The Ecology of Relatedness: Aspects and Effects

by

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ABSTRACT

Why are human societies so psychologically diverse? The discipline of behavioral ecology is rich in both theory and data on how environments shape non-human animal behavior. However, behavioral ecological thinking has not received much attention in the study of human cultural psychological variation. I propose that ecological relatedness—how genetically related individuals are to others in their proximate environment—is one aspect of the environment that shapes human psychology. I present three studies here that examine the influence of ecological relatedness on multiple aspects of psychology. In the first study, I find that higher levels of ecological relatedness at the nation level is associated with a greater willingness to put oneself at risk for others, greater localized trust, and a stronger sense of belonging to one's community. In the second and third studies, using experimental manipulations of perceived ecological relatedness, I examine the effects of ecological relatedness on helping behavior across situations, monetary sharing on a dictator game, interpersonal judgments, and alloparenting behaviors. I find that individuals led to perceive higher ecological relatedness became more sensitive to need in potential helping situations. The implications of ecological relatedness for thinking about psychological variation across groups are discussed.

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CHAPTER 1

INTRODUCTION

In the mountains of the western U.S., a female Belding ground squirrel sees a coyote. She gives off an alarm call. The call alerts surrounding group members of the approaching danger, and they scatter in search of cover. But at the same time, the squirrel has now put herself in mortal danger, as the coyote now turns its attention towards her.

Halfway around the world, an earthquake in Japan led to the destabilization of a nuclear power plant, leading to the world's worst nuclear disaster since Chernobyl (Bradsher & Tabuchi, 2011). In the midst of evacuation, 50 employees stayed in the plant, risking their own lives to prevent a nuclear meltdown. Since then, these individuals have been dubbed the "Fukushima 50", and lauded around the world for their bravery.

Here are individuals from two different species, putting themselves at risk to save others. But why would such behaviors even exist *in the first place*? Any living organism that sacrifices itself to save other individuals would be unlikely to pass on its genes to future generations, relative to individuals that do not engage in such behavior. Over multiple generations, such behavior (and genetic predispositions towards it) would have been selected against by evolution and disappeared over time.

However, from an evolutionary perspective, self-sacrificing behaviors can be biologically adaptive in special circumstances. Simply, sacrificing oneself to save other individuals can be adaptive if the individuals saved are genetically related to oneself (and sufficiently so). If this is indeed the case, then conditional self-sacrificing behavior could have evolved. The general argument is as such: *if* individuals in our species have faced varying levels of genetic relatedness with members of their groups, *and* different

behaviors are more or less adaptive in social environments of differing relatedness (e.g., sacrificing oneself to save others is more adaptive when others are highly genetically related), *then* evolution would have selected for flexibilities that alter an individual's behaviors depending on how related the individual is to others around them (e.g., a flexibility that increases self-sacrificing behavior when there is a high degree of relatedness to others around).

Beyond self-sacrificing, there are many behaviors that may vary in how biologically adaptive they are, depending on how related the individual carrying out these behaviors is to other individuals around him/her. One might therefore expect the evolution of not one, but multiple flexibilities that are sensitive to one's relatedness to others around them. Each of these flexibilities might influence a variety of behaviors. Broadly, I draw upon work from behavioral ecology to generate predictions about the nature of these flexibilities in humans, and the potential psychological effects of what I will refer to as *ecological relatedness*, defined as the extent to which people in a given environment are genetically related to one another.

I first introduce a behavioral ecological approach and the critical concept of phenotypic plasticity. Next, I summarize existing literature on ecological relatedness and the behaviors that it influences in non-human animals. From this, I then derive a set of hypotheses with respect to how ecological relatedness might similarly influence human psychology and behavior. I then present three studies that test these hypotheses using both correlational and experimental methods. Finally, I discuss the implications of the current findings for the concept of ecological relatedness and its relation to human psychological diversity.

Behavioral Ecology and Phenotypic Plasticity

The ground squirrel puts itself at risk to warn its group members. In contrast, the tiger salamander does the opposite. In its larval stage, the tiger salamander can take two physically distinct forms, "typical" or "cannibalistic" (Collins & Cheek, 1983). The latter is morphologically different, having a significantly larger mouth and head shape. True to its name, the cannibalistic form consumes other salamander larva around it.

Both the squirrel's self-sacrifice and the salamander's cannibalism are examples from behavioral ecology—the study of how ecological pressures lead to variation in animal behavior (Davies, Krebs, & West, 2012). Both represent specific examples of *adaptive phenotypic plasticity*—that individuals with the same genes may exhibit different traits under different environments (Dingemanse, Kazem, Reale, & Wright, 2009; Piersma & Drent, 2003; Pigliucci, 2005; West-Eberhard, 1989). Why would plasticity exist in the first place? Simply, if in different environments some behaviors are more biologically adaptive than others, and organisms have encountered varying environments (both temporally and spatially) in their ancestral history, then natural selection would have led to the evolution of environmentally sensitive flexibilities. This is the broad form of the argument presented earlier focusing on the relatedness aspect of environments.

For the tiger salamander, the cannibalistic form tends to emerge under a specific ecology—that of high population density (Collins & Cheek, 1983). The reasoning here is that when there are many other individuals in the environment, there will likely be more competition for resources, space, and mates. Hence, it is more adaptive under such conditions to adopt a form that can remove one's competition—cannibalism in this case.

The plasticity here may be expressed crudely as: if high density, then become cannibalistic. For the ground squirrel, the likelihood of alarm calling when a predator appears increases when a squirrel has more living kin (e.g., sisters, daughters) in close proximity (Sherman, 1977). This plasticity may be expressed as: if high ecological relatedness, then call to warn others. The reasoning, as described earlier, is that putting oneself in danger for others can be adaptive, if the others saved are genetically related to oneself. More formally, this is the idea that organisms have evolved to behave in ways that increase their inclusive fitness (Hamilton, 1964)—the survival and reproduction of their genes, not just in themselves, but also in others who also carry them.

As illustrated by the two examples, both physical and social ecological factors (e.g., population density, group relatedness) can have effects on individual traits. Plasticity can manifest in both physical and behavioral ways, and the range of possible behaviors can be wide, from the cannibalism of others to the sacrifice of the self. The study of plasticity in behavioral ecology has received much attention. And plasticity has been demonstrated in reaction to a wide variety of ecological factors, such as relatedness, population density, disease prevalence, resource availability, predation pressures, sex ratio, and many others (Davies, Krebs, & West, 2012).

In the current proposal, I will focus on the ecological factor of relatedness. In the next section, I summarize existing work on the various aspects of this ecological dimension, and highlight two behaviors that have received considerable study in relation to it: prosociality and alloparenting.

Ecological Relatedness: Aspects and Effects

The prevalence or absence of genetic relatives in an individual's ecology has important fitness implications for the behaviors one might engage in. But how would organisms be able to recognize another individual as a genetic relative in the first place? Individuals are presumably not born with knowledge of who their kin are. Instead, evolution would have selected for the use of cues to infer genetic relatedness, particularly cues that ancestrally have been reliable indicators of kinship (see Waldman, 1988, and Mateo, 2003, for reviews).

Because across our evolutionary history individuals have grown up in close proximity to family, especially siblings—co-residence is one such cue. Indeed, co-residence, especially during early developmental life stages, seems to elicit behaviors typically observed between kin. For example, ground squirrels that were reared together engaged in fewer exploratory behaviors (typically observed between non-kin) when interacting with each other, relative to squirrels that were not reared together (Holmes, 1986). Interestingly, actual genetic relatedness did not matter in this case: genetically related squirrels reared together behaved towards one another in a similar way as *un*related squirrels reared together. In humans, similar effects of co-residence have been found. Siblings who have lived together for a longer period of time are more altruistic towards each other (e.g., are more willing to donate a kidney) and also feel more disgusted when imagining having sexual acts with their opposite-sex sibling (Lieberman, Tooby, & Cosmides, 2007). The disgust reaction presumably functions to avoid inbreeding. Mirroring the animal examples, such effects also occur in contexts where individuals who grow up together are not actual genetic relatives (e.g., Israeli

Kibbutzim); co-residence duration predicts peer-directed altruism and sexual aversion (Lieberman & Lobel, 2012).

A second cue that has been uncovered in humans is maternal perinatal association (MPA)—the close association of one's mother with a particular individual (e.g., through breastfeeding) (Lieberman et al., 2007). This is arguably a good indicator that the individual being cared for by one's mother is a sibling. Co-residence and MPA are interactively used as kinship cues. Specifically, when MPA is not present, both altruism towards and sexual disgust at imagined incest with a sibling are predicted by co-residence duration. However, when MPA is present, co-residence duration does not predict either altruism or incest aversion. Hence, MPA may be considered a more primary cue relative to co-residence, with the latter being relied on more when MPA cues are not available (e.g., when identifying one's older siblings).

A third cue to relatedness is phenotypic similarity. To the extent that greater morphological similarity may reflect shared genes, organisms might use similarity to the self as a cue of relatedness. This process is referred to as self-phenotype matching in behavioral ecology (Hauber & Sherman, 2001; Mateo, 2010), with evidence of it occurring via smell (Mateo, 2009; Olsén, Grahn, Lohm, & Langefors, 1998), sight (Tibbetts & Injaian, 2013), and sound (Rendall, Rodman, & Emond, 1996). For example, in paper wasps, queen wasps tend to preferentially associate and cooperate with other queens that have similar facial patterns (Tibbetts & Injaian, 2013). Again, there is also some evidence for phenotypic matching in humans. For example, when individuals are presented with faces of strangers digitally morphed with their own, they tend to exhibit more prosocial behaviors towards these self-resembling morphed targets (Debruine,

2005; Krupp, Debruine, & Barclay, 2008). Other work also finds that individuals who hold highly similar attitudes (e.g., beliefs about capital punishment) to the self are more likely to be mentally categorized as kin (Park & Schaller, 2005).

From the above, one might expect individuals to be sensitive to the prevalence of cues of relatedness in their proximate ecology, allowing an estimate of the average relatedness of themselves to others in their ecology. For example, if individuals reside in an ecology where they are surrounded by many individuals who have lived with them since they were a child (i.e., co-residence cue), this might lead to a perception of high ecological relatedness. Another possibility is if individuals are currently in an ecology where they are surrounded by many individuals who are physically similar (or similar in other phenotypic aspects) to themselves, this could also lead to perceptions of high ecological relatedness.

Having outlined potential aspects of ecological relatedness, I now summarize some existing work on its effects, specifically on prosocial behavior and alloparenting.

Prosociality. Recall the ground squirrel example. Alarm calling is a behavior that seems maladaptive, given the mortal danger that the calling squirrel puts itself in. Yet such seemingly maladaptive behavior can be adaptive if there are many genetically related individuals (or few but extremely highly related individuals) who would benefit from it. In behavioral ecology, such seemingly altruistic behaviors posed an early puzzle in evolutionary thinking. The most striking example is arguably the eusocial insects (e.g., ants, bees, wasps), in which whole castes of workers sacrifice their own reproduction to aid the reproduction of the colony queen. It was difficult to explain how behaviors such as these—individual sterility while aiding the reproduction of others—could have

evolved. A key insight came from the unique genetic structure of the eusocial insects, which is such that workers were actually more closely related to the siblings they help raise (75%) than their own potential offspring (50%) (Hamilton, 1972).[1] Hence, behaviors that benefit others at a cost to the self can evolve if the net benefit to one's *genes* outweighs the costs.

Subsequently, relatedness has often been examined in terms of its effects on prosocial behavior. Across multiple species, animals in proximity of genetically-related individuals tend to affiliate more with and engage in more prosocial behavior towards these individuals (e.g., Hesse, Bakker, Baldauf, & Thunken, 2012; Holmes, 1995; Lihoreau & Rivault, 2009; Mateo, 2010; Sherman, 1977; Sherman, 1985; Wilkinson, 1985). For instance, urban cockroaches, across all developmental stages, prefer socializing with genetically related individuals (compared to non-relatives), even when they have never encountered these individuals before (Lihoreau & Rivault, 2009). Like the ground squirrels, prairie dogs, upon detecting predators, are more likely to alarm call when there are genetic relatives in proximity (Hoogland, 1983). Finally, vampire bats are more likely to regurgitate and share blood with related individuals (Wilkinson, 1985).

Note that greater prosociality under high relatedness conditions does not necessarily imply lower levels of competition. In the animal literature, related individuals

[1] Note that subsequent work has argued that the genetic structure of the eusocial insects is, by itself, an insufficient condition for the evolution of eusociality. Other conditions, such as monogamy, need to have also been present for the evolutionary emergence of such a phenomenon (e.g., Boomsma, 2009).

have sometimes been found to be just as or even more competitive towards one another than unrelated individuals are (Bernstein & Ehardt, 1986; Packer & Pusey, 1982; Wahaj et al., 2004). One reason this can occur is because genetically similar individuals may draw upon the same kinds of resources, leading to greater competition over limited resource pools (Waldman, 1988). However, what is crucial here is that such competition between related individuals, even when high, should be unlikely to become lethal. Given that kin may also be potential competitors, one might expect the effects of relatedness on prosocial behavior to more strongly emerge when related individuals are actually facing mortal danger, as in the case of the ground squirrel example.

Similar effects have also been found in humans. As highlighted by examples earlier, people behave in a more prosocial manner towards individuals of (perceived) higher relatedness. Individuals are more likely to trust people whose faces have been morphed to be similar to their own (Debruine, 2005; Krupp, Debruine, & Barclay, 2008). Siblings who have co-resided for a longer duration of time report a greater likelihood of engaging in costly helping behaviors towards one another (Lieberman, Tooby, & Cosmides, 2007). Finally, in self-reports about helping behavior, individuals are more likely to help highly related individuals, particularly when faced with life-or-death situations (e.g., when forced to choose between saving a sister or cousin from a burning building) (Burnstein, Crandall & Kitayama, 1994). Hence, individuals in our species also behave in more prosocial ways towards genetically related others.

From this, one might predict that general prosocial behavior should also vary according to ecological relatedness, with greater prosociality emerging under conditions of higher ecological relatedness. In addition, such greater prosociality may be most likely

to emerge when the potential benefit to inclusive fitness is high, or more relevant to the various examples described, when the potential inclusive fitness costs (if help is not provided) are high.

Besides one's own prosocial behavior, one might also consider how the prosocial or anti-social behaviors of *others* might be evaluated in ecologies of varying relatedness. In a high relatedness ecology, given that the prosocial behavior of another can lead to greater inclusive fitness benefits for an individual, individuals in high relatedness ecologies (relative to low) might evaluate prosocial individuals especially positively. On the flip side, however, individuals in higher-relatedness ecologies might evaluate anti-social behaviors, particularly lethal ones (e.g., physical aggression, homicide), especially negatively, due to the greater inclusive fitness *costs* imposed by such anti-social behaviors. Therefore, a second prediction is that individuals in high relatedness ecologies will be more polarized in their evaluations of prosocial versus anti-social behaviors. That is, prosocial behaviors will be judged more positively than anti-social ones in general, but this difference should be greater in high relatedness ecologies.

To summarize, I hypothesize that individuals in high relatedness ecologies will be more prosocial, especially under conditions when potential inclusive fitness costs for not helping are high. My second hypothesis is that when evaluating the behaviors of *others*, individuals will tend to judge prosocial behaviors more positively in high-relatedness conditions, but will also judge anti-social behaviors more negatively.

Alloparenting. Alloparents are individuals that care for offspring that are not their own. The example of the eusocial insects is one instance of this. This is also referred to as the "helper at the nest" phenomenon, or cooperative breeding. Alloparenting has

been documented across multiple species, with the most extensive empirical work being done in birds (e.g., Clarke, 1984; Cockburn, 1998; Curry, 1988; Dierkes et al., 2005; Emlen, 1978; Komdeur & Hatchwell, 1999; Mumme, 1992; Nam, Simeoni, Sharp, & Hatchwell, 2010; Wright, McDonald, Marvelde, Kazem, & Bishop, 2009). For instance, in white-fronted bee-eaters, the probability of individuals being a helper at the nest increased with the degree of relatedness of the individual to the nestlings (Emlen & Wrege, 1988). In long-tailed tits, when both kin and non-kin nests were in similar proximity, more than 90% of individuals chose to help at the nest with kin (Russell & Hatchwell, 2001). Finally, in a meta-analysis across 18 species, higher levels of relatedness generally predicted a higher probability of helping another's offspring, and this was particularly so in species for which there was a strong benefit of such helping on offspring survival (Griffin & West, 2003; see also Cornwallis, West & Griffin, 2009). Interestingly, there was no general effect of relatedness on the *amount* of helping, which is argued to be influenced by many other factors, such as the helper's own physical condition, and may subsequently be a more noisy measure.

This connects to a critical question in cooperative breeding: *who* are the individuals that help? As mentioned, one factor here is how related individuals are to the potential recipients of help. But even amongst related individuals, there are both breeders and helpers. While the body of work documenting alloparenting is substantial, the individual differences between breeders and non-breeders (helpers) are less well understood. Some work has documented that helpers are often young juveniles—individuals that have not reached reproductive status themselves (e.g., Brown, 1987; Stacey & Koenig, 1990; Valencia, de la Cruz, & Gonzalez, 2003). Other work, however,

finds the opposite, with older individuals investing more in cooperative breeding (e.g., Boland, Heinsohn, & Cockburn, 1997; Clutton-Brock et al., 2001; Dickinson, Koenig & Pitelka, 1996). In general, it seems that these inconsistencies may be the result of the interplay of two factors: the provisioning ability of the helper (i.e., older individuals may be more successful at foraging and subsequently have more to give) and the independent reproductive options of the helper (i.e., younger individuals may be less able to successfully compete for mates and therefore more likely to invest in indirect reproduction—alloparenting).

Cooperative breeding has also been observed in some hunter-gatherer groups (Kaplan, Hill, Lancaster & Hurtado, 2000; Mace & Sear, 2005). Males in the Ache were much more likely than females to be food providers to breeding pairs, and this was particularly so for unmarried and younger males (Hill & Hurtado, 2009). The sex difference may be because males experience greater variation in reproductive success (i.e., more males than females end up not reproducing at all), and are subsequently more likely to invest in alloparenting as a means of indirect reproduction. That unmarried and younger males are more likely to engage in cooperative breeding may simply reflect fewer resource demands on these males.

In sum, theory and data in behavioral ecology suggest that (1) organisms have evolved to detect cues of relatedness in other individuals in their ecology, and (2) higher levels of ecological relatedness generally lead to both greater prosocial behavior and a greater prevalence of alloparenting. Also, such effects of relatedness can be moderated by other factors, both ecological and individual (e.g., potential reproductive success). From this, one might expect humans to also be sensitive to the average relatedness of their

proximate group, and alter their behaviors accordingly, depending on what would be more adaptive in their specific ecology.

Note that I am not proposing that ecological relatedness accounts for the origin of widespread human cooperation, as actual mean genetic relatedness between adults in modern hunter gatherer groups is relatively low (mean relatedness coefficient is about 0.05; Hill et al., 2011). What I am proposing is that individuals detect *variation* in average group relatedness that can occur both temporally and spatially, and that this variation should lead to adaptive shifts in social behaviors. Below, I summarize my primary hypotheses and overview three studies testing these hypotheses.

Overview

Broadly, I hypothesize that, as a form of adaptive phenotypic plasticity, individuals are sensitive to how related they are to others in their immediate ecology, and that they subsequently adjust their behaviors in predictable ways depending on ecological relatedness. I outline my three main predictions below:

H1. Individuals in ecologies of high relatedness will be more prosocial. This effect may emerge specifically when the inclusive fitness costs of not helping are high, such as "life-or-death" scenarios, or when one's entire group is under external threat.

H2. Individuals in ecologies of high relatedness will be more polarized in their evaluations of prosocial and anti-social behaviors of others; they will judge prosocial behaviors more positively (due to the greater inclusive fitness benefits) and anti-social behaviors more negatively (due to the greater inclusive fitness costs).

H3: Individuals in an ecology of high relatedness will be more likely to exhibit alloparenting behavior—caring for children who are not their own. This effect may emerge only, or be strongest, for individuals who are less able to reproduce themselves and hence most likely to engage in indirect reproduction. From work reviewed earlier, such individuals may be males not currently in a reproductive life stage (men without children), or males who expect to have low success in finding a mate (men with low desirability as a mate).

I first present a preliminary study, in which I examine the relationships between a proxy of ecological relatedness at the nation level—the prevalence of cousin marriages in a country—and various psychological traits that it should theoretically influence. Then, in my two dissertation studies, I use an experimental manipulation of ecological relatedness and examine its effects on prosocial helping, evaluations of prosocial and antisocial others, and alloparenting tendencies.

CHAPTER 2

PRELIMINARY STUDY: NATION-LEVEL RELATEDNESS

One way of testing the effects of ecological relatedness is examining psychological differences across groups that live in ecologies of varying relatedness. Existing work has tested other ecological hypotheses using nations as units of analysis. For instance, people in nations with historical higher pathogen prevalence have been found to be lower in extroversion and openness, and are less inclined towards casual sexual relationships (Schaller & Murray, 2008). Such tendencies are presumably adaptive in environments with high pathogen loads, as they function to help avoid exposure to disease. Other ongoing work finds that psychological variation across nations is predicted by population density, with people in more dense nations exhibiting traits that correspond to a slower (as opposed to faster) life history strategy, which includes traits such as being more future-oriented, investing in building one's skills, having fewer children, and investing more in each child (Sng, Neuberg, Varnum, & Kenrick, under review). A slow life history strategy is presumably more adaptive in highly dense environments due to intense social competition between conspecifics, which increases the need to invest in building one's competitive ability and to focus resources on fewer offspring in order to increase reproductive competitiveness of offspring themselves.

In a similar vein, I predict that average relatedness at the nation level is related to predictable psychological differences. Note that although one might operationalize ecological variables at the nation level, this should not be taken to imply that it is the ecology of an entire nation that is exerting an effect on any specific individual. In the two examples of ecological disease and density mentioned above, there is presumably

considerable local variation *within* nations in both pathogen prevalence and social density. Measuring ecologies at the nation level serves as a crude estimate, at best, of the more proximate ecologies that individuals are more likely to interact with and be exposed to in their everyday lives (e.g., one's own town or neighborhood). Hence, an indicator of average relatedness at the nation level is presumed to reflect, to some degree, relatedness of one's proximate group within the nation. If anything, that nation-level ecological measures may miss finer ecological variation within a nation would lead to a more crude and conservative test of my hypotheses.

To assess ecological relatedness, I used existing data on the frequency of cousin marriages as a proxy. The presumption here is that the higher the prevalence of cousin marriages, the higher the average degree of relatedness individuals will have with others around them. I then examined the relationship of this proxy with similar nation-level data on general willingness to defend one's country (as a measure of potential self-sacrifice), trust, and sense of connectedness towards various groups.

Method

Ecological Relatedness. To assess relatedness, I obtained secondary data on the proportion of consanguineous marriages at the nation level (Hoben, Buunk, Fincher, Thornhill & Schaller, 2010). These are defined as marriages between individuals who are second cousins (sharing a same great-grandparent) or closer. The original data were gathered from reviews of past clinical genetics research beginning from the 1950s (Bittles, 2001) and can be found on www.consang.net. Data were available for 71 geopolitical regions. Data for both consanguineous marriages and the psychological measures of interest were available for a subset of 36 regions. The mean percentage of

consanguineous marriages in this subset was 16.8% (*S.D.* = 17.8), and ranged from .1% (Croatia) to 51.7% (Kuwait).

Dependent Measures. Data on relevant dependent measures were gathered from the sixth and most recent wave of the World Values Survey (WVS), which was carried out between the years 2010-2014. Interviews were conducted across 60 different countries, with samples in each country numbering 1000 individuals or more.

The first dependent measure was a single item that asked about people's willingness to defend their country. The item was phrased: "Of course, we all hope that there will not be another war, but if it were to come to that, would you be willing to fight for your country?" Participants responded either yes or no. I used the percentage of individuals in each country who responded yes. This represents a proxy to prosocial behavior, specifically when one's group is under threat.

A second set of dependent measures captures self-reported trust towards a variety of groups. Previous work has found that individuals are more likely to trust others who show cues of relatedness (e.g., facial similarity; Debruine, 2002). One might therefore expect higher ecological relatedness to be associated with greater trust, but specifically towards one's own group members. I focus here on three theoretically relevant groups. Participants in the WVS were asked how much they trust their family, people from their neighborhood, and people of another nationality. They responded to these three items on a 4-point scale (1= Do not trust at all, 4 = Trust completely). I use the aggregate score at the nation level for each of these three items. Neighbors represent potential own group members, while people of another nationality should not. The prediction is therefore that individuals will be more trusting towards their neighbors in high-relatedness ecologies,

but not necessarily towards individuals of another nationality. For trust towards family members, I had no strong prediction. It is possible that higher relatedness will also lead to greater trust amongst family members (e.g., if an individual's parents are cousins, then he/she is likely also more highly related to his/her siblings than if their parents were unrelated), and hence potentially higher trust. However, it is also possible that trust towards family members may simply be extremely high to begin with, and that there is little room for further variation.

A final set of dependent measures captures perceptions of the self. One distinction made in the psychological literature of the self is that of independent-interdependent selves. An interdependent self is a conception of the self as being inextricably connected to others, and is associated with behaviors that put the interests of one's group before the self, along with greater social empathy and regard for others (Cross, Bacon, & Morris, 2000; Markus & Kitayama, 1991). I examined three relevant items on the WVS. Participants were asked how strongly they agree or disagree with three statements: "I see myself as part of my local community", "I see myself as part of the [PARTICIPANT'S NATION]", and "I see myself as a world citizen" (1 = Strongly Disagree, 4 = Strongly Agree). Again, the aggregate score at the nation level for each of these three items was used. The prediction here is that higher relatedness should be associated with a more interdependent self but once again specifically with own group members (community and possibly fellow citizens), but not with the world at large.

Results and Discussion

All analyses presented here are Pearson correlations. First, the prevalence of cousin marriages was indeed correlated in the predicted direction with willingness to

fight for one's country. The higher the relatedness, the more people in a country were likely to say they would be willing to fight for their country under conditions of war, $r = .41$, $p = .013$. For trust, the higher the relatedness, the more trusting people were towards their neighbors ($r = .53$, $p < .001$). There was no relationship between relatedness and trust towards family or foreigners ($r = .08$, $p = .65$, and $r = -.15$, $p = .39$, respectively). Finally, for perceptions of the self, the higher the relatedness, the more people saw themselves as part of their community and country ($r = .45$, $p = .006$, and $r = .35$, $p = .036$ respectively). There was no relationship between relatedness and perception of the self as world citizen ($r = -.05$, $p = .78$).

Using prevalence of cousin marriages as a crude proxy of ecological relatedness, I find meaningful relationships between relatedness and theoretically relevant psychological traits. First, higher levels of ecological relatedness are associated with a greater willingness to put oneself at risk for the group, in this case being willing to fight for one's country if there was a war. Second, higher ecological relatedness was also associated with greater interpersonal trust of one's proximate group (neighbors), but *not* beyond (foreigners). Finally, individuals in higher relatedness ecologies saw their selves as more connected to proximate groups (community and country), but not beyond (world citizenship). Again, it is important to remind here that the conceptual argument being made is that the average relatedness of others around is what is influencing individual psychology, not the average relatedness of everyone in a country. The use of a country-level indicator is useful because it is assumed to be associated to some extent to ecological relatedness at smaller geographical scales within the country (e.g., neighborhoods). To the extent that this association is imperfect, the use of the country-

level relatedness proxy would have underestimated the strength of the relationships I am finding.

Nevertheless, this preliminary study is limited in multiple ways. Correlational analyses do not provide evidence for direct causality. There have also been methodological issues raised with regard to how correlations across cultures should be interpreted (e.g., Hruschka & Hackman, 2014; Pollet, Tybur, Frankenhuis, & Rickard, 2014). In addition, data on measures more directly relevant to my main hypotheses (e.g., interpersonal judgments, alloparenting) were not available. Hence, in focal Studies 1 and 2, I use experimental manipulations of ecological relatedness to carry out more precise tests of my hypotheses. Specifically, I provide individuals with information that ostensibly alters their perceptions of ecological relatedness, and examine its subsequent effects on prosocial behavior and evaluations of others' anti/prosocial behavior (Study 1), and alloparenting tendencies (Study 2).

CHAPTER 3

STUDY 1

In this study, I examine two central hypotheses. First, I propose that individuals in ecologies of higher relatedness will tend to behave more prosocially, but particularly so when there are strong potential implications for inclusive fitness (e.g., life-or-death situations, when one's entire group is under external threat). Second, I propose that individuals in ecologies of higher relatedness will be more polarized in their judgments of prosocial behaviors relative to antisocial behaviors, judging prosocial behavior even more positively and antisocial behaviors even more negatively. Again, the rationale is that such behaviors carry greater inclusive fitness implications in a high relatedness ecology (e.g., antisocial behaviors may inflict harm on not just oneself, but also genetically related others, in a high relatedness ecology).

To test these hypotheses, I use an experimental manipulation designed to alter perceptions of ecological relatedness—popular science news articles that present research showing that individuals are more, or less, genetically related to one another than previously known to be.

Method

Participants. Two-hundred and fifty participants (119 women) were recruited from Amazon's Mechanical Turk and compensated $1.00 for their participation. The mean age of these participants was 35.4 years (SD = 11.8).

Procedure. Participants signed up for a "Social Memory Survey." Participants previewing the task read the participant consent form and were then directed to a link

where they could complete the survey. Upon entering the survey, participants were randomly assigned to either the high or low ecological relatedness conditions.

Participants in the high ecological relatedness condition read a fictitious newspaper article titled "Surprisingly, DNA survey finds that people are genetically similar to the strangers around them," which described how recent scientific research had discovered that people were much more genetically related to those around them than previously expected. For example, as part of the article, participants read:

> Whether you hail from Richmond, Ulan Bator or Nairobi, your genetic make-up is strikingly similar to that of people around you, a new analysis concludes. Scientists have long recognized that, despite physical differences, most human populations are genetically similar. The new work concludes that people within a population may share many more genetic similarities with one another than previously assumed. The estimates are striking, indeed. In layman terms, according to the new study, about 1 in 4 people we encounter in our everyday lives may have a great-great-grandparent in common. The results of the study, published today in the journal *Science*, have implications for understanding population change and human migration, said Professor Morris Feldman of Harvard University who led the team. "These new estimates of relatedness can seem surprising, especially given that we all seem to look so different from one another. But there is growing evidence suggesting that very small differences in DNA may be all that underlie the things that make us look different. At the genetic level, we are far more similar than meets the eye…"

Participants in the low ecological relatedness condition read a similarly formatted article titled “Surprisingly, DNA survey finds that people are genetically dissimilar to those around them,” which described the reverse—that recent research had discovered that people were much less genetically related than expected to those around them (for full essays see Appendix A).

Everyday vs. life-or-death helping. After reading either the high or low relatedness article, participants then completed a measure of helping in everyday versus life-or-death situations. Participants read two imaginary scenarios (see Appendix B for full scenarios). In one scenario (everyday helping), participants imagined coming across a person whose car seemed to have broken down, on their way to a meeting. They were then asked how likely they would stop to help this person, on a scale of 0% (*Definitely not help*) to 100% (*Definitely help*).

In the other scenario (life-or-death helping), participants imagined coming across a burning building and hearing a call for help by someone presumably stuck in the building. Again, they were then asked how likely they would enter the burning building to help this person, on the same scale of 0% (*Definitely not help*) to 100% (*Definitely help*). The presentation order of the two scenarios was randomized.

Helping under external threat vs. without external threat. After completing the everyday/life-or-death helping scenarios, participants then completed a measure of helping under external threat or without threat (Appendix C).

For helping without threat, participants were told to imagine that the U.S. was currently not at war, and that the U.S. president had given a television address announcing a proposal to raise taxes for military funding, and had asked Americans to

support this proposal. For helping under external threat, participants were now told to imagine that another country had attacked the U.S., and there would likely be severe casualties. Again, the president had given a similar television address announcing a proposal to raise taxes for military funding, and was asking for American support. After reading each situation, participants were asked to rate their likelihood of supporting the tax raise proposal on a scale of 1 (*Not at all support*) to 9 (*Definitely support*). The order of presentation for each of the two situations was randomized.

Dictator game. Following the helping measures, participants then played a dictator game (see Appendix D). Participants were told that they had now been given a bonus amount of $0.50, from which they were to decide how much to allocate to another randomly chosen participant in the study versus keep for themselves. They were told that whatever amount they chose to keep would be allocated to them as a bonus payment at the end of the study.

Booster Manipulation. Upon completing the dictator game, participants then completed an experimental manipulation "booster", in which they were asked to recall the newspaper article (i.e., the manipulation of high or low ecological relatedness) they read at the beginning of the study, and to write a few sentences summarizing the content of the article. The purpose of such a procedure is to bring to memory the experimental manipulation, due to the potential decay of the psychological effects of the manipulation over time. Similar procedures have been used in previous research (e.g., Griskevicius, Cialdini, & Kenrick, 2006).

Social Evaluation. After the booster manipulation, participants were then presented with the profiles of two hypothetical target individuals (see Appendix E). Each

target individual had supposedly completed a questionnaire containing items adapted from a measure of the Dark Triad (i.e., Narcissism, Psychopathy, Machiavellianism) (Jonason & Webster, 2010). Two sample items are "I tend to exploit others towards my own end" and "I tend to manipulate others to get my way", on scale from 1 (*Strongly Disagree*) to 5 (*Strongly Agree*). The scores of the two hypothetical targets were such that one appeared to engage in more anti-social behavior (i.e., strongly agreeing to the item "I tend to exploit others towards my own end") than the other (referred to here as the pro-social target).

After viewing the questionnaire profile of each target, participants then evaluated how positive-negative they felt about the target (1 = *Extremely Negative*, 9 = *Extremely Positive*), and how much they liked or disliked the target (1 = *Strongly Dislike*, 9 = *Strongly Like*). Ratings of the two items for each target were averaged to form a general evaluation score (*r*s = .70 for prosocial target, .84 for antisocial target)—higher scores mean greater positivity/liking. Finally, participants also reported how much they would like each target as a potential neighbor, friend, or family member (1 = *Strongly Dislike*, 9 = *Strongly Like*). The three ratings for each target were also combined to create a general social choice score for each target (prosocial target: $\alpha = .96$; antisocial target: $\alpha = .94$)—higher scores mean greater preference of a target as a social partner.

Results

I present the findings for each set of measures in the same sequence as they were presented in the study. For each measure, I first reiterate my predictions, followed by the analyses testing the prediction.

Everyday vs. life-or-death helping. I predicted that people will be more willing to help when they believe that others around them are highly related to themselves. This effect, however, should be greater for life-or-death helping than everyday helping, given that there are higher potential inclusive fitness costs for not helping genetic relatives. To test this, I performed a 2 (Relatedness condition: High/Low ecological relatedness) X 2 (Helping type: Everyday/Life-or-death) mixed measures ANOVA.

There was no main effect of Relatedness Condition, $F(1, 246) = .08$, $p = .77$. There was a main effect of Helping Type, $F(1, 246) = 40.46$, $p < .001$; participants reported being more likely to help in the life-or-death scenario than the everyday scenario. This was, however, qualified by a significant Relatedness Condition X Helping Type interaction, $F(1, 246) = 4.62$, $p = .033$ (see Figure 1). From pairwise comparisons, participants were more likely to help in the life-or-death scenario than the everyday scenario in both relatedness conditions (both *p*s < .01), but this difference was greater in the high relatedness condition. In other words, participants led to believe that they were in a high relatedness ecology seemed to *differentiate more strongly between life-or-death and everyday helping*. For the simple effects of relatedness condition on each helping type, neither were statistically significant (everyday helping: $p = .15$; life-or-death helping: $p = .30$)—there was no difference in helping between the low and high relatedness conditions for both everyday and life-or-death helping.

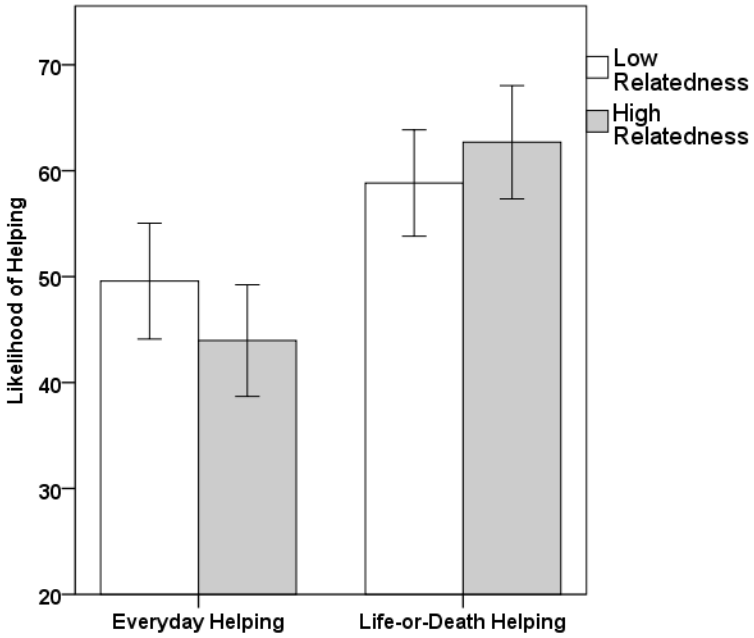


Figure 1. Everyday versus life-or-death helping by relatedness condition. Error bars are 95% confidence intervals.

Helping under external threat vs. without external threat. My second prediction was that people would be more willing to help under higher ecological relatedness, but particularly so when the group is facing an external threat. To test this, I performed a 2 (High/Low Relatedness Condition) X 2 (Helping under External Threat/No Threat) mixed measures ANOVA.

Contrary to predictions, there was no interaction effect, $F(1, 248) = .05$, $p = .82$ (Figure 2). There was also no effect of Relatedness Condition, $F(1, 248) = .04$, $p = .85$. There was a main effect of Helping type, $F(1, 248) = 181.60$, $p < .001$; people were more willing to support the tax increase if the U.S. was facing external threat, compared to when not.



Figure 2. Helping with/without external threat by relatedness condition. Error bars are 95% confidence intervals.

Dictator game. I predicted that individuals in the high relatedness condition, to the extent that they engage in more prosocial behavior, would also give more in the dictator game. I performed an independent samples *t*-test to examine this. There was, however, no effect of Relatedness Condition on amount shared in the dictator game, $t(247) = .98$, $p = .33$ (Figure 3).

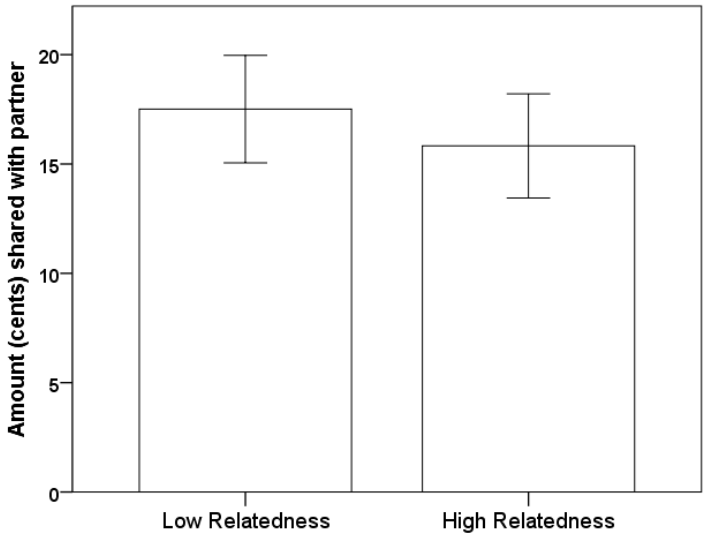


Figure 3. Average amount shared in dictator game by relatedness condition. Error bars are 95% confidence intervals.

Social Evaluation. Finally, I predicted that participants in the high relatedness condition will be more polarized in their evaluations of prosocial and antisocial others—they will judge prosocial others more positively and antisocial others more negatively. This is due to the potential greater inclusive fitness benefits of prosocial actors, and correspondingly greater inclusive fitness costs of antisocial actors, in high relatedness environments. To test this, I performed a 2 (High/Low Relatedness Condition) X 2 (Prosocial/Antisocial Target) mixed measures ANOVA on the general evaluation and social choice measures separately.

For general evaluation, contrary to predictions, there was no interaction effect, $F(1, 242) = .93$, $p = .34$. There was also no effect of Relatedness Condition, $F(1, 242) = 1.45$, $p = .23$. The only significant effect was that of Target Type, $F(1, 242) = 405.66$, $p < .001$; the antisocial target was evaluated more negatively than the prosocial target

(Figure 5, left panel). For the social choice measure (i.e., preference for target as neighbor/friend/family member), there was also no interaction effect, $F(1, 244) = .23$, $p = .63$, but both the Target Type and Relatedness Condition main effects were significant (Figure 5, right panel). First, the antisocial target was also generally less favored relative to the prosocial target, as a social partner, $F(1, 244) = 558.67$, $p < .001$. In addition, participants in the high relatedness condition rated both targets less favorably than those in the low relatedness condition, $F(1, 244) = 4.83$, $p = .029$. This finding was not predicted, and I discuss this briefly below.

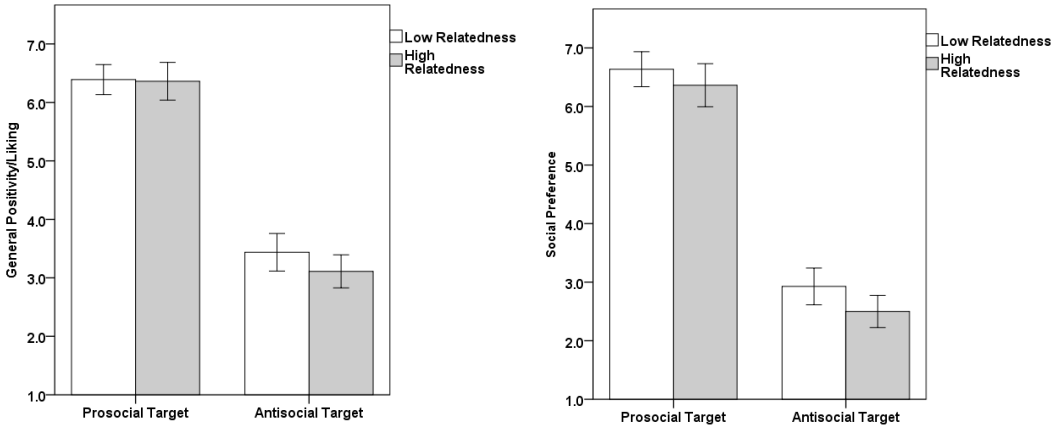


Figure 4. General positivity/liking (left) and social preference (right) for prosocial and antisocial targets by relatedness condition. Error bars are 95% confidence intervals.

Summary and Discussion

In general, the manipulation of ecological relatedness did not have the predicted effects. There was no effect of the relatedness manipulation on helping under external threat (i.e., tax raises to support the military under war conditions), or sharing on the dictator game. However, there did seem to be an effect on helping in life-or-death versus everyday situations. Specifically, although participants generally reported being more

likely to help in the life-or-death situation than the everyday helping situation, this difference was larger for participants who were led to perceive that they were in a high relatedness ecology. In addition, there was an unpredicted general effect of the relatedness manipulation on social preferences—participants in the high (relative to low) relatedness condition disliked both the prosocial and antisocial individuals as potential social partners (neighbors/friends/family members).

That participants reported being more likely to help in the life-or-death than the everyday situation may reflect a general sensitivity towards need—the person in the burning building could have lost their life whereas the person with the flat tire was in no immediate physical danger. If this is indeed so, then one implication is that perceivers in the high relatedness condition (relative to those in the low relatedness condition), in their greater differentiation of reported helping between the two situations, became more sensitive to others' needs (or lack thereof). In a high relatedness ecology, this heightened sensitivity to need might serve the function of prioritizing toward whom an individual directs his or her helping, particularly with the aim of minimizing inclusive fitness costs (i.e., having a genetically related individual die).

Unexpectedly, participants in the high relatedness condition were more likely to dislike both the prosocial and antisocial individuals as potential social partners. My specific prediction had been that participants in the high relatedness condition would be less favorable towards the antisocial individuals but *more* favorable towards the prosocial individual. However, given that this same pattern was not observed for the general positivity measures (i.e., participants in the high and low relatedness conditions did *not* differ in how positively they perceived the hypothetical individuals), I am cautious about

drawing any conclusions from this. In addition, there are some methodological considerations with the current design for testing the social evaluation predictions. I elaborate on these in the General Discussion.

Contrary to predictions, there were no effects of the relatedness manipulation on helping under external threat (i.e., when one's country is at war), or sharing in a dictator game. Methodologically, one possibility is that the effects of the manipulation decayed rapidly, and were no longer exerting psychological effects after the first set of measures (helping under life-or-death/everyday situations). This possibility seems particularly plausible given that the two measures most affected by the manipulation followed immediately either the article manipulation or the booster manipulation. Also, although sharing on the dictator game involved actual money and is thus presumably more reflective of true behaviors (relative to hypothetical decisions), the individuals who participants presumed they would be sharing with are not clearly in need. And the general prediction with respect to relatedness' effects on helping behavior is that they are most likely to emerge when inclusive fitness consequences are high.

Finally, a general issue is that the predictions so far have focused on how higher levels of relatedness engage greater prosocial behavior. Yet there is the possibility of the opposite occurring. As mentioned in the introductory review of behavioral ecological work, individuals do not always act more prosocially toward kin. For example, highly related others may also be competitors to the extent that similar individuals draw upon similar types of resources. I elaborate on this in the General Discussion.

CHAPTER 4

STUDY 2: RELATEDNESS AND ALLOPARENTING

In the second study, I examine the last focal hypothesis: that individuals in ecologies of higher relatedness will be more likely to engage in alloparenting. However, this effect should hold only, or be strongest, for individuals who are less able to reproduce themselves, or who are not yet in the life stage when they would be doing so. As outlined before, such individuals may be men who expect to have low success in finding a mate (men with low desirability as a mate) or men not currently in a reproductive life stage (men without children).

To test these hypotheses, I use similar procedures as Study 1. Participants read either the low or high ecological relatedness manipulation article, and then completed measures of alloparenting tendencies. Finally, they also completed other individual difference measures used to test the specific hypotheses mentioned above.

Method

Participants. Two-hundred and fifty-two participants (128 women) were recruited from Amazon's Mechanical Turk and compensated $0.50. The mean age of these participants was 35.1 years (SD = 12.1).

Procedure. The general procedures of Study 2 were similar to that of Study 1. Participants were randomly assigned to either the high or low ecological relatedness conditions, and read the same articles as described in Study 1. After reading the newspaper article, participants then completed a measure of alloparenting behavior.

Alloparenting Measure. Participants first read a brief description of the Big Brothers Big Sisters of America Program (Appendix F)—a volunteer program dedicated

to finding adult mentors for children between 6 and 18 years of age who come from disadvantaged backgrounds. After reading the program description, participants were asked how much time they would be willing to spend with a child from the program every month, ranging from 0 to 20 or more hours, in 1 hour increments. In addition, they also reported how much money they would be willing to donate to Big Brothers Big Sisters, on a scale from $0 to $100 or more.

Following this, participants also responded to two items that asked how many hours per week (from 0 to 10) they would be willing to spend (a) coaching children's sports teams, and (b) tutoring others' children in reading, writing and arithmetic. The two items (r = .48) were combined to form a composite time investment score.

Mate value. After completing the alloparenting measures, participants then filled out a self-perceived mate value scale (Landolt, Lalumiere & Quinsey, 1995)—a measure of participant's self-perceived mating success. The purpose of the scale is to test the hypothesis that males with lower desirability as a mate would be most likely to engage in alloparenting under high ecological relatedness. A sample item on the scale is "Members of the opposite sex that I like, tend to like me back." (1 = *Strongly Disagree*, 7 = *Strongly Agree*).

Current number of children. At the end of the study, along with other demographic items, participants were asked how many children they currently have. Again, this was to test the prediction that males without children would be most likely to engage in alloparenting under high ecological relatedness.

Results and Discussion

I predicted that individuals will be more likely to engage in alloparenting behavior under a high relatedness condition, but that this will be especially likely for (a) men who have not yet reproduced themselves or (b) who are unlikely to do so (men with a low mate value).

To examine the first prediction, I carried out a 2 (Participant Sex) X 2 (Relatedness Condition: High/Low Ecological Relatedness) X 2 (Reproductive Status: No children/Has children) ANOVAs on the alloparenting measures. For volunteered time for the Big Brother program, contrary to predictions, there were no significant effects (Fs < .96, ps > .32). There were also no significant effects for donation amount (all Fs < 1.98, ps > .16), with the exception of a main effect of reproductive status—individuals with children were willing to donate more than those without children, $F(1, 243) = 7.47$, $p = .007$. Finally, there were no significant effects for the volunteer coaching/tutoring composite (all Fs < 1.24, ps > .26).

To test the second prediction that men with lower mate value would engage in greater alloparenting under high relatedness conditions, I carried out a series of multiple regressions with participant sex, Relatedness Condition, mate value, and the interactions of the three as predictors, with the same three alloparenting measures as dependent variables. Again, there were no significant effects of any of the predictors on all three alloparenting measures (all Fs < 1.62, ps > .10).

In summary, the focal hypotheses were not supported. The relatedness manipulation did not have any effect on alloparenting behavior as measured in the current study. I discuss potential reasons and implications in the General Discussion.

CHAPTER 5

GENERAL DISCUSSION

In one preliminary study and two focal studies, I examined the effects of ecological relatedness on a variety of behaviors, using both correlational and experimental methods. The premise underlying the current work is that individual behaviors vary in how biologically adaptive they are depending on the degree to which others around are genetically related. The argument therefore is that individuals should have evolved to be sensitive to ecological relatedness, and to adjust their behaviors depending on what would be more adaptive in their specific environment. This draws upon the general notion of adaptive phenotypic plasticity in behavioral ecology.

First, examining ecological relatedness at a broad scale using nation level cousin marriages as a proxy, I find that higher ecological relatedness is associated with greater willingness to fight for one's country, more trust towards one's neighbors, and greater connectedness to one's community (but not towards foreigners). These findings track what I expected from the existing literature on kin psychology: individuals act in more prosocial ways towards, and are more trusting of, kin.

The findings from the two experimental studies were less clear. Experimentally manipulated ecological relatedness did not influence group helping under external threat, sharing on a dictator game, evaluations of prosocial and antisocial others, or alloparenting behavior. Individuals led to perceive higher ecological relatedness did, however, become more sensitive towards need in potential helping situations. Specifically, people reported that they were more likely to help a person in a life-or-death situation (someone trapped in a burning building) than a person in a more everyday situation (someone with a broken

down car), but this difference was larger for individuals in a high (relative to low) ecological relatedness condition.

There are several potential reasons for the current findings. Below, I first discuss specific methodological considerations of the current work.

Methodological Considerations

In the preliminary study, I examined the relationship between ecological relatedness, using nation level cousin marriages as a crude proxy, and a variety of psychological measures. It is important to reiterate that I am *not* proposing that the relatedness of the entire nation is what is influencing individual level psychology. Instead, the use of such a proxy is simply due to a lack of equivalent data across societies at a smaller, more psychologically proximate level (e.g., relatedness of the people that an individual interacts with in everyday life). Prevalence of cousin marriages at the nation level is presumably associated with relatedness at smaller, more psychologically proximate, geographical scales. To the extent that this association is imperfect, this would have worked against the ability to detect the predicted effects of relatedness. Another limitation of correlational analyses is the inability to draw causal inferences. Nonetheless, it is worth noting that the data on cousin marriages temporally precede that of the psychological measures—the former were gathered from individual studies across time beginning from the 1950s and the latter were from surveys conducted in 2010 onwards. Future work might seek to test the hypotheses using potential measures at a smaller geographic scale. In addition, if sufficient data across time are available, it would be particularly informative to examine psychological changes across time as they might relate to changes in ecological relatedness.

Focal Studies 1 and 2 attempted to examine the effects of ecological relatedness using experimental methods. With the exception of the potential effects on sensitivity towards need in helping situations, experimental manipulations of ecological relatedness did not seem to exert any psychological effect. One possibility is simply that the current experimental manipulation had extremely short-term effects. This seems likely given that the two measures affected by the manipulation were the two measures presented to participants immediately after the manipulation or booster.

In addition, there may have been specific issues with the dependent measures. For example, for sharing in the dictator game, the effects of relatedness may not have emerged because game partners were not necessarily perceived to be individuals in need (the general prediction is that relatedness should most affect behaviors when there are strong inclusive fitness implications).

Moreover, for social evaluations of the prosocial and antisocial hypothetical individuals, an unexpected effect emerged: Individuals in the high ecological relatedness condition evaluated both the prosocial and antisocial individuals as less desirable social partners. Given that this effect was not consistent across the social evaluation measures, no clear conclusions can be drawn. It is useful to note, though, that the current methods manipulated the hypothetical prosocial/antisocial target individuals by presenting differential ratings on a personality survey capturing a variety of antisocial behaviors (e.g., willingness to deceive and manipulate others). It is possible, then, that the "prosocial" individual, even with the presented lower self-ratings on such items, was not evaluated as prosocial, per se, but simply as *less* antisocial than the "antisocial" individual. If participants had indeed perceived the "prosocial" target as less antisocial, it

is not surprising that the "prosocial" target was also evaluated more negatively in a high ecological relatedness condition (indeed this is what was predicted). Future work could seek to distinguish between the two by having perceivers evaluate individuals described as engaging in clearly prosocial versus antisocial behaviors.

Genetic versus Psychological Cues of Relatedness

As discussed in the Introduction, individuals are not born knowing who their genetic relatives are. Instead, we have evolved to make inferences based on cues that have ancestrally been reliable indicators of kinship. Such cues include co-residence, especially during developmental life stages, and phenotypic similarity. It may not be surprising, then, that abstract information about actual genetic relatedness (the current experimental manipulation), a modern scientific concept, fails to exert the same effects that would be expected from a manipulation of information that would be more ancestrally valid (e.g., putting individuals in an ecology where others look physically very similar to themselves). Indeed, psychological cues of relatedness, and not actual genetic relatedness, should be the fundamental factor influencing kinship inferences. This is captured in the Israeli kibbutzim example, where genetically unrelated opposite-sex individuals raised together as children end up with sexual aversions towards one another (e.g., Lieberman & Lobel, 2012), similar to what would be observed between actual genetic kin. That my preliminary study finds the predicted relationships between ecological relatedness and the various psychological measures may be a result of the relatedness proxy capturing psychological cues of relatedness more strongly than the experimental manipulation in Studies 1 and 2. For example, countries with high frequencies of cousin marriages may also generally be ecologies in which individuals

look more phenotypically similar to one another (due to shared genes), a relatedness cue not contained in a newspaper article that talks about scientific genetic relatedness.

This has interesting implications for thinking about the role of relatedness in human social behavior. Work in hunter-gatherer groups finds that group-level genetic relatedness is extremely low (mean coefficient of relatedness *r* between adults in a band is only about .05; Hill et al., 2011). It is unlikely, therefore, that inclusive fitness benefits can account for the existence of widespread cooperation in hunter-gatherer bands. One possibility, though, is that psychological cues of relatedness (which is what an evolved psychology should utilize) do not always map on to actual genetic relatedness, as in the example of the Kibbutzim highlighted above. Indeed, the social structures of groups may create conditions that lead to psychological inferences of higher degrees of genetic relatedness than there actually are (e.g., coresidence with unrelated individuals, cultural practices that exaggerate phenotypic similarities between individuals). Future work would benefit from considering both actual genetic relatedness and the psychological cues of relatedness together, examining their independent and interactive effects. In addition, a better experimental manipulation of ecological relatedness might utilize more psychological cues of relatedness (e.g., being presented with an array of faces that are phenotypically similar versus dissimilar to oneself).

Mechanisms and the Limits of Plasticity

I have made general predictions about how ecological relatedness influences a variety of behaviors. Behavioral ecology has traditionally relied on what is referred to as the *phenotypic gambit* (Nettle, Gibson, Lawson, & Sear, 2013)—making predictions about behavior without committing to specific underlying mechanisms. This does not

imply that mechanisms are unimportant. Rather, the phenotypic gambit leverages the idea that if the relevant mechanisms exist (in this case adaptive plasticity to ecological relatedness), then one should see differences at the behavioral or trait level. Evolution cannot select for something that is not, at some point in an organism's life, expressed externally. The phenotypic gambit is therefore a tool that allows one to begin scientific inquiry where one might most likely uncover meaningful differences.

Assuming individuals are indeed sensitive to ecological relatedness, what processes might underlie this? One possibility is that a summary judgment is made by aggregating across individual cues of relatedness (e.g., coresidence, phenotypic similarity with each individual in one's group) in one's immediate social ecology. A critical question here is whether such a summary judgment is stored in the mind and retrieved when necessary, or if summary judgments are made "on-the-fly" depending on the immediate context (e.g., other individuals one is currently interacting with). Given that human groups consist of both kin and non-kin, and group compositions can vary considerably depending on the specific social activity, the latter mechanism (situation-specific relatedness evaluations) may be more likely. Indeed, this might be one explanation for the lack of experimental effects in the current work, as my manipulations attempted to alter a general summary judgment stored in the mind rather than alter a situation-specific evaluation.

I must also acknowledge the limits of plasticity. So far, adaptive shifts in prosocial and alloparenting behavior have been conceptualized as potential examples of phenotypic plasticity—in this case, a plasticity that reacts to variations in ecological

relatedness. However, what is the time scale along which such shifts may occur? In other words, how plastic is plasticity?

At one end, one might see indefinite flexibility. Here, organisms react instantly to immediate changes in their ecology, altering their phenotype to maximize reproductive fitness in the new ecology. On the other end, one might see strong canalization—phenotypes are irreversibly set early in life depending on developmental experiences. For example, adult male Pacific salmon can adopt either a hooknose or jack form (Gross, 1991). Hooknoses take longer to mature, but are physically larger in size than jacks (hence better able to compete in direct fights for mates). The two forms also differ in other distinct morphological ways. Whether individual salmon develop a hooknose or jack form depends on various ecological factors (e.g., higher predation pressures lead to more jacks, given the risks of adopting the slow maturing hooknose strategy). Importantly here, becoming either a hooknose or jack is an irreversible process.

Indefinite flexibility is generally not expected, especially when there are substantial costs to plasticity (see DeWitt, Sih, & Wilson, 1998, for a review). For instance, plasticity requires additional energy invested in maintaining sensory mechanisms for gathering ecological information. Ecological information can also be imprecise, leading to phenotypic changes that are maladaptive. Although an important question, current understanding about the costs of plasticity remains in its early stages (Pigliucci, 2005).

One might consider the degree of flexibility expected in the current domain of interest—assessments of relatedness. In the kin detection literature, there have been mixed findings for the existence of a critical developmental period (e.g., Fessler &

Navarette, 2004; Lieberman, Tooby & Cosmides, 2003; Walter & Buyske, 2003; Wolf, 1995), much less accurate estimates of such a critical period. This is further complicated by the different cues that can be used to infer relatedness, each of which theoretically should vary in their time periods of relevance. For instance, co-residence with another individual is likely reliably associated with actual kinship early in life, but this may be less true at older ages. Hence, co-residence may not be as strong a cue of relatedness for individuals of older ages. Maternal-infant association, on the other hand, is a cue that exists precisely to aid kin inference by older individuals (as older siblings may not spend much time co-residing with younger siblings).

The degree of flexibility for assessments of ecological relatedness is therefore an open question. At one extreme, one might be able to influence immediate prosocial and alloparenting behavior by altering an individual's in-the-moment perceptions of ecological relatedness (as presumed by the current experiments). However, if there is strict canalization, an individual's developmental ecological conditions may set a certain degree of prosociality and alloparenting that is relatively inflexible. Of course, it might also be a combination of the two. For example, developmental ecologies may shape an individual's baseline level of prosocial behavior as an adult, but the individual may also react to his or her current ecological relatedness and adjust their behaviors from their baseline accordingly.

Future work might seek to examine the processes through which individuals make judgments of ecological relatedness, the specific cues by which such judgments are made, and the relative effects of developmental and current environments.

When do Kin Care versus Compete?

The broad prediction so far has been that individuals will behave more prosocially toward related individuals, and that this prosocial behavior may be more likely to emerge under certain circumstances. This tracks the general pattern observed in the behavioral ecological literature. Yet it is also recognized that kin can pose competition. For example, although prairie dogs generally engage in less hostile behavior toward kin than non-kin, male prairie dogs do become more hostile toward male kin during breeding season (Hoogland, 1986), presumably due to intense mate competition. In addition, female prairie dogs sometimes kill infants of close kin, once again seemingly due to resource competition coupled with accessibility of these infants (relative to infants of non-kin) (Hoogland, 1985). Indeed, to the extent that highly related individuals may also have more similar preferences for food, habitats, and mates, competition between kin may be even more intense than non-kin (Waldman, 1988). One implication of this is that ecological relatedness may exhibit a curvilinear relationship with competitive behavior, with the competitiveness decreasing from low to moderate ecological relatedness, but potentially increasing again at extremely high levels of relatedness—when others in the vicinity may pose intense competition due to shared preferences. Exactly how high such levels of relatedness need to be is unclear though. One might examine individuals in families with many siblings—who thus may pose strong competition for the same kinds of resources (e.g., many siblings of the same sex as an individual might be a strong source of competition for mates). One might also examine the interaction between ecological relatedness and resource availability. Presumably, under high levels of

resource scarcity, the general prosocial effects of relatedness might be muted, or even reversed.

Conclusion

Striking psychological differences exist between human groups, and have implications for a wide range of social behaviors. I proposed that ecological relatedness—the degree to which individuals are genetically related to others in their surroundings—is one factor that underlies such psychological differences. The findings in the current research provide preliminary tests of this proposal. Greater ecological relatedness is potentially associated with specific forms of prosocial behavior, localized trust, and sensitivity towards the needs of others. Much work remains to be done, in clarifying underlying mechanisms, the limits of plasticity, and the specific conditions under which ecological relatedness would or would not lead to prosocial behavior.

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APPENDIX A

RELATEDNESS MANIPULATION ARTICLES

High Ecological Relatedness Manipulation Essay

Surprisingly, DNA survey finds that people are genetically similar to the strangers around them

By Roger Lowell, Science Editor

12:01AM GMT 20 Dec 2015

Whether you hail from Richmond, Ulan Bator or Nairobi, your genetic make-up is strikingly similar to that of people around you, a new analysis concludes.

Scientists have long recognized that, despite physical differences, most human populations are genetically similar. The new work concludes that people within a population may share many more genetic similarities with one another than previously assumed. The estimates are striking, indeed. In layman terms, according to the new study, about 1 in 4 people we encounter in our everyday lives may have a great-great-grandparent in common.

The results of the study, published today in the journal *Science*, have implications for understanding population change and human migration, said Professor Morris Feldman of Harvard University who led the team. “These new estimates of relatedness can seem surprising, especially given that we all seem to look so different from one another. But there is growing evidence suggesting that very small differences in DNA may be all that underlie the things that make us look different. At the genetic level, we are far more similar than meets the eye.”

The team analyzed DNA from 10,506 people from 65 populations in cities across five geographic world regions: Africa, Eurasia, East Asia, Oceania and the Americas. The research team examined 377 "microsatellites"—short segments of human DNA that occur in specific patterns, which are passed down generation to generation.

"Each microsatellite had between four and 32 distinct types," Professor Feldman said. "We found that, on average, about 24% of people in each city are likely to share a similar microsatellite type, much higher than what one would expect by chance. And even this may be an underestimate, as the specific microsatellites we examined are known to be more diverse in types compared to other microsatellites in the genome.”

For those of us who have lived all our lives in the same town, this may not be surprising. But how could this be possible if we have moved away from our birthplace? Interestingly, recent psychological research has found that people tend to marry and befriend those who are more genetically similar to themselves. Consciously or unconsciously, we may be drawn to places where people are genetically related to ourselves.

“Early estimates of genetic relatedness within populations were usually based on family genealogies, which are known to be notoriously inaccurate. More often than not, a relative gets missed out,” said Professor Richard Hamilton of the Human Genome Research Institute, commenting on the findings of the *Science* article. “With the rapid advancement of genetic testing, it has become much more feasible to include gene assays in human research. The reliability of such tests has also increased tremendously in recent years. So I’m not surprised at these findings. Geneticists have always been aware that individuals within a population may be a lot more highly related to each other than it seems to be. However, exactly how such high degrees of relatedness come about is unclear.”

Research suggests that people often believe they share connections with those around them. Indeed, from the perspective of our genes, the world is full of cousins.

Low Ecological Relatedness Manipulation Essay

Surprisingly, DNA survey finds that people are genetically dissimilar to those around them

By Roger Lowell, Science Editor

12:01AM GMT 20 Dec 2015

Whether you hail from Richmond, Ulan Bator or Nairobi, your genetic make-up is strikingly different from people around you, a new analysis concludes.

Scientists have long recognized that, despite physical differences, most human populations are genetically similar. However, the new work concludes that people within a population may be much more genetically different from one another than previously assumed. The estimates are striking, indeed. In layman terms, according to the new study, only about 1 in 200 people we encounter in our everyday lives may have a great-great-grandparent in common.

The results of the study, published today in the journal *Science*, have implications for understanding population change and human migration, said Professor Morris Feldman of Harvard University who led the team. “These new estimates of relatedness can seem surprising. But there is growing evidence suggesting that very large differences in DNA may nonetheless underlie physical similarities. At the genetic level, we may be far more dissimilar than meets the eye.”

The team analyzed DNA from 10,506 people from 65 populations in cities across five geographic world regions: Africa, Eurasia, East Asia, Oceania and the Americas. The research team examined 377 "microsatellites"—short segments of human DNA that occur in specific patterns, which are passed down generation to generation.

"Each microsatellite had between four and 32 distinct types," Professor Feldman said. "We found that, on average, less than 0.8% of people in each city are likely to share a similar microsatellite type, much lower than what one would expect by chance. And even this may be an overestimate, as the specific microsatellites we examined are known to be less diverse in types compared to other microsatellites in the genome.”

For those who have moved between large cities, this may not be surprising. But how could this be possible for those who still live where they were born? Interestingly, recent psychological research has found that people tend to marry and befriend those who are genetically more dissimilar to themselves. Consciously or unconsciously, we may be drawn to places where people are genetically different from ourselves.

“Early estimates of genetic relatedness within populations were usually based on family genealogies, which are known to be notoriously inaccurate. More often than not, people

who are not actual genetic relatives get included," said Professor Richard Hamilton of the Human Genome Research Institute, commenting on the findings of the *Science* article. "With the rapid advancement of genetic testing, it has become much more feasible to include gene assays in human research. The reliability of such tests has also increased tremendously in recent years. So I'm not surprised at these findings. Geneticists have always been aware that individuals within a population may be a lot less related to each other than we think. However, exactly how such low degrees of relatedness come about is unclear."

Research suggests that people often believe they share connections with those around them. However, from the perspective of our genes, the world is actually full of strangers.

APPENDIX B

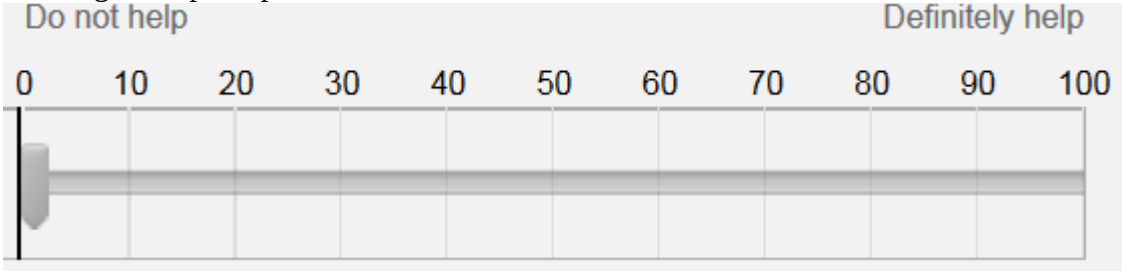
LIFE-OR-DEATH AND EVERYDAY HELPING SCENARIOS

In this next section, you will be presented with some hypothetical situations. You will then be asked about what you would do in each situation.

Life-or-death helping:
On your way back from grocery shopping, you are surprised to see smoke in the air ahead of you. As you turn the corner, you are shocked to see a building on fire. The fire appears to be small, but looks like it's beginning to spread. You vaguely hear someone in the building shouting for help.

You look around and there seems to be no one else there, and you do not hear fire sirens either. The building looks old, and you think the flames could begin to spread soon. Entering the building to help could become dangerous.

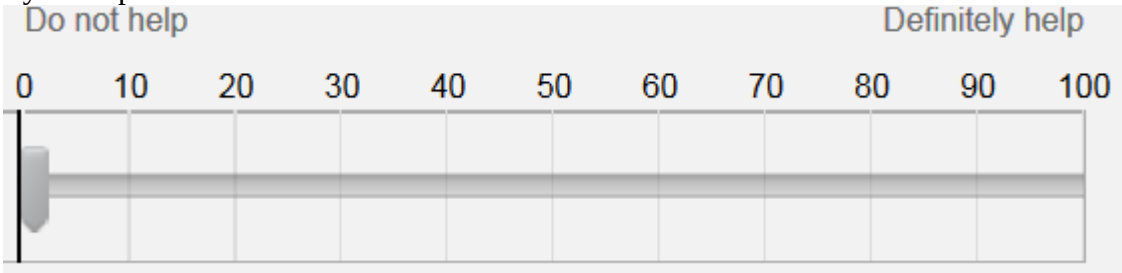
On a scale of 0% (Do not help) to 100% (Definitely help), how likely would you enter the building to help the person?



Everyday helping:
On your way to a meeting, you see a car on the side of the road. It looks like it has broken down and you glimpse a person (presumably the driver) trying to fix it. It looks like the car may have a flat tire. As you approach, the driver hears you and looks up.

You look around and there seems to be no one else there, and this road is not travelled by many people. It looks like the driver could do with some help, although it also does not look serious. If you do stop, you will be late for your meeting.

On a scale of 0% (Do not help) to 100% (Definitely help), how likely would you stop and try to help the driver?



APPENDIX C

HELPING UNDER THREAT AND WITHOUT THREAT SCENARIOS

Helping without external threat:

Imagine that, currently, the United States is not at war.
The President gives a national television address from the White House announcing that he will ask Congress to raise taxes to enhance military effectiveness and strength. He asks Americans to support his proposal—to sacrifice to aid in the nation's defense.
On the scale of 1 to 9 below, to what extent would you support the proposal to raise taxes to enhance U.S. military effectiveness?

1-Not at all	2	3	4	5	6	7	8	9-Definitely
○	○	○	○	○	○	○	○	○

Helping under external threat:

Now, instead, imagine that another country has attacked the U.S.. Given that their military strength is comparable to your own, the war will likely lead to severe casualties on both sides. From their declaration of war, you know that their military forces are unlikely to show mercy. It is not clear where they will strike first.

As before, the President gives a national television address from the White House announcing that he will ask Congress to raise taxes to enhance military effectiveness and strength. He asks Americans to support his proposal—to sacrifice to aid in the nation's defense.

On the scale of 1 to 9 below, to what extent would you support the proposal to raise taxes to enhance U.S. military effectiveness?

1-Not at all	2	3	4	5	6	7	8	9-Definitely
○	○	○	○	○	○	○	○	○

APPENDIX D

DICTATOR GAME

Dictator Game:
Pick a random number between 1 and 10. (NUMBER OPTIONS)

In this task you will be asked to make a decision which can earn you some money, **in addition to** the $0.50 you will be paid for participating in the survey.

In this task you will be partnered with another randomly chosen participant in this study. You have been randomly assigned to be the **distributor**.

You have 50 cents that you must now decide how to distribute between yourself and this other person. No participant will know who their partner was.

For example, if you choose to keep 25 cents for yourself and to give the other 25 cents to this other Turker, you will receive a bonus of $0.25 (in addition to the $0.50 you will already be getting), while the other Turker will receive the remaining $0.25.

How much money do you want to give the other person/keep for yourself?

APPENDIX E

ANTI-SOCIAL/PRO-SOCIAL TARGET PROFILES/EVALUATIONS

In this next section, you will be presented with the survey responses of two individuals. As part of a separate study, both of these individuals were asked to complete a series of personality questions. Below you will see their responses on a subset of these questions. We are interested in how people form impressions about others through profiles like this. When looking at the responses of these two individuals, try to think about what he/she is like. We will ask you some questions about your impressions later.

Individual A:

	1-Strongly DISAGREE	2	3	4	5-Strongly AGREE
I tend to exploit others towards my own end	○	○	○	◉	○
I tend to be callous or insensitive.	○	○	◉	○	○
I tend to manipulate others to get my way.	○	○	○	◉	○
I tend to not be too concerned with morality or the morality of my actions.	○	○	○	◉	○
I have used deceit or lied to get my way.	○	○	◉	○	○

Individual B:

	1-Strongly DISAGREE	2	3	4	5-Strongly AGREE
I tend to exploit others towards my own end	◉	○	○	○	○
I tend to be callous or insensitive.	○	◉	○	○	○
I tend to manipulate others to get my way.	◉	○	○	○	○
I tend to not be too concerned with morality or the morality of my actions.	○	◉	○	○	○
I have used deceit or lied to get my way.	○	◉	○	○	○

Evaluations of Individuals (Example for Individual A)

How much do you like **Individual A**?

1-Strongly Dislike	2	3	4	5	6	7	8	9-Strongly Like
○	○	○	○	○	○	○	○	○

How negative/positive do you feel about **Individual A**?

1-Extremely Negative	2	3	4	5	6	7	8	9-Extremely Positive
○	○	○	○	○	○	○	○	○

How much would you like **Individual A** as a...

	1-Strongly Dislike	2	3	4	5	6	7	8	9-Strongly Like
Neighbor	○	○	○	○	○	○	○	○	○
Friend	○	○	○	○	○	○	○	○	○
Family member	○	○	○	○	○	○	○	○	○

APPENDIX F

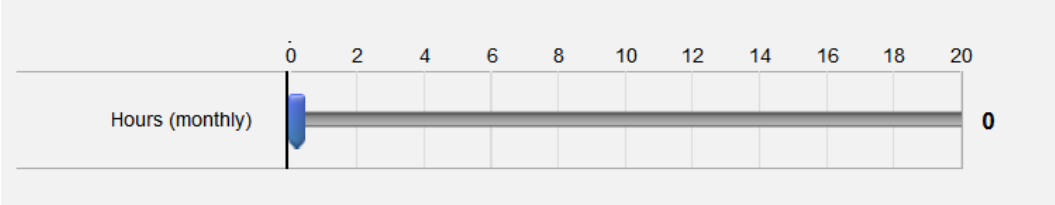
ALLOPARENTING MEASURES

Below, you will read a brief description of the *Big Brothers Big Sisters of America* Program. We are interested in your perceptions of the program and will ask you some questions about it later.



Big Brothers Big Sisters of America is the largest youth mentoring organization in the United States. The program matches adult volunteers ("Bigs") with children ("Littles") aged 6 to 18, with the goal of providing children from disadvantaged backgrounds a positive role model. The program is highly regarded and its positive impact on the Littles has been demonstrated in multiple aspects of their lives.

How much time *per month* would you be willing to volunteer as a Big Brother/Big Sister?



APPENDIX G

MATE VALUE SCALE

I receive sexual invitations from members of the opposite sex.

Disagree Agree

Members of the opposite sex are attracted to me.

Disagree Agree

Members of the opposite sex are not very attracted to me.

Disagree Agree

Members of the opposite sex notice me.

Disagree Agree

APPENDIX H

DEMOGRAPHIC MEASURES

What is your gender?

_____ Male _____ Female

What is your age?

_____ years old

Where were you born?

_____

What is your race or ethnicity? (check all that apply)

_____ African-American
_____ Latino/Latina/Hispanic
_____ Middle Eastern
_____ Other
_____ Asian/Asian-American
_____ Native American
_____ European-American/White

What is your current relationship status? (check one option)

_____ Single and not currently dating
_____ Single and currently dating
_____ In a committed relationship
_____ Married
_____ Divorced/Widowed

How many children do you currently have? (check one option)

_____ None
_____ 1
_____ 2
_____ 3
_____ 4 or more