

Original Article

Human Kin Investment as a Function of Genetic Relatedness and Lineage

Gregory D. Webster, Department of Psychology, Campus Box 345, University of Colorado, Boulder, Colorado 80309-0345, USA. Email: gwebster@psych.colorado.edu.

Abstract: Two independent samples of students were asked to allocate fictional lotteries of varying dollar amounts to their blood relatives. In both studies, a reliable genetic relatedness by lineage interaction emerged, such that the genetic effect was a more positive predictor of percent of money allocated for relatives of a direct lineage (e.g., parents, grandparents) than it was for peripheral relatives (e.g., siblings, aunts and uncles). In a third study, this interaction was replicated in an archival analysis of wills. The implications of accounting for differences in relatives' lineages in studies of kin investment are discussed.

Keywords: Altruism; Genetic relatedness; Inclusive fitness; Kin investment; Lineage; Multilevel modeling; Prosocial behavior; Resource allocation

Introduction

By analyzing the inheritance patterns of 1,000 British Columbian wills, Smith, Kish, and Crawford (1987) found that deceased benefactors allocated the greatest percentage of their estates to their closest genetic relatives, a lesser percentage to their relatives of lesser genetic relatedness, and gave the least to non-kin and organizations. This pattern of resource allocation is what would be expected given Hamilton's (1964) inclusive fitness theory. In a similar study, Judge and Hrdy (1992) examined over 1,500 inheritances from Sacramento, California over the course of a century (1890-1984). They found the same basic pattern predicted Hamilton (1964) and demonstrated by Smith et al. (1987): On average, benefactors gave a greater percentage of their estates to kin of closer genetic relatedness than more distantly related kin and non-kin.

According to inclusive fitness theory, factors such as genetic relatedness and differential fertility (which is related to sex and age) should explain the majority of variation in inheritances within families (Hamilton, 1964; Judge and Hrdy, 1992;

Smith et al., 1987). However, genetic relatives can be further divided into two distinct categories based on whether or not they share a direct lineage to the benefactor or target individual. Relatives of a *direct lineage* are those who are direct descendants or progenitors of the target individual (e.g., grandparents, parents, children, grandchildren), whereas *peripheral* relatives refer to those who are genetically related to the target, but are neither direct descendants nor progenitors of the target (e.g., siblings, aunts/uncles, nieces/nephews, cousins).

Although inclusive fitness theory would predict that resources would be allocated equally among kin of the same genetic relatedness, sex, and age, previous investigations of wills (e.g., Smith et al., 1987) suggest that the genetic relatedness effect is stronger among relatives of direct lineage than it is for peripheral relatives (see Figure 1). Although Smith et al. (1987) did not consider lineage differences as an independent variable, the pattern of estate allocations observed in their archival analysis of wills is suggestive of a substantial genetic relatedness by lineage interaction. Why should the genetic relatedness effect be stronger for direct lineages than it is for peripheral lineages? There are at least four possible explanations.

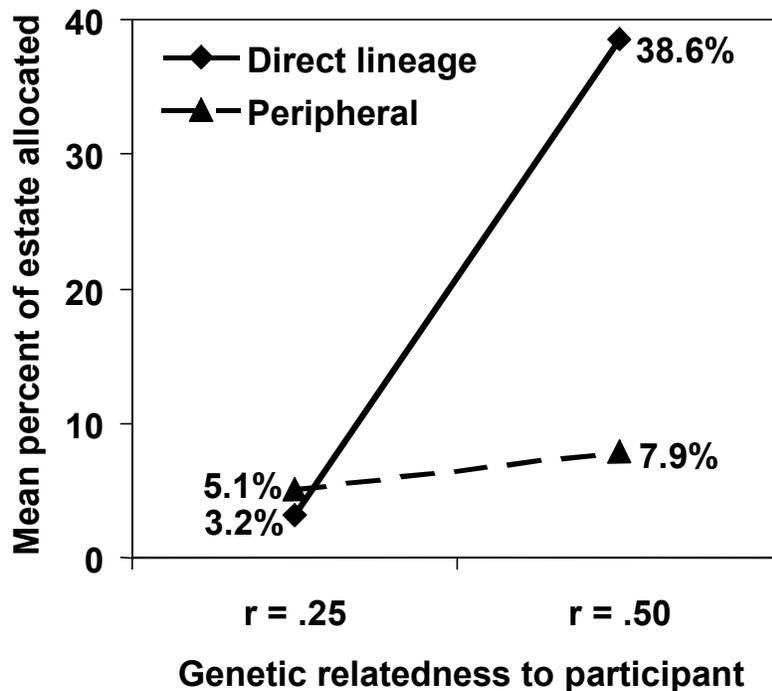


Figure 1: Mean percentages of estates allocated to relatives as a function of genetic relatedness and lineage in archival analyses of wills. Adapted from Smith, Kish, and Crawford (1987) with permission from Elsevier Science.

First, age differences, which were not statistically controlled in Smith et al.'s data, could be driving the interaction, since relatives of equal genetic relatedness—but different lineages—typically differ in age (e.g., daughters vs. sisters, granddaughters vs. nieces). Since age is inversely related to fertility, age differences could partially account for the pattern of means in Figure 1.

Second, there are strong cultural and historical norms that may influence people's inheritance decisions. Although there is substantial amount of variability in inheritances of titles and property within and between cultures over time (Cooper, 1976; Goody, 1983; Le Roy Ladurie, 1976; Radcliffe-Brown, 1950), in many modern Western cultures, people tend to will a larger percentage of their estates to their direct descendants than to their peripheral relatives.

Third, it is possible that favoritism toward relatives of direct lineage results from differences in bonding and competition early in development. For example, perhaps the parent-child and child-parent patterns of attachment are stronger than sibling-sibling attachment patterns (Bowlby, 1969). It is also possible that parent-offspring conflict is more subdued than sibling-sibling conflict when children compete for limited resources (Trivers, 1974).

Fourth, the genetic relatedness by lineage interaction may be associated with individuals' perceptions of relatedness uncertainty. For example, the certainty that a child is one's own may be greater than the certainty that one's sibling is a full or half sibling (particularly among females who are can be certain that their child is their own). For instance, equating relatives on age and sex, it would be more conservative for a woman to invest in two of her children than it would be to invest in her two siblings, given that she cannot be entirely certain if her siblings are full or half siblings, due to paternal uncertainty. Given this fact, over evolutionary time, a resource sharing preference that favored relatives of direct lineage could be beneficial in the context of an individual's inclusive fitness.

Overview of the Present Studies

The purpose of the present studies was to assess the strength of the genetic relatedness by lineage interaction using a survey method (Study 1), to replicate this effect in a subsequent survey study (Study 2), and to observe this effect in actual inheritances (Study 3). In Studies 1 and 2, college students were asked to allocate various fictional lotteries to as many genetic relatives as they wished. In Study 3, the inheritance patterns in a sample of archived wills were analyzed, taking into account differences in lineage between benefactors and their beneficiaries. Across all studies, it was predicted that the effect relatives' genetic relatedness on resource allocations would depend on relatives' lineage to the target individual, such that the genetic relatedness effect would be more positive for relatives of direct lineage to the target than it would be for peripheral relatives.

Study 1: Exploration

Method

Participants. Participants were 133 students (57% males) enrolled in an introductory psychology course at a southern state university and received course credit in return for their participation. This sample originally consisted of 147 students. The 14 excluded participants were nine who failed to list the ages of any of their relatives, four who allocated their entire lotteries to a single relative, and one who indicated that he or she was adopted.

Materials and Procedure. Participants were instructed to allocate a fictional lottery prize of varying dollar amounts to their blood relatives. Each participant was randomly assigned one of three lottery amounts to allocate: US\$10,000, US\$100,000, or US\$1,000,000. Participants were instructed to imagine that they had won one of the three lottery amounts, but that only their blood relatives would be allowed to keep the prize money. Thus, participants were asked to allocate the entire lottery to as many (or as few) relatives as they saw fit, and were allowed to allocate any amount they desired to each relative, so long as the entire lottery was allocated across the set of relatives they chose to list. Participants were asked specifically to list blood relatives (i.e., no step-parents or in-laws). The back side of the instructions served as the response sheet, where participants were asked to list each relative's (a) specific relation to them (e.g., "father's sister" instead of "aunt,"), (b) sex (if not obvious), (c) age in years (or approximate age if unknown), (d) allocated lottery amount in dollars. Following these procedures, students were debriefed on the purpose of the research and thanked for their participation.

Data Analysis. Preliminary analyses within each of the present three studies revealed evidence of neither a sex-of-relative difference in allocations nor a sex-of-participant difference in any of the effects of interest ($ps > .06$). In other words, participant sex moderated neither the main effects of genetic relatedness or lineage, nor their interaction. Thus, all subsequent analyses were run collapsing across male and female relatives and participants.

The data obtained from all three studies yielded a hierarchically nested data structure, with relatives nested within families. Whereas previous studies have ignored problems with statistical dependency in using relatives as the sole unit of analysis (e.g., Smith et al., 1987), the present data were modeled using a more appropriate mixed model in the form of a multilevel random coefficient model (MRCM) in the context of the program Hierarchical Linear Modeling (HLM, Version 5; Raudenbush, Bryk, Cheong, and Congdon, 2000). This procedure involved performing within-participant regressions and then modeling the resulting within-participant regression coefficients as a function of between-participant variables. In MRCM terms, this involved modeling within-participant (or within-family) variance at *Level 1* and between-participant (or between-family) variance at *Level 2* (see Raudenbush and Bryk, 2002).

For the present data, within-participant regression coefficients were estimated predicting percent of money allocated from each relative's genetic relatedness, lineage, and their interaction, controlling for relative's age. Thus, the design of the within-person model was the regression analog of a 2 (genetic relatedness: $r = .25$ vs. $r = .50$) \times 2 (lineage: direct vs. peripheral) analysis of covariance (ANCOVA), with relative's age in years (mean-deviated at the within-person level) as a covariate:

$$\text{PERCENT}_{ij} = \beta_{0j} + \beta_{1j}(\text{AGE})_{ij} + \beta_{2j}(\text{RELATEDNESS})_{ij} + \beta_{3j}(\text{LINEAGE})_{ij} + \beta_{4j}(\text{RELATEDNESS} \times \text{LINEAGE})_{ij} + r_{ij}.$$

In this model, PERCENT_{ij} represents the percent of the lottery money allocated by participant j to relative i and β_{0j} is the random coefficient representing the mean Percent for family j across i relatives for which the participant listed. The coefficients β_{1j} through β_{4j} represent within-person slopes (or difference scores). The variance of r_{ij} is the within-person error variance.

Multilevel models allow for regression coefficients from one level of analysis (Level 1) to be modeled at another level (Level 2). For these data, this meant that the within-participant (or within-family) relationships were modeled as functions of between-participant (or between-family) variables. At level 2, the resulting within-participant regression coefficients from Level 1 were modeled as a function of between-participant differences in lottery amount (or estate amounts in Study 3). Thus, for Study 1, the Level-2 design for the between-participant model was the regression analog of a one-way analysis of variance (ANOVA), which compared the two polynomial effects codes for the three lottery amounts:

$$\begin{aligned} \beta_{0j} &= \gamma_{00} + \gamma_{01}(\text{LINEAR LOTTERY})_j + \gamma_{02}(\text{QUADRATIC LOTTERY})_j + u_{0j} \\ \beta_{1j} &= \gamma_{10} + \gamma_{11}(\text{LINEAR LOTTERY})_j + \gamma_{12}(\text{QUADRATIC LOTTERY})_j + u_{1j} \\ \beta_{2j} &= \gamma_{20} + \gamma_{21}(\text{LINEAR LOTTERY})_j + \gamma_{22}(\text{QUADRATIC LOTTERY})_j + u_{2j} \\ \beta_{3j} &= \gamma_{30} + \gamma_{31}(\text{LINEAR LOTTERY})_j + \gamma_{32}(\text{QUADRATIC LOTTERY})_j + u_{3j} \\ \beta_{4j} &= \gamma_{40} + \gamma_{41}(\text{LINEAR LOTTERY})_j + \gamma_{42}(\text{QUADRATIC LOTTERY})_j + u_{4j}. \end{aligned}$$

In the between-family model, β_{0j} and β_{1j} through β_{4j} represent the within-person intercepts and slopes, respectively. The γ_{0s} represent the means of their respective within-person regression coefficients, controlling for the aforementioned between-person effects. These are the effects that are of particular interest in the present research. For example, the strength of the γ_{40} coefficient addresses the central question, "Does the effect of genetic relatedness on lottery allocations depend on differences in relatives' lineage on average across families, controlling for age differences between relatives and controlling differences in lottery amount between participants?" Lastly, the u_{js} represent the errors of their respective β_{js} , and their variances are the family-level error variances.

Results and Discussion

The effect of genetic relatedness was a strong and reliable predictor of percent of money allocated, with first-order relatives receiving substantially more of the lottery than second-order relatives (see Table 1, left columns, for regression statistics). Lineage was also a strong predictor, with direct lineage relatives receiving a greater share of the lottery than peripheral relatives. However, these main effects were qualified by a reliable relatedness by lineage interaction, such that the genetic relatedness effect on percent of money allocated was stronger and more positive among relatives of direct lineage than it was among peripheral relatives (see Figure 2). Note that the predicted mean percentages of resources allocated in the figures do not sum to 100%. This is because (a) allocations made to distal relatives (e.g., $r = .125$) were excluded from analyses because there was no lineage variation (i.e., none were of direct lineage) and (b) the mean percentages represent within-family means that were subsequently averaged across families. Simple effects within the context of this interaction revealed that the genetic relatedness slopes within relatives of direct lineage and within peripheral relatives were each significantly greater than zero ($ps < .01$). Lastly, none of the within-participant slopes were moderated by the between-participant lottery differences ($ps > .10$).

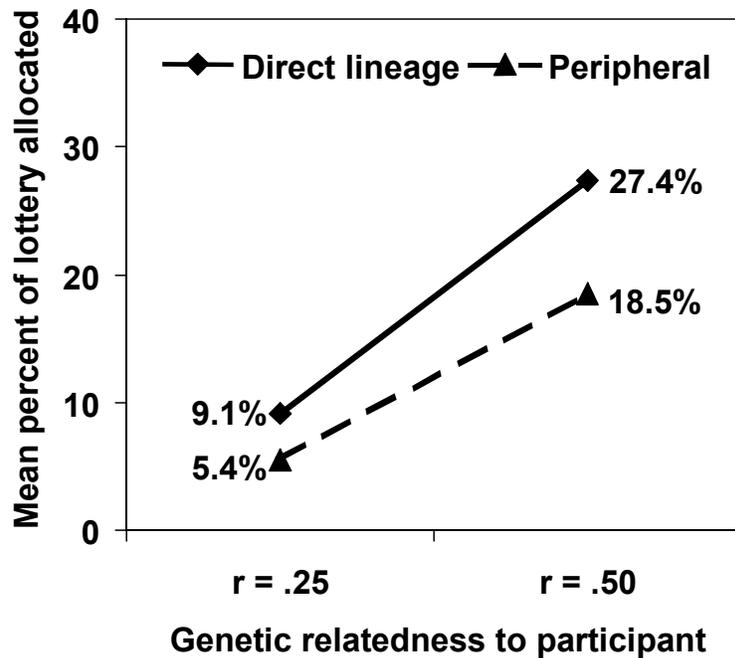


Figure 2: Predicted mean percentages of money allocated to relatives within families for Study 1 as a function of genetic relatedness, lineage, controlling for relatives’ ages and lottery differences.

These results supported the main hypotheses: The relatedness effect was stronger for relatives of direct lineage than it was for peripheral relatives, even when age of relative (which is related to reproductive potential) was statistically held constant. The pattern of means observed in the present study was similar to the pattern reported in previous archival analyses of inheritances (e.g., Smith et al., 1987). This result suggested that the resource sharing patterns reported by younger students were similar to the inheritances specified by older adults in their wills.

Table 1

Percent of Money Allocated to Relatives within Families as a Function of Their Age, Genetic Relatedness, and Lineage, Controlling for Amount of Available Money

	Study 1 (N=133)		Study 2 (N=28)		Study 3 (N=74)	
	Coef.	<i>t</i>	Coef.	<i>t</i>	Coef.	<i>t</i>
Intercept	15.09	35.05**	14.06	10.99**	30.32	4.96**
Age ^a	-0.00	-0.07	0.12	1.31	1.28	0.28
Genetic Relatedness	7.85	9.02**	5.38	4.23**	-1.12	-0.17
Direct Lineage	3.14	3.03**	3.44	1.96*	7.34	1.22
Relatedness x Lineage	1.32	2.15*	6.81	2.02*	10.28	2.37*

^aIn Studies 1 and 2, Age was age in years of relative. In Study 3, Age was generation of relative.

* $p \leq .05$. ** $p \leq .01$.

Study 2: Replication

Although the results of Study 1 clearly supported the hypothesis, the findings were unique in that the effect of lineage and its interaction with genetic relatedness had heretofore never been assessed in an empirical study of within-family resource allocation. To see if these effects were replicable, a second study was conducted using an independent sample of students at a different university. Furthermore, if these effects were as robust as Study 1 had suggested, they should be replicable in a small sample.

Method

Participants. Participants were 28 students (39% males) enrolled in an upper-level psychology course at a western state university and received no compensation for their participation. This sample originally consisted of 35 students. The three excluded participants were two who indicated that they were adopted and one whose regression residual constituted a statistical outlier relative to the rest of the sample.

Materials and Procedure. The procedure and materials used in Study 2 were identical to those used in Study 1, but with one exception: Only two fictional lottery amounts were randomly assigned to participants: US\$10,000 and US\$100,000.

Data Analysis. The model employed in Study 2 was identical to that employed in Study 1, but with one exception: Only a single contrast-coded variable was necessary to model differences in lottery amounts, as this variable had only two levels in Study 2, whereas this variable had an additional level in Study 1 (i.e., US\$1,000,000).

Results and Discussion

The results of Study 2 replicated those of Study 1 (see Table 1, middle columns). Once again, first-order relatives received a greater share of the lottery than second-order relatives. Replicating the lineage effect, relatives of direct lineage to the target were allotted greater amounts of money than peripheral relatives. Moreover, the relatedness by lineage interaction was replicated in the same direction as Study 1, with the genetic relatedness effect being a stronger and more positive predictor among relatives of direct lineage than it was among peripheral relatives (see Figure 3). Simple effects in the context of this interaction revealed that the genetic relatedness slope was significantly different from zero for direct lineage relatives ($p < .01$), but not for peripheral relatives ($p > .50$). None of the within-participant effects were reliably moderated by between-participant differences in lottery amounts ($ps > .05$).

Study 3: Application

Although Studies 1 and 2 demonstrated the moderating effect of lineage differences on the relationship between genetic relatedness and lottery allocation within families, they lacked ecological validity. Specifically, it was not clear whether younger students allocating fictional prize money accurately reflected how older people might actually distribute their estates in wills. To this end, an archival analysis of probated wills was undertaken to support the findings of Studies 1 and 2, and to replicate the patterns of means found in previous archival research (e.g., Smith et al. 1987).

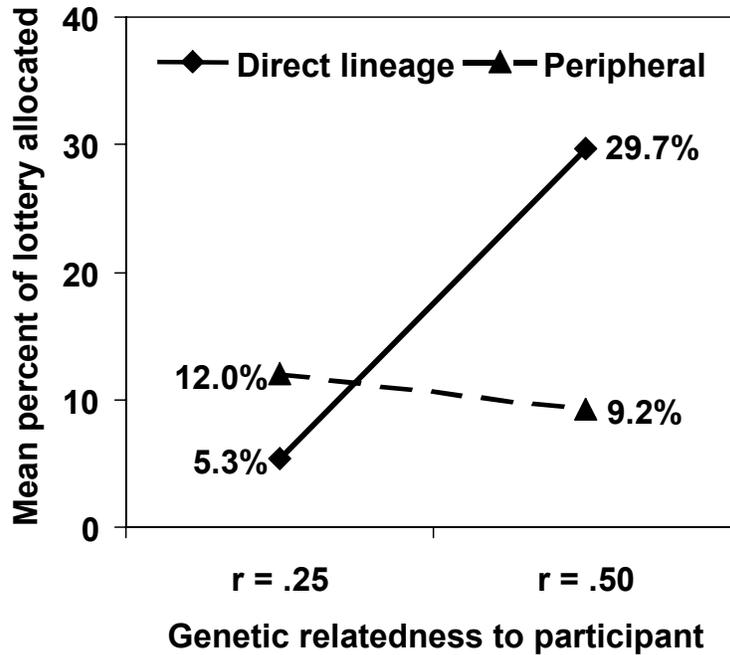


Figure 3: Predicted mean percentages of money allocated to relatives within families for Study 2 as a function of genetic relatedness, lineage, controlling for relatives' ages and lottery differences.

Method

Sample and Procedure. The analyzed sample consisted of the wills of 74 people (62% males) probated in British Columbia in 1954. This sample originally consisted of 191 records. The 117 excluded cases were 67 persons who died intestate, 39 who listed no blood relatives, six whose estates amounted to less than Can\$1, four whose estates were not quantifiable into dollar amounts, and one whose estate exceeded Can\$200,000 (a positive outlier in this sample). The year 1954 was chosen by randomly selecting two adjacent microfilm rolls from a randomly selected file cabinet. Wills were obtained from the British Columbia Archives in Victoria and selected by the order in which they were probated on two microfilm rolls. This population and sampling method were similar to those used by Smith et al. (1987). The median estate was valued at Can\$7,321 (the range was 497 to 89,773). Due to the extreme positive skew of the distribution of estate amounts, and to make these amounts comparable to those of Studies 1 and 2, a \log_{10} transformation was performed. The mean log-transformed estate value was 3.92 ($SD = 0.53$).

Data Analysis. A MRCM was employed, with related beneficiaries nested within families (or target individuals). The Level-1 model was identical to those

presented in Studies 1 and 2, with one exception: Because the actual ages of relatives were not available, ages were estimated by determining what generation the relatives were relative to the target. For example, a mother, sister, daughter, and granddaughter were considered first, second, third, and fourth generation, respectively. These generational distinctions were given a linear coding to reflect categorical age differences (i.e., 3, 1, -1, and -3, respectively). At level 2, log estate amounts were entered as a predictor of the resulting within-family (Level 1) regression coefficients.

Results and Discussion

Neither a reliable genetic relatedness difference nor a lineage difference was detected in these data (see Table 1, right columns). However, a reliable genetic relatedness by lineage interaction did emerge (see Figure 4).

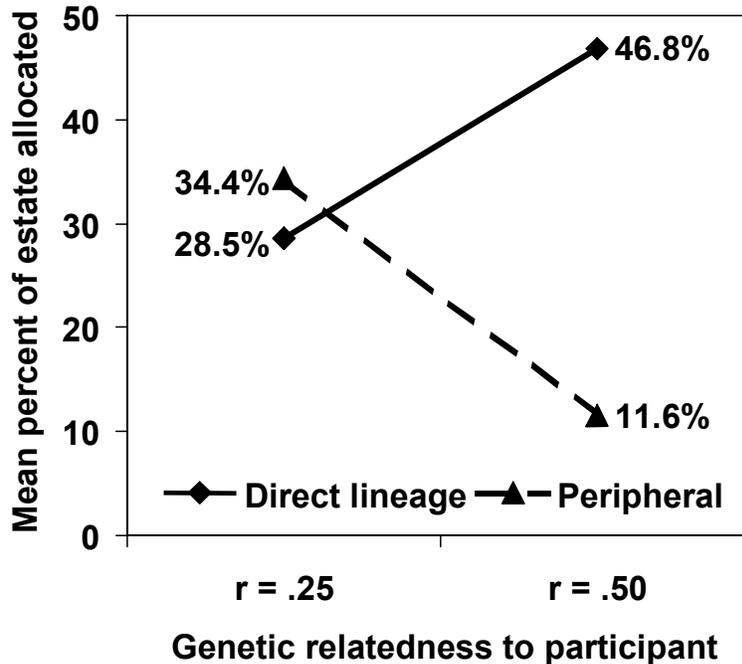


Figure 4: Predicted mean percentages of estates allocated to relatives within families as a function of genetic relatedness, lineage, controlling for relatives' generational ages and estate amount differences.

This interaction was in the same direction as Studies 1 and 2 and in the direction suggested—but not tested—by previous researchers (e.g., Smith et al. 1987). Tests of simple effects in the context of this interaction indicated that neither the positive genetic relatedness slope within relatives of direct lineage ($p = .15$) nor

the negative genetic relatedness slope within peripheral relatives ($p = .29$) differed significantly from zero. None of the within-family effects were moderated by between-person differences in the log estate amounts ($ps > .50$).

These results from the archived wills suggested that the genetic relatedness by lineage interaction was as reliable in real inheritances as it was across two survey studies using college students. Once again, the effect of genetic relatedness on resource allocations was dependent on the lineage of the relative in question. Specifically, the simple relationship between genetic relatedness and allocations of estate amounts was significantly more positive among relatives of a direct lineage than it was among peripheral relatives.

General Discussion

Across two surveys and an archival analysis, the predicted pattern was supported: the extent to which people allocated their resources to kin as a function of their common genes was more positive for relatives of a direct lineage than for other relatives. Across the three studies presented here, this interaction was robust—even when statistically controlling for differences in relatives' ages and differences in amounts of resources to be allocated. This interaction suggests that accounting for differences in relatives' lineages is important to understanding resources sharing within families.

Although these studies were the first to statistically demonstrate the genetic relatedness by lineage interaction in inheritances, they do not explain the mechanism behind this interaction. In the introduction, four possible explanations were given: (a) age-of-relative differences, (b) cultural norms, (c) sibling-sibling competition is stronger than parent-child competition, and (d) relatedness uncertainty. The only explanation that the present research rules out is that of relatives' age differences, which were controlled in all analyses. As for cultural norms, the present research is only generalizable to upper-middle class North Americans, typically of European descent. To evaluate the roll culture plays in the strength of the genetic relatedness by lineage interaction, other cultures—particularly non-Western ones—will need to be investigated.

To assess the possibility that differences in within-family competition for resources could be driving the observed interaction, future research could measure variables relating to sibling-sibling closeness, amount of overlap in years of cohabitation, and socio-economic status of the family. If differences in within-family competition are indeed driving the genetic relatedness by lineage interaction, one would expect the interaction to be stronger as measures of sibling-sibling competition for resources increase.

It is also possible that the genetic relatedness by lineage interaction is related to differences in genetic relatedness stemming from paternal uncertainty within families. Women (but not necessarily men) can be certain that their offspring is indeed their own. Because of paternal uncertainty, however, neither men nor women

can be certain that their brothers and sisters are full or half siblings. Thus, over evolutionary time, individuals who invested more resources in relatives of greater certainty (i.e., direct lineages) than relatives of lesser certainty (i.e., peripheral lineages), were more likely to pass on more of their common genes to future generations, thus perpetuating favoritism towards direct descendants.

Limitations and Implications

One possible limitation of these studies is the ecological validity of having college students allocate fictional lotteries to their relatives in Studies 1 and 2. Specifically, it was not clear if using a survey method with younger participants would accurately reflect the allocation patterns employed by older people when writing their wills. However, the results of an archival analysis of actual inheritance patterns in Study 3 replicated the pattern of findings present in the first two studies. In addition, the three studies presented here reflect the results of previous archival research on large samples of wills (Judge and Hrdy, 1992; Smith et al., 1987). Moreover, this survey method has been used successfully to investigate other kin investment issues in a related study (cf. Webster, 2003). Thus, it appears that younger people faced with a resource allocation task allocate resources to their kin in much the same way that older people do when they create wills. Although survey methods are no substitute archival analyses of inheritances, the similarity of the results across the three studies presented here show convergent validity between the survey and archival methods. Thus, the use multiple methods to assess patterns of kin investment should be encouraged in future investigations.

A second possible limitation of the present research is the lack of replication of the genetic relatedness and lineage main effects in Study 3. There are at least two factors contributing to these null effects. First, the sample size in Study 3 ($N = 74$) was small in comparison to previous analyses of archived wills ($Ns > 1,000$), which resulted in relatively low statistical power to detect effects. Second, real-world data (e.g., archival and field data) are notoriously noisier (i.e., containing more sources of error variance) than data collected in controlled environments (e.g., in classrooms and laboratories; McClelland and Judd, 1993). Thus, it is not unusual for archival studies to show weaker effects than survey studies.

The results of these studies indicate that differences in relative's lineages to a given target should be accounted for in studies of human kin investment or altruism. Not only were relatives of a direct lineage favored over other relatives in the two survey studies, but also this effect determined the extent to which genetic relatedness was associated with resource allocation in an analysis of archived wills. Because the simple relationship between genetic relatedness and resource allocation depends on the lineage of the relative in question, future research should make distinctions between relatives of direct and peripheral lineages.

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