA cue for a given younger sibling, the older sibling's duration of coresidence with that younger sibling does not predict sibling-directed behaviors. This pattern of results is what one expects if MPA is the stronger cue to sibship, and coresidence a fall back cue used by the kin-estimation system when MPA is absent. This interaction of MPA and coresidence duration accounts for previously observed patterns of marital fertility in the Taiwanese minor marriage data (Lieberman, 2009) and was replicated by the Belgian study with psychophysiological measures described above (De Smet et al., 2014).

The evidence implicating MPA in sibling detection raises a related question: Does sibling detection rely on Paternal Perinatal Association (PPA)? Do children track the association between males (fathers) and newborns to determine siblingship in the same manner they appear to track the association between females (mothers) and newborns? To date, no research has examined this possibility despite its potential fitness advantages. Ancestrally, divorce and remarriage would have been somewhat frequent events (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Hill & Hurtado, 1996). As a result, children would have sometimes experienced sets of siblings related only via shared maternity or paternity—the kind of socioecological conditions that might select for fine-grained sib detection capabilities. Therefore, the mind might attend to and register the perinatal association of a candidate sibling not only with a mother (MPA) but also with a father (PPA), and use these independent bits of information to finely calibrate sibling-directed altruism: more toward a younger sibling when both MPA and PPA are present; less toward a younger sibling when PPA is absent, thus facilitating the kinds of marginal fitness gains predicted by inclusive fitness theory (Hamilton, 1964).

Relying on PPA to reckon paternal sibship, however, is not without costs. Women's extrapair sex (Greiling & Buss, 2000; Pillsworth & Haselton, 2006; Scelza, 2011) weakens the association between social fatherhood and genetic fatherhood, and so computing paternal sibship from PPA carries the risk of making false-positive errors. Quantitative estimates of this risk vary considerably across cultures (Schmitt et al., 2004), but evidence suggests that among foraging populations somewhere between 2% to 9% of men unwittingly raise children who are not their genetic offspring (Baker & Bellis, 1995; Neel & Weiss, 1975). Relying on PPA to estimate paternal sibship involves a small but nontrivial probability of incurring a great fitness cost. The danger of generating a false-positive when relying on a PPA cue might be somewhat attenuated by the fact that men condition their parental investment on cues of their mates' sexual fidelity (Apicella & Marlowe, 2004; Daly & Wilson, 1980, 1988; Platek et al., 2003). Thus, if a PPA-based mechanism were to register the right frequency or intensity of PPA, it could "assume" a favorable likelihood of paternity *as per the (putative) father's assessment,* in effect outsourcing the judgment to an actor selected for discriminative solicitude, as it were. Paternity uncertainty, however, cannot be altogether eliminated (Anderson, 2006). A PPA cue, if it exists, should therefore be an inherently weaker predictor of genetic relatedness than the MPA cue, and its relative weight in any evolved sibling detection mechanism correspondingly discounted.

Here, we explore this possibility.

## The Present Study

If the MPA/coresidence model of sibling detection is valid, the predicted pattern of sibling-directed altruism—where coresidence duration positively predicts altruism when the MPA cue is absent—should be replicable. Moreover, if the pattern in question is indeed generated by a species-typical design feature, the mappings between sibship cues on the one hand and altruism on the other hand should be observed across the world's cultures rather than be circumscribed to American culture. And the predicted patterns should be detectable not only in industrial cultures but also in more traditional, nonindustrial cultures.

Here our aim is threefold. (a) We seek to replicate the findings first published by Lieberman, Tooby, and Cosmides (2007), who showed that, among college students in California, the MPA cue moderates the effect of coresidence duration on sibling-directed altruism. (b) Further, we assess whether these findings obtain across cultures. Although cross-cultural evidence supports a role for coresidence duration as a cue to siblingship, it does so largely in the context of sexual aversion without considering sibling-directed altruism. Moreover, such evidence consists mainly of distal measures such as marriage, divorce, and fertility rates (e.g., Wolf, 1995) and does not consider MPA as a possible moderator (for an exception, see Lieberman, 2009). Here we address these lacunae by using data from six studies across four countries (the United States, Argentina, Belgium, and Dominica; the latter a nonindustrial population) to examine whether the effects of coresidence duration on sibling-directed altruism are moderated by the presence of the MPA cue. The United States, Belgium, and Argentina samples are convenience samples found in the vicinity of

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the researchers' workplace. DL was invited and agreed to join a research group in Dominica because it is a small-scale, nonindustrial population with economic and demographic characteristics more similar to what is known about ancestral humans than those of industrial populations (Flinn, 1999; Hill & Hurtado, 1996; Lee & DeVore, 1968; Quinlan, Quinlan, & Flinn, 2003). Several features of Dominica bring its inhabitants closer than industrial citizens to what we know about the human environment of evolutionary adaptedness (EEA) in general and the EEA of sibling detection in particular (Hrdy, 2000; Lee & DeVore, 1968). Kinship is the foundation of economic, social, and reproductive behavior, and most people are related through genetic or affinal bonds (Quinlan & Flinn, 2005). Unlike the typical housing arrangement in a modern nation state, in Dominica various households of closely related kin are often grouped together. Importantly, because commercial baby formula is expensive and hard to obtain, there is little social stigma attached to breastfeeding and so nursing is a common practice (Quinlan et al., 2003). This would provide older-borns ample opportunities to consolidate a register of MPA. Further, a substantial minority of families consists of children with multiple fathers (see below), which is the kind of context that would have selected for the ability to independently track maternal and paternal sibship. Thus, although not considered non-Western, Dominica bears features that make it a useful comparison sample. (c) Our third goal is to extend research on kin detection by examining whether PPA serves as a cue to siblingship; the use of this cue may allow the discrimination of younger full siblings from younger maternal or paternal half siblings, and a finer calibration of sibling-directed altruism.

## Method

Each of the following six studies was conducted in the native language of the participants: English (Studies 1–4 in Santa Barbara, Hawaii, and Dominica), Dutch (Study 5 in Ghent, Belgium), and Spanish (Study 6 in Buenos Aires, Argentina). The stimuli were created by native speakers of those languages.

### Study 1: Santa Barbara, California

**Subjects.** Subjects included 163 University of California Santa Barbara undergraduate students (49 men and 114 women) between the ages of 16 and 21 ($M = 18.44$, $SD = 0.82$).

**Procedure and materials.** Subjects completed a paper and pencil survey asking about each of their siblings. From these questions, the following variables were computed.

***Coresidence duration.*** We computed the number of years the subject coresided with each sibling between the subject's ages of 0 and 18 from the sibling-specific coresidence begin and end ages provided by the participant.

***Maternal perinatal association (MPA).*** MPA was computed from the following information: (i) whether the individual shared the same biological mother with the target sibling, (ii) whether the individual lived with their biological mother right after the target sibling was born, and (iii) whether the individual lived with the target sibling right after that sibling was born. A value of "1" was assigned if all three questions were answered in the affirmative, and a "0" was assigned if otherwise.

***Paternal perinatal association (PPA).*** PPA was computed for each subject–sibling pair from the following information: (i) whether the individual shared the same biological father with the target sibling, (ii) whether the individual lived with their biological father right after the target sibling was born, and (iii) whether the individual lived with the target sibling right after that sibling was born. A value of "1" was assigned if all questions were answered in the affirmative. A "0" was assigned if otherwise.

***Sibling-directed altruism.*** For each sibling, subjects answered a question concerning their motivation to help a sibling in a hypothetical life-threatening situation: "Provided that your sibling needs a new kidney, how willing would you be to donate one of your kidneys? In this hypothetical situation, you're not the only person who could help your sibling." (Likert scale: 0 = *not willing at all*; 6 = *completely willing*; $M = 5.46$, $SD = 1.09$). A second measure of sibling-directed altruism involved real-life behavior: "In the previous month, did you provide your sibling a favor? If so, how many? (e.g., by helping)" (measured on a 12-point scale with discrete values 0–10, and more than 10; $M = 2.12$, $SD = 2.34$). Both measures were derived from Lieberman et al. (2007). For each sibling, both measures were $z$ scored and then averaged together to create a dependent measure of altruism ($z$ score range: $-2.96$ to 1.93; $M = 0$, $SD = 0.79$).

**Data analysis.** Of the 163 subjects that we recruited in this study, 158 provided complete information (i.e., coresidence duration, MPA, PPA, and altruism) regarding one or more siblings. These 158 subjects generated 294 subject–sibling pairs (75 subjects provided data on one sibling; 46 on two siblings; 21 on three siblings; 16 on four siblings; $M = 1.86$ siblings per subject).

### Study 2: Santa Barbara, California

**Subjects.** Subjects included 112 University of California Santa Barbara undergraduate students (37 men and 75 women) between the ages of 18 and 44 ($M = 21.02$, $SD = 3.76$).

**Procedure and materials.** Subjects completed a computer-based survey asking about each of their siblings (up to eight same-sex and eight opposite-sex siblings). The variables coresidence duration, MPA, and PPA were measured as in Study 1.

To measure sibling-directed altruism, for each sibling, subjects answered four questions, all rated on 7-point Likert type scales with anchor points *not willing at all* and *extremely willing*: (a) "How willing would you be to loan your sibling $1,000?" (b) "How willing would you be to give your sibling $1,000?" (c) "How willing would you be to donate a kidney to this sibling?" (d) "Assume your sibling needs your help to finish their education. If, for some reason, nobody else could help, how willing would you be to interrupt your education, career, or life for an entire year to work and help pay for your sibling's education?" Factor analysis revealed that these questions loaded onto the same factor above a .50 cut-off criterion; they were averaged to form a composite measure, altruism (range: 0–6; $M = 3.93$, $SD = 1.61$). For analyses, we $z$ scored responses to each question and then averaged them: (range: $-2.11$ to 1.02; $M = 0$, $SD = 0.81$).

**Data analysis.** Of the 112 subjects that we recruited in this study, 109 provided complete information (i.e., coresidence duration, MPA, PPA, and altruism) regarding one or more siblings. These 109 subjects generated 234 subject–sibling pairs (48 subjects provided data on one sibling; 27 on two siblings; 18 on three siblings; eight on four siblings; six on five siblings;

one on six siblings; one on 10 siblings; $M = 2.15$ siblings per subject).

## Study 3: Honolulu, Hawaii

**Subjects.** Subjects included 128 University of Hawaii undergraduate students (29 men, 99 women) between the ages of 18 and 31 ($M = 20.96$, $SD = 2.59$).

**Procedure and materials.** Subjects completed a questionnaire on a computer regarding family attitudes. The variables coresidence duration, MPA, and PPA were measured as in Study 1. Sibling-directed altruism was measured as in Study 2; range: 0–6; $M = 4.11$, $SD = 1.74$, $N = 245$. For analyses, we $z$ scored responses to each question and then averaged them: (range: −2.17 to 0.94; $M = 0$, $SD = 0.87$).

**Data analysis.** Of the 128 subjects that we recruited in this study, 122 provided complete information (i.e., coresidence duration, MPA, PPA, and altruism) regarding one or more siblings. These 122 subjects generated 245 subject–sibling pairs (54 subjects provided data on one sibling; 39 on two siblings; 15 on three siblings; six on four siblings; five on five siblings; two on six siblings; one on seven siblings; $M = 2.01$ siblings per subject).

## Study 4: Dominica

**Subjects.** Subjects included 86 residents (51 women, 35 men) between the ages of 16 and 76 ($M = 33.34$, $SD = 12.34$; one subject did not report their age) of a small, remote coastal village on the Caribbean island of Dominica. This village has been visited by anthropologists conducting fieldwork since 1988, and extensive information has been collected on genealogies, education, social networks, and health (e.g., Flinn & England, 1997; Flinn, 1999). Dominica was occupied by British and French colonists, and remained less well-developed than the nearby islands of Guadeloupe, Martinique, and Antigua due to mountainous terrain, limited opportunities for large-scale agriculture, and rocky coasts. At the time of data collection in 2003, the population of the village consisted of about 600 individuals of mixed Carib, European, and African ancestry. In the village, land is communally owned by kin groups, and may be allocated for individual use. Most villagers cultivate vegetables and fruits for subsistence, as well as work cash crops (bay leaves and bananas) for pay. Approximately half the homes have electricity, and water is obtained at pipe stations and nearby creeks. Women begin having children in their late teens or early twenties, typically out of wedlock (Quinlan & Flinn, 2005). While the majority of women have children with only one man, about 20% of families consist of children with multiple fathers. In this community, marriage often occurs only after a woman has had children (for more information on this population, see Quinlan et al., 2003; Quinlan & Flinn, 2005).

**Procedure and materials.** Individuals from the village were approached during the 2003 field season and asked if they wanted to participate in a study on family relationships. They were told that the study would involve a 20-min interview and that they would be given 10 Eastern Caribbean dollars for their participation (~US$3.70). All participants were informed that they could withdraw at any time during the interview for any reason and still receive EC$10. Three people declined the request for an interview.

Subjects were interviewed about their family composition during childhood. Due to the size of most families (mean number of siblings = 7.5, $SD = 3.2$) and the desire to occupy the participant for only a brief period of time, the researcher asked the subject to choose two siblings (an older sibling and a younger sibling when possible) and continued the interview focusing on only these two siblings. For each selected sibling, participants were asked to indicate the gender and age of the sibling, the participant's age when they started and stopped living with their sibling, whether or not they shared the same biological mother and father, and, separately, whether they lived with their biological mother, biological father, and their sibling right after the sibling was born. The variables coresidence duration, MPA, and PPA were measured as in Study 1.

For each of the two selected siblings, participants answered three questions regarding hypothetical situations that involve altruistic behavior toward a sibling. Answers were recorded on a 9-point Likert-type scale with endpoints *not willing at all* and *extremely willing*: (a) "How willing would you be to give this sibling half of your earnings from participating in this study?" (b) "How willing would you be to care for this sibling if he or she got sick?" (c) "If this sibling committed a crime and was sent to jail, how willing would you be to do some or all of the jail time for this sibling?" Participants were asked to point to the position on the scale that corresponded with their feelings. The participants were familiarized with this method of answering questions before the interview began, and no one had a problem using the scale. Factor analyses revealed that all three questions loaded on the same factor (factor loadings > .5), and we averaged responses across items to create a composite variable labeled altruism (range: 1–9, $M = 6.52$, $SD = 1.78$, $N = 133$). For analyses, we $z$ scored responses to each question and then averaged them: (range: −2.77 to 0.89; $M = 0$, $SD = 0.73$).

**Data analysis.** Of the 86 subjects that we recruited in this study, 73 provided complete information (i.e., coresidence duration, MPA, PPA, and altruism) regarding one or more siblings. These 73 subjects generated 133 subject–sibling pairs (13 subjects provided data on one sibling; 60 on two siblings; $M = 1.82$ siblings per subject).

## Study 5: Ghent, Belgium

**Subjects.** Subjects included 150 Ghent University students (76 men, 74 women) between the ages of 18 and 28 ($M = 20.24$, $SD = 1.97$; two subjects did not report their age).

**Procedure and materials.** Subjects were recruited at the Faculty of Law and the Faculty of Psychology of Ghent University to participate in a study about sibling relations. In the first part of the study, subjects completed a questionnaire on a personal computer. In the second part, subjects' physiological responses were registered while they were asked to imagine different kinds of scenarios involving siblings and nonfamily members (the physiological data are reported in De Smet et al., 2014). Subjects were paid €8 for their participation in the entire study (60 min). No subject withdrew from participation during the procedure.

The variables coresidence duration, MPA, PPA, and altruism were measured as in Study 1. Altruism is the average of the $z$ scores created from the questions regarding donating a kidney and providing a favor, also as in Study 1 (range: −1.55 to 1.65; $M = 0$, $SD = 0.80$).

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**Data analysis.** Of the 150 subjects that we recruited in this study, 139 provided complete information (i.e., coresidence duration, MPA, PPA, and altruism) regarding one or more siblings. These 139 subjects generated 249 subject–sibling pairs (84 subjects reported on one sibling; 26 on two siblings; 15 on three siblings; five on four siblings; six on five siblings; three on six siblings; average = 1.79 per subject).

## Study 6: Buenos Aires, Argentina

**Subjects.** Subjects were 225 Universidad de Buenos Aires undergraduate students (113 men; 110 women; two unreported) between the ages of 18 and 35 ($M$ = 21.07, $SD$ = 2.73). Twenty-four subjects reported not having any siblings, thus leaving an effective sample size of 201. Subjects were paid ARS 10 (about US$3 at the time of the study) for their participation.

**Procedure and materials.** Students were invited to participate in a paid survey. The survey was administered in a large classroom. Each subject completed a questionnaire including measures about one sibling, and other measures to be reported elsewhere. If the subject had more than one sibling, they were instructed to choose the one whose first name appeared first in alphabetical order.

***Coresidence duration.*** This was measured as in Study 1.

***Maternal perinatal association (MPA).*** Subjects indicated whether they lived in the same home as their sibling during the sibling's first year of life. The question read "Were you living in the same home as your sibling during the latter's first year of life? (yes)/(no [I hadn't been born, then])/(no [I was living in another home])." MPA was assigned a value of 1 if the subject answered "yes" and a value of 0 otherwise. This differs from the above (and previous) measures of MPA, but nevertheless captures the general categorization of whether a subject physically could have observed MPA or not.

***Altruism.*** The participant's willingness to help the target sibling was measured with the item "If your sibling needed help, to what extent could they count on you?"; scoring was done on a 1 (*not at all*) to 9 (*extremely*) scale, range: 3–9; $M$ = 8.57, $SD$ = 1.04.

**Data analysis.** Subjects were split into two groups: MPA-present individuals versus MPA-absent individuals. The MPA-present group included 107 participants: 106 individuals with a younger sibling and one individual with a twin. The MPA-absent group included 94 participants: 92 individuals with an older sibling and two individuals with a younger sibling for whom MPA was absent. There were thus 201 total participants. Because subjects in this study were asked to report on only one sibling, a data set of 201 subject–sibling pairs resulted.

## Data Analyses

For Studies 1–5, some subjects reported on more than one sibling, potentially violating the assumption of independence. To determine whether our data indeed violated the assumption of independence, for each of these studies we conducted and then compared the results of two different linear mixed models (LMMs) using IBM SPSS Statistics (Version 22), one which included a Level 2 subject variable and one which did not. LMM analyses that included the Level 2 variable improved model fit significantly for all five studies and thus LMM was deemed the appropriate method of analyses for these studies (see Supplementary Information #1).

To answer whether the MPA/coresidence prediction replicates across cultures, in the LMM analyses reported for Studies 1–5 we followed recommendations of Peugh and Enders (2005) and included a random intercept, subject as a random effect, and MPA, coresidence duration, and their interaction as fixed-effect covariates. When reported, culture was included as a fixed-effect factor. We used the maximum likelihood estimation method.

To compute $R^2$ for each LMM, we compared the residual variance of a LMM with all fixed effects (i.e., the main effects of MPA and coresidence duration and their interaction) with the residual variance of a LMM without any fixed effects (i.e., just the intercept model). Specifically, we followed Hox (2010) and computed: $R^2$ = (residual variance of two-level intercept only model minus residual variance of model that also includes the predictors) divided by (residual variance of two-level intercept only model). Study 6 only contained data for one sibling per subject; these data were analyzed using SPSS Univariate General Linear Model.

Given the intercorrelations between our predictor variables (e.g., MPA, PPA, and coresidence duration), we examined the variance inflation factor (VIF) associated with each main effect to assess multicollinearity and found that all VIFs for all analyses were less than 6 and thus did not exceed the commonly accepted maximum threshold of 10 (Stevens, 2002).

# Results

## Replication and Cross-Cultural Tests: Does the Effect of Coresidence Duration on Sibling-Directed Altruism Depend on the Presence of MPA?

Mixed model analyses for the California, Hawaii, Dominica, and Belgium samples (Studies 1–5) revealed significant interactions between MPA and coresidence duration on measures of sibling-directed altruism, California Study 1: $F(1, 234) = 5.25$, $p = .023$; California Study 2: $F(1, 202) = 10.56$, $p = .001$; Hawaii Study 3: $F(1, 221) = 29.01$, $p = 1.83 \times 10^{-7}$; Dominica Study 4: $F(1, 126) = 5.98$, $p = .016$; Belgium Study 5: $F(1, 239) = 21.19$, $p = .000007$. Univariate general linear model analysis of the Argentina sample (Study 6) revealed a marginally significant interaction effect between MPA and coresidence duration: $F(1, 197) = 2.85$, $p = .093$, $\eta_p^2 = .014$ (see Table 1).

We conducted simple correlations to examine the size of the effect of coresidence duration on altruism, for cases with MPA and, separately, for cases without MPA. We ran analyses on data from subsamples from each study. To create subsamples, in each of Studies 1–5, that would not violate the assumption of independence, we randomly sampled approximately 50% of dyads using the SPSS select cases function. For each study, we then conducted a set of LMM analyses (identical to those described in Supplementary Information #1) to determine for this random sample whether the assumption of independence was violated or not, and, thus, whether we could run meaningful simple correlations. As reported in Table 2, in each study, for the randomly selected subsample, the LMM including both fixed and random effects did not significantly differ from the LMM including just fixed effects, that is, it did not include the Level 2 subject variable (at $\alpha = .01$

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Table 1
*Replications and Cross-Cultural Tests of the Effects of MPA and Coresidence Duration on Sibling-Directed Altruism*

| | California, Study 1 | | California, Study 2 | | Hawaii, Study 3 | | Dominica, Study 4 | | Belgium, Study 5 | | Argentina, Study 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fixed effects | *F* | Parameter estimate β (*SE*) | *F* | Parameter estimate β (*SE*) | *F* | Parameter estimate β (*SE*) | *F* | Parameter estimate β (*SE*) | *F* | Parameter estimate β (*SE*) | *F* | β (*SE*) |
| Intercept | 49.19*** | −.70 (.10) | 30.15*** | −.65 (.12) | 75.44*** | −.93 (.11) | 14.33*** | −.41 (.11) | 36.89*** | −.51 (.08) | 540.17*** | 7.73 (.33) |
| MPA × Coresidence | 5.25* | −.04 (.02) | 10.56*** | −.07 (.02) | 29.01*** | −.09 (.02) | 5.98* | −.05 (.02) | 21.19*** | −.08 (.02) | 2.85τ | −.06 (.04) |
| MPA | 10.78*** | .76 (.23) | 19.76*** | 1.41 (.32) | 42.68*** | 1.51 (.23) | 10.31** | .72 (.22) | 34.02*** | 1.29 (.22) | 4.67* | 1.16 (.54) |
| Coresidence duration | 51.12*** | .05 (.01) | 26.37*** | .04 (.01) | 92.67*** | .07 (.01) | 15.75*** | .04 (.01) | 49.43*** | .05 (.01) | 4.87* | .05 (.02) |
| Covariance parameters | | | | | | | | | | | | |
| Residual | | .23 (.03) | | .29 (.04) | | .23 (.03) | | .34 (.06) | | .28 (.03) | | |
| Intercept variance[a] | | .28 (.05) | | .26 (.06) | | .21 (.04) | | .14 (.06) | | .19 (.04) | | |
| $R^{2b}$ | .25 | | .24 | | .27 | | .26 | | .31 | | .04 | |

*Note.* MPA = maternal perinatal association. Tests and estimated parameters of fixed effects from linear mixed model analyses. Dependent measure is sibling-directed altruism, which varied in composition across studies and was the only variable centered.
[a] Intercept variance is of the Level 2 subject variable, which includes family from which sibling pairs were sampled. [b] See additional information regarding data analyses section in Methods.
$^{\tau}p < .10$. $^{*}p < .05$. $^{**}p < .01$. $^{***}p \leq .001$.

Table 2
*Analyses to Determine Whether a Random Sample of Approximately 50% of Dyads Violates Assumption of Independence, for Correlation Analyses*

| | −2 Log likelihood | | | |
|---|---|---|---|---|
| Study | Model without random effect | Model with random effect | $\chi^2(df)$ | *p* |
| 1 | 294.29 | 290.66 | 3.63 (1) | .057 |
| 2 | 349.78 | 347.23 | 2.55 (1) | .110 |
| 3 | 395.88 | 390.69 | 5.19 (1) | .023 |
| 4 | 282.91 | 282.61 | .30 (1) | .584 |
| 5 | 261.78 | 258.72 | 3.06 (1) | .080 |

for all studies; at $\alpha = .05$ for Studies 1, 2, 4, 5), indicating that these subsamples did not violate the assumption of independence. Having established this, we then conducted simple correlations on these subsamples to examine the size of the effect of coresidence duration on altruism, for cases with and without MPA.

The effect sizes of these correlations are displayed in Figure 1, and show that when MPA is absent, coresidence duration significantly predicts altruism (Study 1: $r = .50$, $p = 3.01 \times 10^{-7}$, $N = 92$; Study 2: $r = .47$, $p = .000119$, $N = 61$; Study 3: $r = .63$, $p = 3.83 \times 10^{-10}$, $N = 79$; Study 4: $r = .35$, $p = .016$, $N = 47$; Study 5: $r = .41$, $p = .000108$, $N = 82$). By contrast, when MPA is present, coresidence does not predict altruism: (Study 1: $r = -0.10$, $p = .454$, $N = 55$; Study 2: $r = -0.11$, $p = .515$, $N = 39$; Study 3: $r = -0.28$, $p = .058$, $N = 46$; Study 4: $r = -0.28$, $p = .195$, $N = 23$; Study 5: $r = -0.03$, $p = .851$, $N = 39$). (Notice, in Figure 1, that most of the effects are at least as extreme

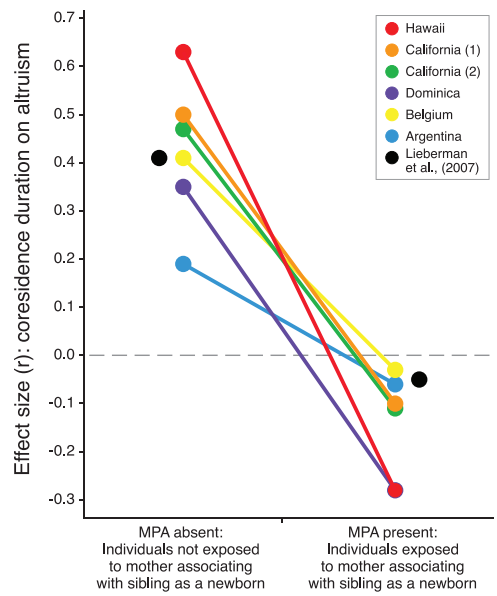


*Figure 1.* Maternal perinatal association (MPA) moderates the relationship between coresidence duration and sibling-directed altruism. The figure displays the effect sizes of coresidence duration on altruism for subjects without access to the MPA cue and for subjects with access to the MPA cue; see Method for description of analyses. See the online article for the color version of this figure.

as those in the original report; Lieberman et al., 2007.) The difference in the effect size of coresidence between MPA-absent and MPA-present cases is significant in each study (Fisher's $Z$ transformation of $r$: Study 1: $Z = 3.72$, $p = .0002$; Study 2: $Z = 2.92$, $p = .0035$; Study 3: $Z = 5.42$, $p < .0001$; Study 4: $Z = 2.42$, $p = .0155$; Study 5: $Z = 2.32$, $p = .0203$).

When inspecting the first order correlations in Argentina (Study 6), we see the same overall pattern observed in our other samples: For MPA-absent subjects, coresidence duration marginally predicted a subject's willingness to help a sibling, $r = .19$, $p = .061$, $N = 94$, whereas for subjects with access to the MPA cue, it did not, $r = -.06$, $p = .56$, $N = 107$. The difference in the effect size of coresidence between MPA-absent and MPA-present cases was marginally significant (Fisher's $z$ transformation of $r$: $Z = 1.76$, $p = .0784$). Replicating past findings, duration of coresidence with a sibling predicted sibling-directed altruism only when MPA was absent.

## What Are the Effects of Sibling Age Difference, Beliefs About Relatedness, and Culture?

Although the findings reported above are consistent with the hypothesis that MPA and coresidence duration interact to predict sibling-directed altruism, there are potential confounds that could provide an alternative explanation for the results. One such confound is absolute sibling age difference (see also below for separate analyses on younger vs. older siblings). In general, the closer in age two siblings are, the longer their coresidence duration. Another potential confound is explicit knowledge regarding relatedness as captured by Hamilton's coefficient of relatedness, r. To examine the effects of these variables, increase statistical power, and probe more carefully for a possible effect of culture, we combined data from the studies that used the same independent *and* dependent measures, leading to two supersets of data: Studies 1 and 5 (1/5) and Studies 2 and 3 (2/3).

In both data supersets, coresidence duration significantly correlated with absolute sibling age difference (Studies 1/5: $r = -.53$, $p < .001$, $N = 542$; Studies 2/3: $r = -.59$, $p < .001$, $N = 479$) and with degree of relatedness (Studies 1/5: $r = .67$, $p < .001$, $N = 543$; Studies 2/3: $r = .71$, $p < .001$, $N = 478$). Likewise, MPA also correlated with absolute sibling age difference (Studies 1/5: $r = -.15$, $p < .001$, $N = 542$; Studies 2/3: $r = -.18$, $p < .001$, $N = 479$) and with degree of relatedness (Studies 1/5: $r = .32$, $p < .001$, $N = 543$; Studies 2/3: $r = .33$, $p < .001$, $N = 478$).

However, when we included sibling age difference, degree of relatedness, and culture in LMM analyses, we observed the same pattern of results as the one displayed in Table 1 (see Table 3). The interaction between MPA and coresidence continued to significantly predict altruism, Studies 1/5: $F(1, 480) = 17.49$, $p = .000034$, $N = 542$; Studies 2/3: $F(1, 444) = 19.40$, $p = .000013$. Degree of relatedness independently predicted

Table 3
*Tests of Possible Confounds on the Effects of MPA and Coresidence Duration on Sibling-Directed Altruism*

| | Studies 1/5 ($N$ = 542) | | Studies 2/3 ($N$ = 478) | |
|---|---|---|---|---|
| Fixed effects | $F$ | Parameter Estimate β ($SE$) | $F$ | Parameter Estimate β ($SE$) |
| Intercept | 69.69*** | −.80 (.10) | 72.71*** | −1.11 (.13) |
| MPA × Coresidence | 17.49*** | −.05 (.01) | 19.40*** | −.06 (.01) |
| MPA | 27.49*** | .84 (.16) | 32.35*** | 1.17 (.20) |
| Coresidence duration | 22.10*** | .03 (.01) | 29.17*** | .05 (.01) |
| Culture[a] | .44 | −.04 (.06) | 1.11 | .09 (.08) |
| Sibling age difference | .55 | .01 (.01) | 2.44 | .01 (.01) |
| Degree of relatedness (r) | 22.25*** | 1.00 (.21) | 5.88* | .76 (.31) |
| Covariance parameters | | | | |
| Residual | | .24 (.02) | | .25 (.02) |
| Intercept variance[b] | | .20 (.03) | | .25 (.04) |
| $R^{2c}$ | .33 | | .30 | |
| | Mean ($SD$)[d] | Range | Mean ($SD$)[e] | Range |
| Coresidence duration | 10.66 (6.56) | 0–18 | 11.51 (6.15) | 0–18 |
| MPA | .35 (.48) | 0–1 | .39 (.49) | 0–1 |
| Sibling age difference | 5.51 (4.14) | 0–22 | 6.04 (5.13) | 0–39 |
| Degree of relatedness | .38 (.18) | 0–.5 | .42 (.15) | 0–.5 |

*Note*. MPA = maternal perinatal association. Tests and estimated parameters of fixed effects from linear mixed model analyses. Dependent measure is sibling-directed altruism, which was the same in Studies 1 and 5 and the same in Studies 2 and 3 allowing for the combination of data sets; see test for more information. Sibling-directed altruism was the only centered variable.
[a] Study 1/5: estimate for Belgian location provided; University of California Santa Barbara (UCSB) estimate set to zero; Study 2/3 estimate for UCSB location provided; Hawaii estimate set to zero. [b] Intercept variance is of the Level 2 subject variable, which includes family from which sibling pairs were sampled. [c] See additional information regarding data analyses section in Method. [d] In Studies 1/5, total $N = 543$ for all variables, except sibling age, where $N = 542$. [e] Studies 2/3 total $N = 479$ for all variables, except $r$, where $N = 478$.
* $p < .05$. *** $p \leq .001$.

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altruism in the predicted direction across both supersets of data, Studies 1/5: $F(1, 512) = 22.25$, $p = .000003$; Studies 2/3: $F(1, 456) = 5.88$, $p = .016$; however, culture and sibling age difference did not.

## When MPA Is Present, What Is the Level of Altruism Reported?

Because MPA would have had high sensitivity and specificity as a cue to sibship in human ancestral environments, it should regularly produce high estimates of sibship. If this is so, then when MPA is present, levels of sibling-directed altruism should be elevated across *all* durations of coresidence, as previously reported (Lieberman et al., 2007). This is indeed the case. For individuals lacking the MPA cue, altruism increases with the number of years the subject has coresided with their sibling, but for individuals with the MPA cue altruism is elevated across all periods of coresidence (see Figure 2).

In sum, access to the MPA cue sets sibling-directed altruism at high levels, irrespective of coresidence duration. When MPA is absent, however, sibling-directed altruism increases in lockstep with coresidence duration. Thus, MPA moderates the effect of

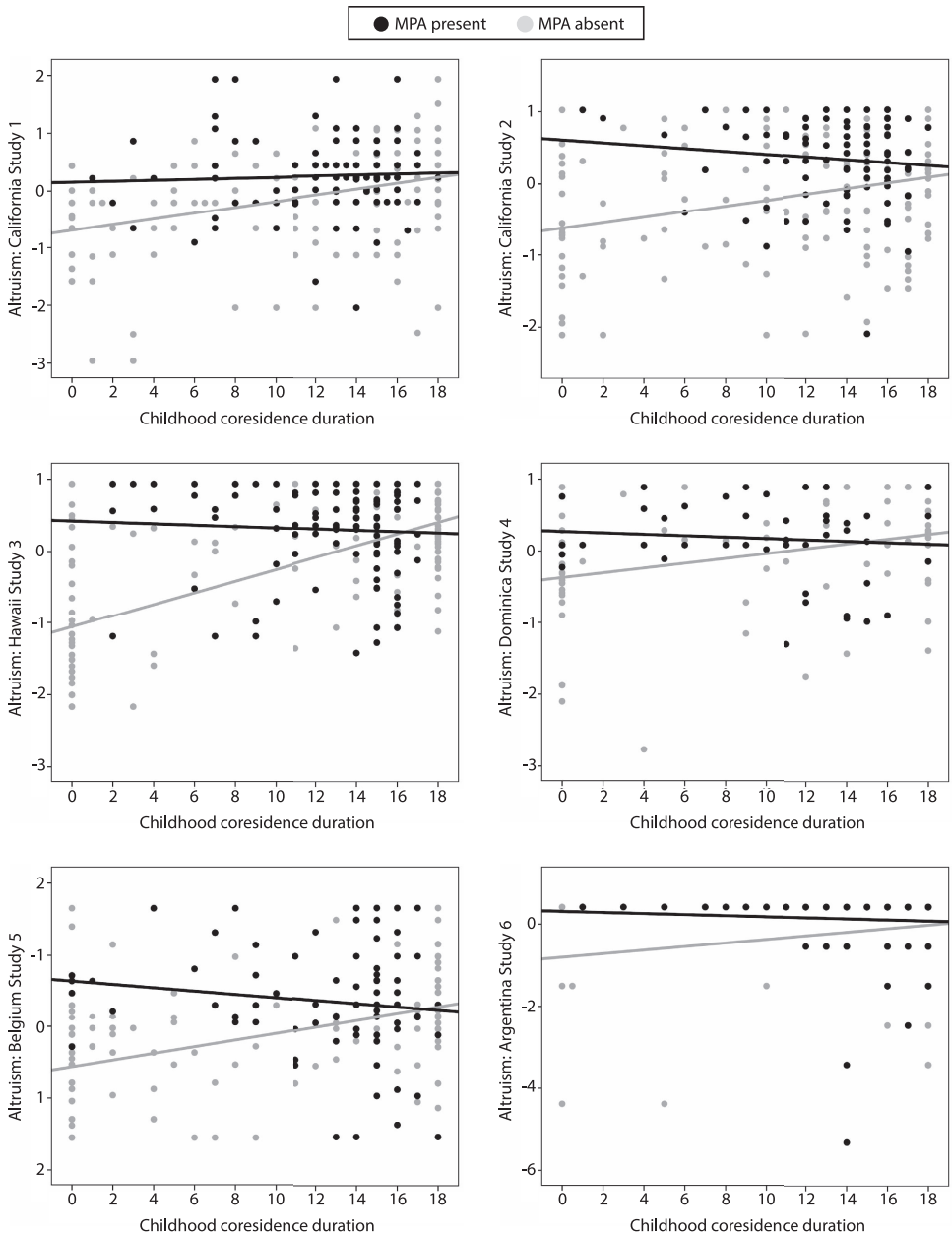


*Figure 2.* Scatterplots of how coresidence duration predicts altruism when maternal perinatal association (MPA) is present versus when MPA is absent, across the six studies.

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coresidence on sibling-directed altruism, and, by implication, the effect of coresidence on the estimation of sibship. This pattern of results is highly replicable. Further, this pattern is not an idiosyncrasy of American culture: It obtains across cultures, including a nonindustrial culture. These are the results one would observe if the MPA moderation of coresidence were indeed part of a species-wide psychological mechanism designed to reckon sibship from ecologically valid cues.

## Does PPA Predict Sibling-Directed Altruism?

In the above analyses, we replicated the effects of MPA and coresidence duration on sibling-directed altruism and showed this effect to be robust after controlling for culture, sibling age difference, and explicit knowledge regarding relatedness. But are the effects of MPA actually driven by maternal associations rather than paternal associations, that is PPA? Across studies, MPA and PPA are highly correlated ($r$s $>$.6), and thus PPA might be the important variable, not MPA. To examine the role of PPA as a potential cue to siblingship, we conducted the same analyses as those reported in Table 1, but this time controlling for PPA. Our results remain unchanged and the effects of PPA were not significant (see Table 4).

The analyses examining the effect of PPA, reported in Table 4, include both older and younger siblings. But only subjects with younger siblings could, in principle, have access to the MPA and PPA cues. Might individuals with access to MPA also utilize information regarding PPA to discern siblings from nonsiblings, and possibly (younger) full siblings from (younger) half siblings? To test the effects of PPA, we restricted our analyses to subject-and-younger-sib pairs. To enhance power and to test for culture effects, we conducted analyses on our combined data sets (Studies 1/5 and Studies 2/3).

We conducted separate LMM analyses for Studies 1/5 and Studies 2/3 on subject-younger sib pairs, entering MPA, PPA, and coresidence duration as covariates, culture as a factor, and altruism as the dependent measure (both data sets violated the assumption of independence and so LMM was again the appropriate statistical method to use). As reported in Table 5, the only significant predictor of altruism was MPA, Studies 1/5: $F(1, 237) = 16.89$, $p = .000055$, $N = 250$; Studies 2/3: $F(1, 181) = 24.77$, $p = .000001$, $N = 228$. PPA, coresidence duration, culture, and the interaction between MPA and PPA did not predict altruism.

The data reported in Table 5 include a mix of biological, half, step, and adopted younger siblings. LMM analyses focusing only on maternal and paternal half siblings yielded the same results: Both in studies 1/5 and in studies 2/3, when MPA and PPA were entered into LMM analyses, MPA had an effect on altruism but PPA did not, MPA: Studies 1/5: $F(1, 30) = 5.21$, $p = .03$, $N = 53$; Studies 2/3: $F(1, 19) = 48.38$, $p = .000001$, $N = 33$; PPA: Studies 1/5: $F(1, 27) = 0.09$, $p = .764$, $N = 53$; Studies 2/3: $F(1, 17) = .23$, $p = .636$, $N = 33$.

We further examined the effects of MPA and PPA on altruism by comparing younger siblings for whom: MPA and PPA were both present, only MPA was present, only PPA was present, and neither was present. Figure 3 displays sample compositions. We conducted multiple independent samples $t$ tests on all subject-and-younger-sib pairs within our data supersets (Studies 1/5 and Studies 2/3). First we assessed whether, for individuals with MPA, the presence of PPA increased levels of altruism. For all subject and younger sibling pairs, we compared altruism scores between the set of subjects with MPA and PPA (MPA+/PPA+: Study 1/5: $M = 0.17$, $SD = 0.69$, $N = 156$; Study 2/3: $M = .18$, $SD = .62$, $N = 166$) and the set of subjects with MPA but no PPA (MPA+/PPA–: Study 1/5: $M = 0.28$, $SD = 0.53$, $N = 31$; Study 2/3: $M = -0.04$, $SD = .94$, $N = 22$). There was no difference in reported altruism between these two groups, Studies 1/5: $t(185) = .98$, $p = .33$; Studies 2/3: Levene's $F = 6.64$, $p = .011$, $t(24) = 1.09$, $p = .289$. Thus, it appears that adding PPA to MPA does not contribute to sibling-directed altruism (or, by implication, to the kinship estimate).

By contrast, for individuals with PPA, the presence of MPA increased levels of altruism. There was a marginally greater level of altruism in MPA+/PPA+ subjects than in MPA–/PPA+ subjects, Study 1/5: MPA–/PPA+: $M = -0.25$, $SD = 0.67$, $N = 9$, $t(163) = 1.74$, $p = .084$; Study 2/3: MPA-/PPA+: $M = -0.24$, $SD = 0.21$, $N = 3$ (too few subjects to conduct meaningful

Table 4
*Replications and Cross-Cultural Tests: Tests and Estimated Parameters of Fixed Effects From Linear Mixed Model Analyses*

| | California, Study 1 | | California, Study 2 | | Hawaii, Study 3 | | Dominica, Study 4 | | Belgium, Study 5 | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fixed effects | $F$ | Parameter estimate β ($SE$) | $F$ | Parameter estimate β ($SE$) | $F$ | Parameter estimate β ($SE$) | $F$ | Parameter estimate β ($SE$) | $F$ | Parameter estimate β ($SE$) |
| Intercept | 48.83*** | −.70 (.10) | 32.25*** | −.68 (12) | 75.94*** | −.93 (.11) | 14.38*** | −.41 (.11) | 38.25*** | −.52 (.08) |
| MPA × Coresidence | 5.09* | −.04 (.02) | 12.80*** | −.08 (.02) | 26.34*** | −.10 (.02) | 5.89* | −.05 (.02) | 22.68*** | −.08 (.02) |
| MPA | 10.64*** | .75 (.23) | 12.35*** | 1.20 (.34) | 37.69*** | 1.48 (.24) | 5.69* | .69 (.29) | 23.66*** | 1.17 (.24) |
| Coresidence duration | 51.02*** | .05 (.01) | 28.42*** | .04 (.01) | 93.09*** | .07 (.01) | 15.82*** | .04 (.01) | 50.95*** | .05 (.01) |
| PPA | .12 | .05 (.14) | 2.95 | .37 (.21) | .23 | .09 (.19) | .02 | .04 (.27) | 1.34 | .21 (.18) |
| Covariance parameters | | | | | | | | | | |
| Residual | | .23 (.03) | | .28 (.03) | | .23 (.03) | | .33 (.06) | | .28 (.03) |
| Intercept variance[a] | | .28 (.05) | | .26 (.06) | | .20 (.04) | | .14 (.07) | | .19 (.04) |
| $R^{2b}$ | .25 | | .26 | | .27 | | .26 | | .32 | |

*Note*. MPA = maternal perinatal association; PPA = paternal perinatal association. Analyses are of all subject–sibling pairs. Dependent measure is sibling-directed altruism, which varied in composition across studies and was the only variable centered.
[a] Intercept variance is of the Level 2 subject variable, which includes family from which sibling pairs were sampled. [b] See additional information regarding data analyses section in Method.
* $p < .05$. *** $p \leq .001$.

Table 5
*Cues Used to Detect Younger Siblings*

| Fixed effects | Study 1/5 ($N$ = 250 younger siblings) $F$ | Study 1/5 Parameter estimate β (*SE*) | Study 2/3 ($N$ = 228 younger siblings) $F$ | Study 2/3 Parameter estimate β (*SE*) |
|---|---|---|---|---|
| Intercept | 20.12*** | −.43 (.11) | 46.84*** | −.89 (.14) |
| MPA | 16.89*** | .66 (.16) | 24.77*** | .95 (.19) |
| PPA | 2.13 | .35 (.24) | 3.68 | .71 (.37) |
| MPA × PPA | 1.69 | −.37 (.28) | 3.33 | −.74 (.40) |
| Coresidence duration | .06 | .00 (.01) | .39 | .01 (.01) |
| Culture[a] | .14 | −.03 (.09) | .65 | .09 (.12) |
| Covariance parameters | | | | |
| Residual | | .26 (.03) | | .22 (.03) |
| Intercept variance[b] | | .19 (.04) | | .31 (.06) |
| $R^2$ | .07 | | .37 | |

*Note*. MPA = maternal perinatal association; PPA = paternal perinatal association. Tests and estimated parameters of fixed effects from linear mixed model analyses. Study 1/5: combined data sets of Studies 1 and 5; Study 2/3: combined data sets of Studies 2 and 3. Dependent measure is sibling-directed altruism, which varied in composition across studies and was the only variable centered.
[a] Study 1/5: estimate for Belgian location provided; University of California Santa Barbara (UCSB) estimate set to zero; Study 2/3 estimate for UCSB location provided; Hawaii estimate set to zero. [b] Intercept variance is of the Level 2 subject variable, which includes family from which sibling pairs were sampled.
*** $p \leq .001$.

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analysis). In light of the sample size, we cannot be conclusive, but these data suggest that whereas adding PPA to MPA has no effect on altruism, adding MPA to PPA does have an effect.

For the Study 1/5 combined sample we also asked whether PPA had any effect on altruism when MPA was absent (there were too few subjects in the Study 2/3 data set who were MPA–/PPA+; $N$ = 3). It did not. Subjects with no MPA but with PPA reported statistically similar levels of altruism as subjects with no MPA and no PPA ($M$ = −.57, $SD$ = .74, $N$ = 54), $t(61)$ = 1.20, $p$ = .236.

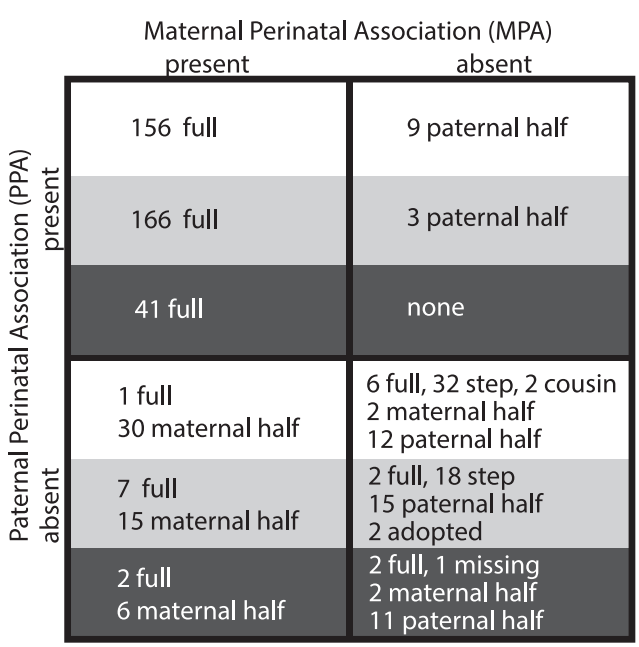


*Figure 3.* Breakdown of subject and younger sibling pairs by MPA and PPA status from combined data set for Studies 1/5 (white boxes), combined data set for Studies 2/3 (light gray boxes), and Study 4 (dark gray boxes).

We note that despite our efforts to enhance power by merging samples with like measures, there were few PPA-absent and MPA-absent subjects. Post hoc analyses suggested that the PPA + versus PPA- test among MPA + subjects was sufficiently powered to detect an effect size of .5 or greater, but that the remaining tests were likely underpowered (Faul, Erdfelder, Lang, & Buchner, 2007). Prior work suggests that the effect size of MPA on sibling-directed altruism is around .4 (Lieberman et al., 2007). The PPA effect on the reckoning of sibship, if any, is probably weaker than the MPA effect—the fact that paternity is uncertain suggests that the mind would have evolved to weight PPA less strongly than MPA. Everything else is not equal, however: Fathers down-regulate their investment in a child when they suspect nonpaternity (Anderson, Kaplan, & Lancaster, 2007; Daly & Wilson, 1980), and so any positive paternal investment (PPA) would likely have occurred conditional on determining offspring paternity. Still, paternal judiciousness is unlikely to completely avoid investment in unrelated infants (Anderson, 2006). The upper bound of a PPA effect would thus be about .4. Our independent samples tests are likely underpowered to detect a PPA effect, though our LMM analyses reported in the main text were not. Nevertheless, higher-powered replications as well as matched unrelated controls may yet reveal a role for PPA. In sum, whereas adding PPA to MPA does not contribute to sibling-directed altruism (or by implication, to the kinship estimate), adding MPA to PPA does.

## For Younger Siblings, Are Beliefs Regarding Relatedness a Confounding Factor?

The analyses above are based on the availability of ecological cues to sibship and suggest that altruism is regulated by MPA, not PPA. However, there is a strong relationship between the presence

of MPA and PPA on one hand and the propositionally known sibling category on the other hand. As shown in Figure 3, for subjects and their younger siblings, having MPA and PPA perfectly predicts being a full sibling. However, the opposite is not true: Being a full sibling *does not* perfectly predict having both MPA and PPA. Thus, the overlap between explicit knowledge and cue presence is not perfect. Yet, this raises the question of whether beliefs regarding relatedness confound the relationship between MPA and altruism reported in Table 5. To examine this possibility, we reran the analyses presented in Table 5, but this time including degree of relatedness. We found the same pattern. MPA significantly predicted altruism, Studies1/5: $F(1, 222) = 10.58$, $p = .001$; Studies 2/3: $F(1, 206) = 9.69$, $p = .002$. However, we also found that degree of relatedness independently predicted altruism for subjects and younger siblings, significantly so in Studies1/5: $F(1, 194) = 4.68$, $p = .032$, and marginally in Studies 2/3: $F(1, 213) = 3.08$, $p = .081$. We examined the VIFs for all the main effects and found that, across both supersets, they were all lower than 6 (range: 1.02–5.03), and thus do not exceed the commonly accepted maximum of 10 (Stevens, 2002). Thus, although MPA is a kinship cue predicting relatedness of younger siblings, it does not appear to be the only factor (see Discussion for more).

## Do Full Siblings Elicit More Altruism Than Half Siblings, Regardless of How the Discrimination Might Be Done?

A separate, but related question is whether there are differences in altruism toward different categories of siblings (i.e., full, maternal half, paternal half, and step sibs). To answer the question of how altruism varies by sibling type, we focused on our two combined data sets (Studies 1/5 and Studies 2/3), and compared the levels of altruism between full sibs, maternal half sibs, paternal half sibs, and step sibs (descriptive statistics in Tables 6 & 7).

To compare across data sets, we plotted the *z*-scored altruism means from both combined data sets (see Figure 4). Inspection of subject and younger sibling pairs (Figure 4, panel a) reveals that for both combined data sets, younger full siblings and younger maternal half siblings did not differ in the altruism they elicited (*p*s $>.30$). On the other hand, both younger full siblings and younger maternal half siblings elicited more altruism than younger paternal half siblings, Studies 1/5: full versus paternal half: $t(182) = 3.55$, $p < .001$; maternal half versus paternal half: $t(51) = 4.06$, $p < .001$; Studies 2/3: full versus paternal half: (Levene's test for equality of variances was significant, $F = 4.15$, $p = .043$; when Levene's test is significant, we report *t*-values with equal variances not assumed), $t(19) = 4.14$, $p = .001$; maternal half versus paternal half: $t(31) = 2.49$, $p = .018$. Likewise, younger full siblings and younger maternal half siblings also elicited more altruism than younger step siblings, Studies 1/5: full versus step: $t(193) = 5.65$, $p < .001$; maternal half versus step: (Levene's test for equality of variances was significant), $F = 5.75$, $p = .019$, $t(54) = 5.40$, $p < .001$; Studies 2/3: full versus step: Levene's: $F = 13.02$, $p < .001$; $t(18) = 4.39$, $p < .001$; maternal half versus step: $t(31) = 2.87$, $p = .007$. But there was no difference in altruism reported toward a younger paternal half sibling and a younger step sibling, *p*s $>.35$.

This pattern of altruism toward younger siblings can be accounted for—at least in part—by differences in MPA presence. Participants with younger full siblings and maternal half siblings are mostly or completely MPA+. In Studies 1/5, 96% (157 of 163) of participants with younger full siblings were MPA+ and 94% (30 of 32) of participants with younger maternal half siblings were MPA+. Similarly, in Studies 2/3, 99% (173 of 175) of participants with younger full siblings were MPA+ and 100% (15 of 15) of participants with younger maternal half siblings were MPA+. By contrast, 0% of participants with younger paternal half sibs and younger step sibs were MPA+. Thus, for participants with younger siblings, a critical factor in assessing sibship appears to be MPA.

Table 6
*Sibling-Directed Altruism Variable (Centered) for Each Type of Older and Younger Sibling in the Combined Data Sets*

| | Subject–younger-sibling pairs | Subject–older-sibling pairs |
|---|---|---|
| | *M* (*SD*), *N* | *M* (*SD*), *N* |
| Studies 1/5 | | |
| Full | .25 (.72), 163 | .15 (.69), 195 |
| Maternal half | .39 (.55), 32 | −.21 (.61), 23 |
| Paternal half | −.35 (.77), 21 | −.52 (.65), 33 |
| Step | −.56 (.82), 32 | −.84 (.61), 41 |
| Studies 2/3 | | |
| Full | .33 (.59), 175 | .10 (.69), 182 |
| Maternal half | .20 (.76), 15 | −.22 (.77), 15 |
| Paternal half | −.49 (.82), 18 | −1.15 (.98), 36 |
| Step | −.67 (.96), 18 | −.92 (1.00), 16 |

*Note*. Study 1/5: combined data sets of Studies 1 and 5; Study 2/3: combined data sets of Studies 2 and 3.

A separate question is whether other factors might also influence patterns of altruism directed toward younger siblings. For instance, past research has found that sibling age affects altruism (e.g., Burnstein et al., 1994). Younger siblings might have more need for aid as compared to older siblings. We sought to examine for subject and younger sibling pairs whether MPA continues to predict sibling directed altruism even after controlling for the younger sibling's age. It does. For both supersets of data, LMM analyses including MPA, sibling age difference, and degree of genetic relatedness as covariates revealed that MPA continues to predict sibling-directed altruism, even controlling for how much younger a sibling is relative to the subject and for explicit beliefs regarding relatedness, Studies 1/5: $F(1, 203) = 11.49$, $p = .001$; Studies 2/3: $F(1, 205) = 11.62$, $p = .001$. Sibling age difference independently predicts altruism as well, Studies 1/5: $F(1, 219) = 9.68$, $p = .002$; Studies 2/3: $F(1, 165) = 13.74$, $p = .000286$. In general, the younger a younger sibling is relative to the participant, the greater the participant's altruism toward that sibling. Last, explicit beliefs regarding relatedness significantly predicted altruism, but only in one database Studies 1/5: $F(1, 210) = 3.25$, $p = .073$; Studies 2/3: $F(1, 213) = 4.02$, $p = .046$.

Examining subject and older sibling pairs (Figure 4, panel b), we found that older full siblings elicited more altruism than (a) older maternal half siblings, Studies 1/5: $t(216) = 2.40$, $p = .017$; marginally so in studies 2/3: $t(195) = 1.74$, $p = .083$; (b) older paternal half siblings, Studies 1/5: $t(226) = 5.19$, $p < .001$; Studies 2/3: Levene's: $F = 8.81$, $p = .003$, $t(42) = 7.31$, $p < .001$; and (c) older step siblings, Studies 1/5: $t(234) = 8.48$, $p < .001$; studies 2/3: Levene's: $F = 8.79$, $p = .003$, $t(16) = 4.01$, $p = .001$. In turn,

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Table 7
*Breakdown by Sibling Type and Coresidence Durations for Younger and Older Siblings*

| Study | Full bio | Half (maternal) | Half (paternal) | Step | Adopted, A Cousin, C | Coresidence range | Coresidence *M* (*SD*) |
|---|---|---|---|---|---|---|---|
| | | | Subject–younger-sibling pairs | | | | |
| 1 | 83 | 22 | 14 | 7 | 2 C | 0–17 | 10.85 (5.30) |
| 2[a] | 86 | 3 | 8 | 9 | 0 | 0–17 | 11.61 (5.27) |
| 3[b] | 89 | 12 | 10 | 9 | 2 A | 0–17 | 10.83 (5.60) |
| 4[c] | 45 | 8 | 12 | 0 | 0 | 0–18 | 7.68 (6.23) |
| 5[d] | 80 | 10 | 7 | 25 | 0 | 0–18 | 9.23 (6.59) |
| 6[e] | 102 | 6 | | | | 0–18 | 14.33 (4.04) |
| | | | Subject–older-sibling pairs | | | | |
| 1 | 111 | 15 | 17 | 22 | 1 C | 0–18 | 11.85 (6.13) |
| 2[a] | 93 | 7 | 20 | 7 | 0 | 0–18 | 11.65 (6.09) |
| 3[b] | 89 | 8 | 16 | 9 | 0 | 0–18 | 12.02 (7.30) |
| 4[c] | 40 | 13 | 14 | 0 | 0 | 0–18 | 9.46 (7.59) |
| 5[d] | 84 | 8 | 16 | 19 | 0 | 0–18 | 10.28 (7.88) |
| 6[e] | 84 | 6 | | 2 | | 0–18 | 15.79 (4.75) |

[a] Study 2, University of California Santa Barbara: Table is missing one older sibling for whom there was no *r* provided. [b] Study 3, Hawaii: One person did not indicate *r* toward sibling; total in table is 244. [c] Study 4, Dominica: One subject indicated that their sibling was half, but did not indicate whether he/she was maternal or paternal half; this subject has been omitted; this is why total sib pairs = 132; also there is one twin pair, included in younger bio sibling group. [d] Study 5, Belgium: There are six twin pairs included in younger sibs bio group. [e] Study 6, Argentina: One person with a younger sibling did not indicate *r* toward sibling; table total = 200; also there is one twin pair, included in younger bio sibling group; half siblings were not specified as either maternal or paternal.

older maternal half siblings elicited more altruism than both older paternal half siblings, marginally in Studies 1/5, $t(54) = 1.80$, $p = .078$, significantly in Studies 2/3, $t(49) = 3.25$, $p = .002$, and older step siblings, Studies 1/5: $t(62) = 3.94$, $p < .001$; Studies 2/3: $t(29) = 2.16$, $p = .039$. With respect to older paternal half siblings and older step siblings, in Studies 1/5 we found a significant difference, with subjects reporting greater altruism toward older paternal half siblings, $t(72) = 2.18$, $p = .032$. However, in Studies 2/3, there was no difference between older paternal half sibs and older step sibs, $p = .456$.

The difference in altruism toward the different types of older siblings appears to be due, at least in part, to differences in durations of coresidence. In Studies 1/5, older full siblings ($M = 14.41$, $SD = 4.99$, $N = 195$) coresided for longer times than older maternal half siblings ($M = 10.17$, $SD = 5.57$, $N = 23$), $t(216) = 3.80$, $p < .001$, older paternal half siblings ($M = 3.55$, $SD = 5.09$, $N = 33$), $t(226) = 11.53$, $p < .001$, and older step siblings ($M = 2.34$, $SD = 4.04$, $N = 41$), $t(234) = 14.51$, $p < .001$. The same held for Studies 2/3: Older full siblings ($M = 14.93$, $SD = 4.06$, $N = 182$) coresided for longer times than (a) older maternal half siblings ($M = 7.60$, $SD = 6.38$, $N = 15$, Levene's $F = 12.12$, $p = .001$), $t(15) = 4.38$, $p = .001$, (b) older paternal half siblings ($M = 2.08$, $SD = 3.83$, $N = 36$), $t(216) = 17.53$, $p < .001$, and (c) older step siblings ($M = 2.50$, $SD = 4.00$, $N = 16$), $t(196) = 11.77$, $p < .001$.

In both combined data sets, there was a significant difference between coresidence duration times for older maternal half siblings and coresidence duration times for both older paternal half siblings, Studies 1/5: $t(54) = 4.61$, $p < .001$; Studies 2/3: Levene's $F = 11.66$, $p = .001$, $t(18) = 3.12$, $p = .006$, and older step siblings, Studies 1/5: Levene's: $F = 7.08$, $p = .01$, $t(35) = 5.93$, $p < .001$; Studies 2/3: Levene's: $F = 7.00$, $p = .013$, $t(23) = 2.65$, $p = .014$. However, despite the difference in altruism between older paternal half siblings and older step siblings (at least in Studies 1/5), there was no difference in coresidence lengths between older paternal half siblings and older step siblings for either study, Studies 1/5: $t(72) = 1.14$, $p = .26$; Studies 2/3: $t(50) = .36$, $p = .722$. The increased altruism directed toward older paternal half siblings over older step siblings in Studies 1/5 thus suggests other kinship cues, in particular cues to shared paternity, might be involved.

We conducted a final set of LMM analyses to examine the effect of coresidence duration on altruism for subject and older siblings controlling for sibling age difference and explicit beliefs regarding relatedness. We found that in both supersets of data, coresidence duration with an older sibling continued to predict altruism toward that older sibling, Studies 1/5: $F(1, 291) = 11.27$, $p = .001$; Studies 2/3: $F(1, 243) = 13.24$, $p = .000335$. Explicit beliefs regarding relatedness also predicted altruism, Studies 1/5: $F(1, 289) = 18.97$, $p = .000018$; Studies 2/3: $F(1, 234) = 4.95$, $p = .027$. However, age difference did not, Studies 1/5: $p = .066$; Studies 2/3: $p = .955$, suggesting that the effect of age difference found above for subject-and-younger sibling pairs might be explained by the greater need of younger siblings in our samples.

## Discussion

Here, we produced multiple replications of the prior finding that maternal perinatal association (MPA) moderates the effect of coresidence duration on sibling-directed altruism. In all six samples there was a positive relationship between coresidence duration and altruistic dispositions for individuals lacking the MPA cue, and in five of these samples the effect was statistically significant. This is consistent with the proposal that in the absence of MPA, internally

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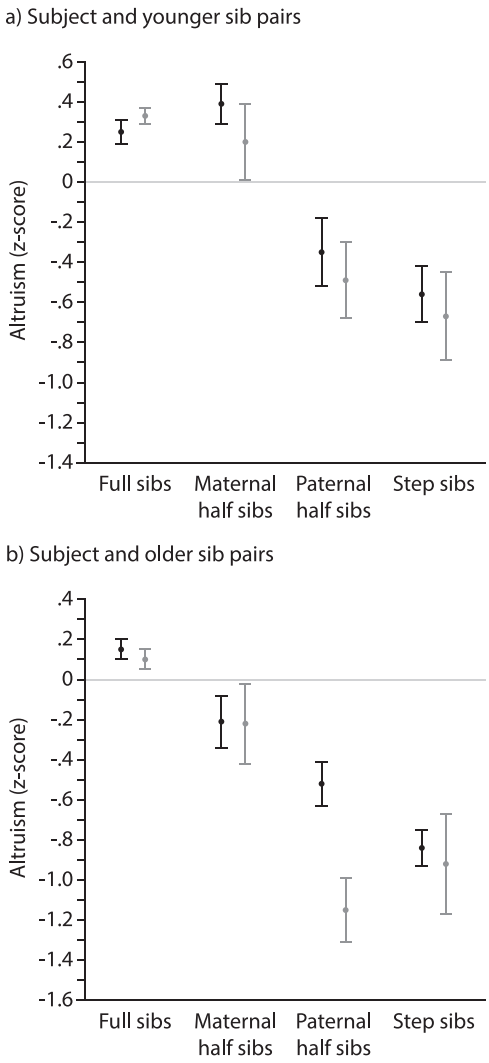


*Figure 4.* Altruism scores for full siblings (sibs), half siblings, and step siblings ($M \pm SE$). Black bars represent data from Studies 1 and 5 combined data set; gray bars represent data from Studies 2 and 3 combined data set.

computed sibship estimates increase with the duration of coresidency. By contrast, for individuals with MPA, none of the six samples showed a relationship between coresidence duration and altruism. Instead, reported altruism was elevated across all durations of coresidence, consistent with the hypothesis that, once perceived, the MPA cue leads to a high and fixed sibship estimate. The noncompensatory cue-integration model of sibship reckoning, whereby coresidence informs the sibship estimate but not when MPA is present, appears to be valid across multiple cultures, including a society of nonindustrial horticulturists. In all, this pattern of data is consistent with the hypotheses that (a) sibship reckoning may be the output of an evolved, species-wide neurocognitive mechanism designed for computing sibship from ecological information, and (b) sibling-directed altruism may be lawfully governed in proportion to the sibship estimate. We cannot, of course, rule out the possibility that cultural elements inherited from a common cultural ancestor (e.g., the use of English as a first language among Dominican and American participants, and the British influence in Dominica and the United States) or convergent evolution in transmitted culture, and not specialized neural circuitry evolved by natural selection, led to these cross-cultural consistencies (see, e.g., Mesoudi, Whiten, & Laland, 2006). Studies with a larger array of more distantly related cultures could address these issues (Norenzayan & Heine, 2005).

We found no evidence that PPA regulates sibling-directed altruism or, by implication, serves to detect siblings. This should not be taken to imply that males do not associate with their newborns or even that humans cannot reckon paternal and maternal sibship independently. Rather, we found no evidence that the observation of males (fathers) associating with newborns is associated with increased sibling-directed altruism. From a selectionist perspective, it would be advantageous to distinguish maternal half siblings from full siblings, especially in a species like ours in which the children of a failed mateship likely stayed with their mother—as they still tend to do today. Indeed, our data suggest that, at least regarding older siblings, humans do distinguish between the two: subjects reported significantly more altruism toward an older full biological sibling than an older maternal half sibling, a pattern that maps onto differences in durations of coresidency.

It would also be advantageous to tell paternal half siblings from nonsiblings. For younger siblings, however, our data suggest no such discrimination—at least in terms of altruism as was measured here. It is possible that measures of sexual aversions, a second domain of behavior governed by kinship cues, might reveal differences in attitudes toward paternal half siblings versus step and nonsiblings. But here, subjects did not distinguish between younger paternal half siblings and younger step siblings. As for older siblings, our data are mixed. One set of studies found no difference between paternal half siblings and step siblings, while another set did.

One reason we might not have found a robust difference between paternal and step siblings is because we focused on association-based kinship cues. The mind might rely on other types of cues—for instance, those based on phenotype matching—to make these discriminations. Recent research has explored the possibility that humans use phenotype matching as a mechanism for detecting kin (DeBruine, 2005; Marcinkowska, Moore, & Rantala, 2013; Park & Schaller, 2005; Park et al., 2008). Phenotype matching systems can be self or other-referencing. As discussed in the Introduction, other-referencing phenotype matching requires a prior mechanism for identifying kin, such as the association-based cues discussed herein. However, humans might use self-referential matching systems to identify possible relatives, one candidate being the olfactory signatures derived from the catabolism of proteins associated with the MHC (Singer, Beauchamp, & Yamazaki, 1997). There are multiple ongoing debates about the MHC: whether the MHC influences kinship relevant behavior (e.g., mate choice) in humans (Kostyu, Dawson, Elias, & Ober, 1993; Ober et al., 1997; Wedekind & Füri, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995; but see Hedrick & Black, 1997; Norlander, Hammarström, Lindblom, & Edvard Smith, 1983); whether MHC-dependent mate choice evolved to function as an inbreeding avoidance system and/or as a system for seeking genetic compatibility, good genes, or both (see Grob, Knapp, Martin, & Anzenberger, 1998); and whether the effects of MHC on mate

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choice are self- or other-referential (e.g., Jacob, McClintock, Zelano, & Ober, 2002; Penn & Potts, 1998). In any case, MHC-based discrimination appears to be neither necessary nor sufficient to detect kin: genetically unrelated (and therefore less phenotypically similar) individuals reared together in Israeli Kibbutz peer groups still develop sexual aversions toward one another (Lieberman & Lobel, 2012), but genetically related siblings reared apart can find one another very sexually attractive when reunited in adulthood (Childs, 1998). Additional work is needed on the role of phenotype matching systems in human kin detection and how they stack up against the effects of association-based cues, including childhood coresidence duration and MPA.

This work extends past work on sibling detection by demonstrating that the effects of MPA and coresidence duration are highly replicable and therefore unlikely to be a false positive. Further, the data indicate that the effect is not a quirk of citizens of industrial societies—the type of sample that makes up the vast majority of published research in psychology (Henrich, Heine, & Norenzayan, 2010). In fact, the effect generalizes to a nonindustrial horticulturist population with demographic, technological, and social characteristics more similar to an ancestral foraging lifestyle than those of industrial populations. The Dominica population tested here is more likely than industrial populations to feature more developmentally valid contexts for the operation of the mechanism under discussion. The effect sizes of the former are well within the range of those of the latter, suggesting the cues involved are fairly abstract, and therefore robust to particulars that may be present in industrial societies but absent in small-scale ones (e.g., bottle feeding).

Despite its horticultural economy, kin-based sociality, extended-kin households, and widespread breastfeeding practices, Dominica has had substantial exposure to the liberal West, including hundreds of years of European influence, European languages, and some degree of market access and modern technology. Thus, as we stated above, data from a larger set of less Westernized and more EEA-like groups could profitably assess the true source of the effects found here.

Also, to our knowledge this work is among the first to test for different relatedness estimates mapping onto different genomes (maternal and paternal). Ancestrally, the probability that a maternal sibling would also have been a paternal sibling would have been better than chance, but far from perfect (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000); this may have selected for the independent computation of maternal and paternal relatedness (Cosmides & Tooby, 1981; Fox et al., 2009; Widdig, 2007). Although the present results are negative regarding PPA, further research may uncover other cues for the identification of paternal siblings, perhaps based on different *types* of cues (e.g., phenotype matching) given the issue of paternity uncertainty.

During the review process, it was noted that the weakest effect was observed in the one sample where participants were asked to report on one sibling only (Argentina). Might the larger effects in the other samples, which queried about multiple siblings, be unduly inflated? Which research design yields the most accurate estimation of effect size? If the true effect is best captured by a one-sibling design, then the results from the other samples should be discounted accordingly. But we note that Argentina is also the sample with a dependent variable featuring the smallest number of items (1), which likely makes it the noisiest of dependent variables. Also, the Argentina data probably have higher error variance due to the between-subjects design, compared to the other samples' repeated-measures design. So it is not clear whether the estimation of the true effect is inflated in the other samples or deflated in Argentina. Assuming the source of the weaker Argentina effect is the one versus multiple siblings feature, this could be driven by an altruistic psychology that is sensitive to an implicit reference class, as one of our reviewers suggested. In making altruistic decisions the psychology of allocations appears to implicitly weight the welfare of another not only relative to the welfare of the self but also relative to the welfare of third parties (Delton, 2010). Thus, the welfare of a given sibling might be weighted more uniformly (highly) against an implicit generic other (in the one-sibling Argentina design), thereby weakening the sib-detection effect, but more precisely as a function of sibship cues against other siblings featuring different levels of sibship cues (in the other, multiple-sibling designs). Further research could address this question. We note, however, that even if an Argentina-like effect size turns out to be the "true" effect, this effect would be, though modest, still as predicted by the MPA/coresidence model of sibling detection.

## Limitations

One limitation of the present data is their reliance on self-reports. Self-reported intentions to behave altruistically may be mere "cheap talk" (but see Charness & Dufwenberg, 2006; Schniter, Sheremeta, & Sznycer, 2013), and so should be interpreted with caution. We note, however, that the predicted pattern of altruism was observed both with a prospective motivation item (e.g., willingness to help) and with a retrospective behavioral item (favors provided in the last month; see Supplementary Information #2). More critically, a mere inflation of self-reported altruism (social desirability) is unlikely to yield the particular pattern of results that we predicted and observed—not without assuming the very specific hypotheses that we derived from evolutionary and ecological considerations. Of course, there may be a main effect of social desirability in our data, though previous studies have shown that controlling for social desirability does not affect the pattern of results (Lieberman, 2003). Nevertheless, further research using behavioral measures—for instance, the pain endurance paradigm employed by Madsen et al. (2007)—may profitably test whether the coresidence/MPA model of sibling-directed altruism replicates across cultures.

Another limitation of these data is the observed covariance between propositionally known sibling category on the one hand and ecological cues to sibship on the other hand. For instance, in our samples, all younger siblings for whom MPA and PPA were present were full biological siblings. However, we note that the reverse was not true—some full biological siblings lacked PPA, or both PPA and MPA. Checks on multicollinearity did not point to serious concern, and propositionally known sibling category (degree of relatedness) shared just 10% and 11% of its variance with MPA, and 45% and 50% of its variance with coresidence, in studies 1/5 and 2/3, respectively. Thus, our finding that both MPA and degree of relatedness independently predict altruism toward a younger sibling suggests that beliefs alone cannot explain patterns of sibling-directed altruism.

Consistent with this interpretation, past research by Lieberman et al. (2007) found that an ecological cue to sibship trumped beliefs when those things were in conflict with each other: For younger subjects believing their older siblings were step- or adoptive siblings, coresidence duration (still) predicted sexual aversion and altruism toward the older siblings. This finding parallels Shepher's (1971) findings regarding the Israeli Kibbutz: Coresidence was associated with low marriage rates even though the subjects knew explicitly that they were not genetic relatives. Nevertheless, our findings of independent significant effects of MPA and relatedness beliefs on altruism point to the need for future research with samples featuring one type of cue but not the other. These kinds of studies will profitably clarify the issue of the contribution of different types of cues to the kinship estimate and to downstream motivation and behavior.

Future research might also fruitfully dissect the concept of MPA. MPA was operationalized here as affirmative answers to each of the following three questions: (a) whether the individual shared the same biological mother with the target sibling, (b) whether the individual lived with their biological mother right after the target sibling was born, and (c) whether the individual lived with the target sibling right after that sibling was born. Further work might attempt to narrow in on more specific cues—for instance those used to assess "motherness" and other cues available during the MPA time period—that might be taken as input by systems that assess siblingship.

## Conclusions

MPA and coresidence duration appear to be relational cues that the mind reliably attends to and integrates in the service of computing sibship. A vast territory remains uncharted, however: Does the mind reckon paternal sibship? If so, how? How are other kin relationships (e.g., mother, father, offspring, extended family members) estimated? How does the mind integrate information about kinship with other information regarding social value (e.g., trustworthiness, skills) to regulate behavior in different domains (e.g., altruism, aggression, sex)? There is still much work to be done and an evolutionary-cognitive approach is a fruitful avenue to answer these and other questions regarding our intuitive sense of kinship.

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