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Lineage, Sex, and Wealth as Moderators of Kin Investment

Evidence from Inheritances

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Abstract Supporting Hamilton's inclusive fitness theory, archival analyses of inheritance patterns in wills have revealed that people invest more of their estates in kin of closer genetic relatedness. Recent classroom experiments have shown that this genetic relatedness effect is stronger for relatives of direct lineage (children, grandchildren) than for relatives of collateral lineage (siblings, nieces, nephews). In the present research, multilevel modeling of more than 1,000 British Columbian wills revealed a positive effect of genetic relatedness on proportions of estates allocated to relatives. This effect was qualified by an interaction with lineage, such that it was stronger for direct than for collateral relatives. Exploratory analyses of the moderating role of benefactors' sex and estate values showed the genetic relatedness effect was stronger among female and wealthier benefactors. The importance of these moderators to understanding kin investment in modern humans is discussed.

Keywords Genetic relatedness · Inclusive fitness · Inheritance · Kin investment · Lineage · Prosocial behavior · Resource allocation · Wills

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Kinship plays a central role in human social cognition (Daly et al. 1997), and archival analyses of wills have produced a wealth of information on how people make decisions about kin investment. Based on Hamilton's (1964) inclusive fitness theory, archival analyses of inheritance patterns have shown a positive effect of shared genetic relatedness on resource sharing within families (Judge 1995; Judge and Hrdy 1992; Smith et al. 1987): People invest more in kin with whom they share a greater proportion of common genes. Although this genetic relatedness effect is well established, comparatively little research has examined possible moderators of its strength, such as differences in relatives' lineage and benefactors' wealth and sex.

Hamilton's (1964) inclusive fitness theory proposes that altruistic tendencies would be selected for if the benefit to the recipients' fitness—weighed by the degree of relatedness between the altruist and the recipients—were greater than the cost of altruism to the altruist's fitness. To quantify inclusive fitness theory, Hamilton developed the inequality $C<rB$, where C represents the cost to the altruist, r represents the coefficient of relatedness between the altruist and the target(s), and B represents the reproductive benefit to the target(s). An example of Hamilton's inequality can be expressed via shared genetic relatedness coefficients (r). An individual animal ($r=1.0$) would be wise to sound a distress call upon spotting a predator if doing so would allow, for instance, three siblings ($r=0.5\times 3=1.5$) to escape unharmed, because copies of the individual's genes contained within its siblings exceed its own relatedness to itself (i.e., $1.5>1.0$). On the other hand, an individual might choose to avoid detection from a predator if only a single sibling is within earshot (i.e., $0.5<1.0$). Although these examples demonstrate altruism in its most extreme form (where the altruist's survival is threatened), less extreme examples of prosocial behavior, such as resource sharing, are certainly possible using Hamilton's model.

According to inclusive fitness theory (Hamilton 1964), factors such as genetic relatedness and reproductive value, which is related to sex and age, should explain the majority of variation in inheritances within families (Judge and Hrdy 1992; Smith et al. 1987). Genetic relatives, however, can be 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 descendents or progenitors of the target individual (e.g., grandparents, parents, children, grandchildren), whereas *collateral* relatives refer to those who are genetically related to the target but are neither direct descendents nor progenitors of the target (e.g., siblings, aunts/uncles, nieces/nephews, cousins). In a series of studies, Webster (2004) had college students allocate fictional lotteries to their blood relatives (Studies 1 and 2) and also examined inheritance patterns in a small sample of 74 wills (Study 3). In each study, a reliable lineage by genetic relatedness interaction emerged, such that the genetic relatedness effect was stronger (i.e., more positive) for relatives of direct lineage than it was for collateral relatives. These interactions were not moderated by benefactors' wealth. Judge (1995) has also shown a similar lineage difference in a larger sample of wills, although a lineage by genetic relatedness interaction was not empirically tested.

Relatedness uncertainty, which is typically due to paternal uncertainty, has been shown to play an important role in inclusive fitness and kin investment (e.g., DeKay 1995). First, because women carry their offspring until birth, they are assured that their child is in fact their own. Second, because women have concealed ovulation and can engage in extra-pair copulations, men cannot be certain that the child of a woman with whom they have had intercourse is in fact their own. Thus, fathers cannot be entirely certain whether they are raising their own offspring or are being cuckolded by raising another man's offspring.

Numerous researchers have found that people invest more in relatives of greater certainty than those of lesser certainty, which is largely a function of paternal uncertainty (DeKay 1995; Euler and Weitzel 1996; Euler et al. 2001; Gaulin et al. 1997; McBurney et al. 2002; Pashos 2000; Webster 2003). For example, in contrast to students given larger lotteries, students given smaller lotteries were more likely to allocate their fictional money to relatives of increasingly certain relatedness (Webster 2003). Further, aunts and uncles tend to invest more in their sisters' offspring than in their brothers' offspring, thus exhibiting a matrilateral bias, owing to the possibility of paternal uncertainty (Gaulin et al. 1997; McBurney et al. 2002). Because maternal grandmothers can be more certain of their grandchild's legitimacy than either maternal grandfathers or paternal grandmothers—who are in turn more certain than paternal grandfathers—researchers have found that maternal grandmothers tend to invest more in their grandchildren than do paternal grandfathers (DeKay 1995; Euler and Weitzel 1996). These patterns of differential grandparental investment have been replicated in three different European countries (Euler et al. 2001; Pashos 2000). Paternal uncertainty, however, is only one way in which sex differences play an important role in inclusive fitness theory.

Men and women appear to differ in their knowledge (or perhaps memory) of the structure of their families, and how they choose to allocate resources to them. Salmon and Daly (1996) found that, among opposite-sex sibling pairs (who by definition have identical family trees), women recalled reliably more relatives than did men. Moreover, women were more likely than men to mention their status within their families (e.g., "I am a sister/daughter"). Recent laboratory research with undergraduates has shown that women use genetic relatedness to determine resource allocations in their families to a greater extent than men (Webster 2003). Thus, benefactor sex may also moderate the effect of genetic relatedness on kin-based resource allocation. As Salmon and Daly (1996) suggested, a sex difference in kin knowledge could support either (*a*) an evolved adaptation that may be consistent with women's larger role in attracting kin support for parental investment (Trivers 1972; Table 1) or (*b*) a cultural difference based on sex roles, since, in other societies such as the Yanomamö of Venezuela (Chagnon 1988), there is a greater emphasis placed on men's knowledge of their kin network than on women's. In the present study, we sought to replicate the sex difference that Webster (2003) observed in a classroom experiment to a large sample of actual wills.

The lineage by genetic relatedness interactions that were observed primarily in classroom experiments (Webster 2004) have not been replicated in a large sample of wills because no study (of which we are aware) has empirically examined this effect. To this end, the purpose of the present research was to evaluate moderators of the genetic relatedness effect in kin investment (i.e., lineage, sex, and wealth). Given the literature reviewed above, we predicted that the genetic relatedness effect should be stronger (i.e., more positive) for direct relatives than for collateral ones (Webster 2004). Additionally, we performed exploratory analyses of benefactors' wealth and sex as possible moderators of the genetic relatedness effect and its interaction with lineage.

Method

Sample and Procedure

The sample consisted of the probate records of wills probated in British Columbia from 1971 to 1980 and included 1,240 benefactors and their 4,819 listed beneficiaries. Note that this sample of wills was independent of the sample used by Smith et al. (1987). The benefactors were 406 men (32.7%) and 783 women (63.1%); no record of sex was available for 51 records (4.1%). Other descriptive statistics for this sample are shown in Tables 1 and 2. Estate values (Can$), which were positively skewed, were normalized via a natural log transformation and mean-centered for all analyses. Note that certain characteristics of these data limit their generalizability. First, female benefactors outnumbered male benefactors by nearly a 2:1 ratio. Second, only five spouses were listed as beneficiaries in the sample. Third, the benefactors were somewhat homogenous in that most were upper-middle-class British Columbians who happened to draft wills. Thus, the present sample can adequately address questions regarding neither spousal resource allocations nor cross-cultural kinship variability. In addition, beneficiaries' descriptions were not detailed enough to allow us to make accurate inferences about paternal uncertainty (e.g., it was unclear whether terms such as "grandson" referred to "daughter's son" or "son's son"). Finally, since beneficiaries' ages were not available in the records, we recorded their generation as an imperfect proxy measure of age.

Data Analysis

The dependent variable was the arcsine of the square root of the proportion of the total estate value allocated to each beneficiary. This arcsine transformation, $\sin^{-1}(p^{1/2})$, corrected heterogeneity-of-variance problems that are typical for proportion data (Judd and McClelland 1989:525–526). The predicted percentages presented in the Results section were obtained by reverse-transforming the predicted arcsine scores into proportions, which were then converted to percentages.

Benefactors' sex was coded −1 (female) and 1 (male). The beneficiary-level independent variables of interest were the sex, lineage, and generation of the beneficiary, as well as the beneficiaries' proportion of common genetic relatedness to the benefactor. Beneficiaries' sex was coded −1 (female), 0 (unknown; e.g., cousins), and 1 (male). Beneficiaries' lineage was coded −1 (collateral relatives; e.g., siblings, nieces, nephews) and 1 (direct relatives; e.g., children, grandchildren). Beneficiaries' generation was estimated using a linear, categorical generational code: −2 (e.g., great grandchildren), −1 (e.g., grandchildren), 0 (e.g., children), 1 (e.g., siblings), and 2 (e.g., parents). Beneficiaries' shared genetic relatedness with their benefactor was expressed using four different levels of relatedness coefficients (i.e., r values): 0.0 (e.g., spouses, charities, friends, in-

Table 1 Percentage of sample and estate allocated for each beneficiary category (N=4,819)

	Beneficiary category			% of sample	% of estate
Kin				79.3	84.44
	r=0.50			48.9	69.75
		Direct		*38.0*	*56.22*
		Offspring		37.7	55.99
			Sons	17.7	26.47
			Daughters	20.1	29.52
		Parents		0.2	0.23
			Fathers	0.1	0.02
			Mothers	0.1	0.21
		Collateral		*11.0*	*13.53*
		Siblings		11.0	13.53
			Brothers	3.3	4.47
			Sisters	7.7	9.06
	r=0.25			26.7	13.03
		Direct		*14.0*	*4.00*
		Grandchildren		14.0	4.00
			Grandsons	6.9	2.08
			Granddaughters	7.2	1.92
		Collateral		*12.6*	*9.03*
		Nephews and nieces		12.3	8.88
			Nephews	5.3	3.43
			Nieces	7.1	5.45
		Half-siblings		0.2	0.13
			Half-brothers	0.1	0.09
			Half-sisters	0.1	0.04
		Uncles and aunts		0.1	0.02
			Uncles	<0.1	<0.01
			Aunts	0.1	0.02
	$r \leq 0.125$			3.7	1.66
		Direct		*1.1*	*0.22*
		Great grandchildren		1.1	0.22
			Great grandsons	0.2	0.21
			Great granddaughters	0.8	0.02
		Collateral		*2.7*	*1.44*
		Cousins		1.3	1.16
			Male cousins	0.2	0.02
			Female cousins	0.7	0.65
			Cousins (sex not reported)	0.4	0.49
		Grand nephews and grand nieces		1.3	0.28
			Grand nephews	0.6	0.14
			Grand nieces	0.8	0.13
	Direct (total)			53.1	60.44
	Collateral (total)			26.2	24.00
Non-kin[a]				20.7	15.55
Grand total[b]				100.0	100.00

[a] Includes five spouses

[b] Rounding error accounts for discrepancies between values and totals

laws), 0.125 (e.g., cousins, great grandchildren), 0.25 (e.g., nieces, nephews, grandchildren), and 0.5 (e.g., siblings, children). Note that because spouses represented only 0.1% of the sample (Table 1), they were treated as non-kin for analyses.

Table 2 Descriptive statistics for benefactors and beneficiaries

Descriptive statistic	Benefactors (N= 1,240)			Beneficiaries (N= 4,819)	
	Age at death[a]	Estate value		Allocations	
		Can$	log	Can$	%[b]
Mean	80.34	76,283	10.65	19,629	25.7
Standard deviation	11.33	141,198	1.12	50,502	27.8
Minimum	28.00	230	5.44	0	0.0
25th percentile	74.00	21,461	9.97	1,579	3.4
Median	82.00	47,640	10.77	7,204	16.7
75th percentile	88.75	88,368	11.39	20,426	33.3
Maximum	108.00	3,176,510	14.97	1,578,255	100.0

[a] Age of death in years; N=1,189

[b] Percentage of estate allocated to recipients

To test the effect of genetic relatedness within blood relatives (excluding unrelated beneficiaries, such as friends and charities), the relatedness variable (r) was centered at its midpoint by subtracting 0.3125 from each beneficiary's r. Thus, third-, second-, and first-order relatives had r values of −0.1875, −0.0625, and 0.1875, respectively. Since only blood relatives were used for the analyses presented in this study, this re-centering strategy was used in all subsequent models, except where otherwise noted.

The data yielded a hierarchically nested structure, with beneficiaries nested within benefactors. Whereas previous archival studies of wills (e.g., Judge 1995; Judge and Hrdy 1992; Smith et al. 1987) have ignored problems with statistical dependency by collapsing across benefactors within beneficiaries (Table 1), the current study used more-appropriate multilevel random coefficient models (MRCMs; Raudenbush and Bryk 2002) via the program hierarchical linear modeling (HLM, version 6.02; Raudenbush et al. 2004). This procedure involved performing within-benefactor (or, equivalently, between-beneficiary) regressions for each benefactor and then modeling the resulting within-benefactor regression coefficients as a function of between-benefactor differences in sex and log estate values. For example, when the lineage by genetic relatedness interaction model was tested (Table 3, right half), the beneficiary-level model was

$$\begin{aligned}\sin^{-1}\left(\text{Proportion}^{1/2}\right)_{ij} &= \beta_{0j} + \beta_{1j}(\text{Genetic relatedness})_{ij} + \beta_{2j}(\text{Sex})_{ij} \\ &\quad + \beta_{3j}(\text{Lineage})_{ij} + \beta_{4j}(\text{Generation})_{ij} \\ &\quad + \beta_{5j}(\text{Lineage} \times \text{Genetic relatedness})_{ij} + r_{ij}\end{aligned}$$

where $\sin^{-1}$ $(\text{Proportion}^{1/2})_{ij}$ represents the arcsine transformation of the estate proportion allocated to beneficiary i by benefactor j. The random coefficient β_{0j} is a within-benefactor intercept that represents the mean of the transformed proportions allocated to the beneficiaries listed by benefactor j. The random coefficients β_{1j} through β_{5j} are within-benefactor regression slopes that represent the effects of genetic relatedness, sex, lineage, generation, and the lineage by genetic relatedness

Table 3 Estate allocations as functions of genetic relatedness, sex, lineage, generation, and benefactors' estate values (log Can$)

Variable	Simultaneous regression			Lineage × genetic relatedness		
	Coef.	t_{1149}	pr^2	Coef.	t_{1149}	pr^2
Genetic relatedness	1.072	8.10****	0.054	1.023	6.06****	0.031
× log estate value	0.472	5.08****	0.022	0.213	1.88**	0.003
Sex of beneficiary	−0.004	−1.10	0.001	−0.006	−1.09	0.001
× log estate value	−0.003	−0.81	0.001	−0.004	−0.83	0.001
Lineage	0.071	3.52****	0.011	0.007	0.30	0.000
× log estate value	−0.044	−2.89***	0.007	−0.004	−0.26	0.000
Generation	0.017	0.57	0.000	0.049	1.20	0.001
× log estate value	−0.090	−4.51****	0.017	−0.047	−1.69*	0.002
Lineage × genetic relatedness	–	–	–	0.419	6.32****	0.034
× log estate value	–	–	–	0.165	3.23***	0.009

*$p<0.10$, **$p<0.06$, ***$p<0.01$, ****$p<0.001$

interaction (respectively) on transformed proportions for benefactor j. The error term, r_{ij}, represents the residual within-benefactor variance for benefactor j.

In MRCMs, regression coefficients generated at one level of analysis can be analyzed at a higher level of analysis. To this end, the within-benefactor coefficients were modeled as a function of between-benefactor differences in grand-mean-centered log estate values

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\text{log estate value})_j + u_{0j},$$
$$\beta_{1j} = \gamma_{10} + \gamma_{11}(\text{log estate value})_j + u_{1j},$$
$$\beta_{2j} = \gamma_{20} + \gamma_{21}(\text{log estate value})_j + u_{2j},$$
$$\beta_{3j} = \gamma_{30} + \gamma_{31}(\text{log estate value})_j + u_{3j},$$
$$\beta_{4j} = \gamma_{40} + \gamma_{41}(\text{log estate value})_j + u_{4j},$$
$$\beta_{5j} = \gamma_{50} + \gamma_{51}(\text{log estate value})_j + u_{5j},$$

where γ_{00} is a between-benefactor intercept representing the mean of the within-benefactor intercepts (i.e., the β_{0j} values) at the mean log estate value. The other intercepts, γ_{10} through γ_{50}, represent the between-benefactor means of the within-benefactor effects of genetic relatedness, sex, lineage, generation, and the lineage by genetic relatedness interaction (respectively) at the mean log estate value. The coefficients γ_{01} through γ_{51} are between-benefactor slopes that represent the extent to which their respective within-benefactor effects are moderated by between-benefactor differences in log estate value. For instance, γ_{11} describes the extent to which the effect of genetic relatedness on estate allocations changes as a function of log estate value. The error terms, u_{0j} through u_{5j}, represent the residual between-benefactor variances for their respective within-benefactor effects.

We chose to examine two types of models. First, we examined within-benefactor models that were unconditional at the between-benefactor level (i.e., contained no moderating variables). Second, we examined within-benefactor models that were conditional on one or more between-benefactor variables (e.g., benefactors' wealth and sex). These two types of models tell us different things about the effects of interest. For example, in an unconditional model, the genetic relatedness coefficient represents the mean linear genetic relatedness effect averaged across all beneficiaries. In contrast, when the grand-mean-centered log estate values are added as a between-benefactor moderator, then the model becomes conditional on that variable, and the genetic relatedness coefficient now represents the linear genetic relatedness effect for a benefactor with the mean log estate value. Thus, it was important to examine both the unconditional and conditional models, since each addresses a different question.

Note that, owing to the nature of these MRCMs, the predicted mean percentages presented later do not sum to 100%, since these numbers represent the mean percentage given to a particular class of beneficiaries within benefactors, which are then averaged across benefactors.

The main purpose of the present study was to examine kin-based resource allocation. Because 89 of the benefactors listed no blood relatives, they were excluded from subsequent analyses, yielding a sample of 1,151 benefactors. Since we had no way of knowing the sex of some of these benefactors because of incomplete records, the sample size was reduced to 1,105 benefactors when benefactor's sex was examined as a variable.

Results

Simultaneous Regressions

When beneficiaries' genetic relatedness, sex, lineage, and generation were entered as simultaneous predictors of estate allocations, only genetic relatedness ($\gamma_{10}=1.42$, $t_{1150}=6.06$, $p<0.001$, $pr^2=0.031$) emerged as a significant predictor (other three variables: p values>0.16; a squared partial correlation or pr^2 is a measure of the proportion of variance explained in an outcome variable by a single predictor variable of interest, controlling for other covariates in that model). For this model, the mean estate percentage for relatives with r values of 0.125%, 0.25%, and 0.5% were 1.9%, 9.7%, and 38.7%, respectively.

When log estate values were added to this model, both genetic relatedness and lineage emerged as significant predictors (Table 3, left columns). Moreover, the effects of genetic relatedness, lineage, and generation were each moderated by log estate value (Figs. 1, 2, and 3, respectively). Here and in subsequent simple effects tests, "more wealthy" corresponds to testing the within-benefactor effect of interest at 1 SD above the mean log estate value, whereas "less wealthy" corresponds to testing the effect at 1 SD below the mean log estate value (following procedures outlined by Cohen et al. 2003:270–280; Judd and McClelland 1989:338–341). First, among more wealthy benefactors, the effect of genetic relatedness was significantly positive ($\gamma_{10}=1.59$, $t_{1149}=9.27$, $p<0.001$, $pr^2=0.070$), whereas among less wealthy benefactors, it was only marginally positive ($\gamma_{10}=0.55$, $t_{1149}=1.82$, $p=0.068$, $pr^2=0.003$). Second, among more wealthy benefactors, the effect of lineage was not significant ($p=0.40$), whereas among less wealthy benefactors, this effect was significantly positive ($\gamma_{30}=0.12$, $t_{1149}=2.80$, $p=0.006$, $pr^2=0.007$). Third, among more wealthy benefactors, the effect of relative's generation on estate

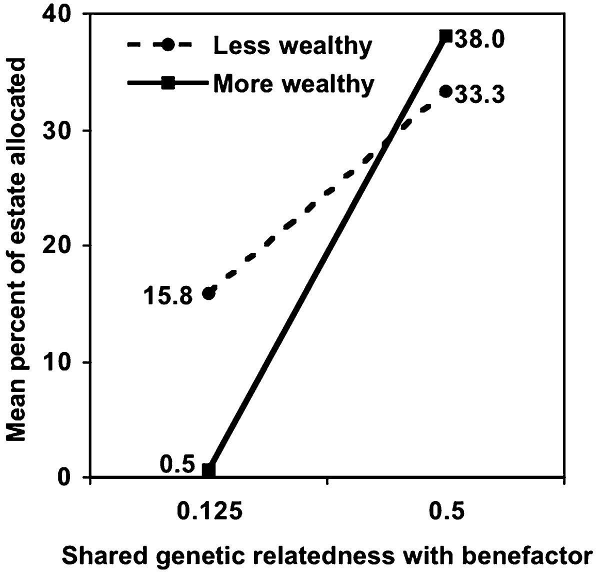


Fig. 1 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex, generation, and lineage, as a function of beneficiaries' shared genetic relatedness with benefactor and benefactor's wealth (i.e., mean log estate value ± 1 SD)

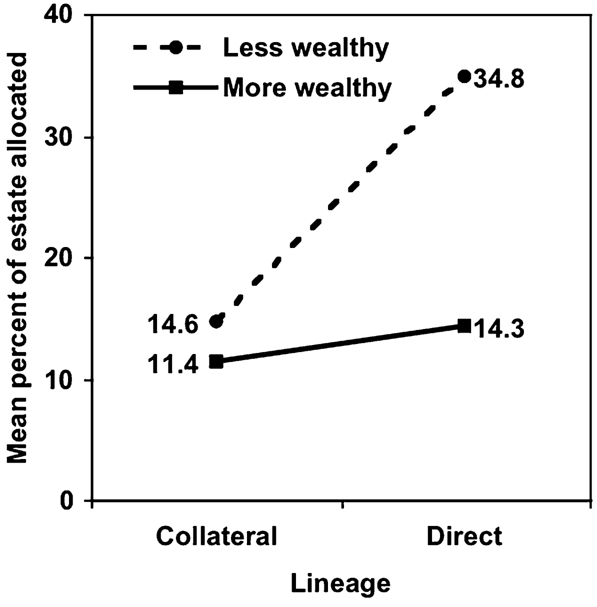


Fig. 2 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex, generation, and beneficiaries' shared genetic relatedness with benefactor, as a function of beneficiaries' lineage (i.e., collateral vs. direct) and benefactor's wealth (i.e., mean log estate value ± 1 SD)

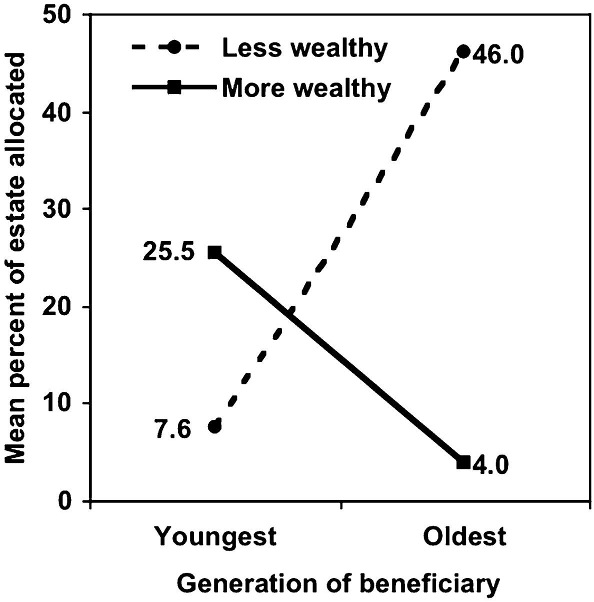


Fig. 3 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex, lineage, and beneficiaries' shared genetic relatedness with benefactor, as a function of benefactor's wealth (i.e., mean log estate value ± 1 SD) and beneficiaries' generation (a proxy measure of age), where "youngest" refers to relatives that are three generations junior to the benefactor (e.g., great grandchildren) and "oldest" refers to relatives one generation senior to the benefactor (e.g., parents)

allocations was significantly negative (γ_{40}=−0.082, t_{1149}=−2.22, p=0.026, pr^2= 0.004), whereas among less wealthy benefactors, this effect was marginally positive (γ_{40}=0.12, t_{1149}=1.65, p=0.098, pr^2=0.002). One possible explanation for this generation by wealth interaction is that the younger relatives of wealthy benefactors may benefit via generation-skipping trusts.

When benefactors' sex was added to this model, male benefactors showed a significantly stronger generation effect than female benefactors (γ_{42}=0.081, t_{1102}= 2.04, p=0.041, pr^2=0.004; Fig. 4), such that men showed an allocation preference for older relatives (γ_{40}=0.16, t_{1102}=2.22, p=0.027, pr^2=0.004), whereas women showed no such preference (p=0.99). More importantly, female benefactors showed a significantly stronger genetic relatedness effect than male benefactors (γ_{12}=−0.35, t_{1102}=−1.96, p=0.049, pr^2=0.003; Fig. 5), such that women showed a significantly positive effect (γ_{10}=1.22, t_{1102}=5.32, p<0.001, pr^2=0.025), whereas men showed a positive effect that was not even marginal (γ_{10}=0.51, t_{1102}=1.60, p=0.11, pr^2= 0.002). Lastly, benefactors' sex moderated neither the lineage effect (p=0.26) nor the effect of relatives' sex (p=0.50).

Lineage by Genetic Relatedness Interaction

To compare the effects of lineage between second-and first-order relatives, the genetic relatedness variable was re-centered at the midpoint between r=0.25 and r= 0.5 by subtracting 0.375 from each beneficiary's r prior to calculating its interaction

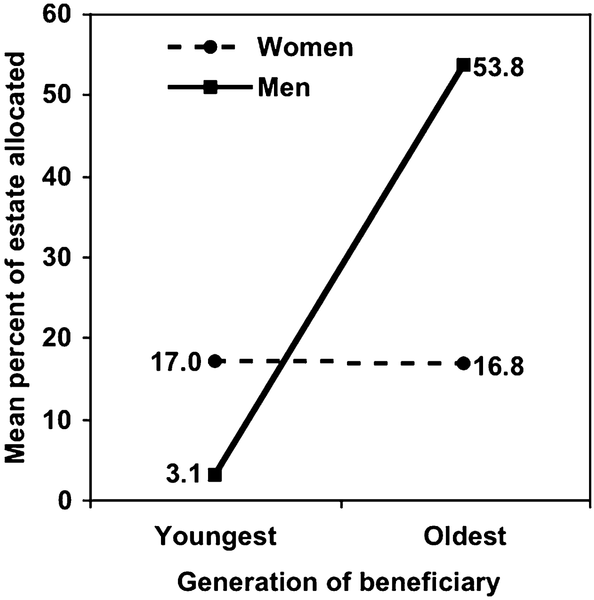


Fig. 4 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex, lineage, beneficiaries' shared genetic relatedness with benefactor, and benefactor's wealth (log estate value), as a function of benefactor's sex and beneficiaries' generation (a proxy measure of age), where "youngest" refers to relatives that are three generations junior to the benefactor (e.g., great grandchildren) and "oldest" refers to relatives one generation senior to the benefactor (e.g., parents)

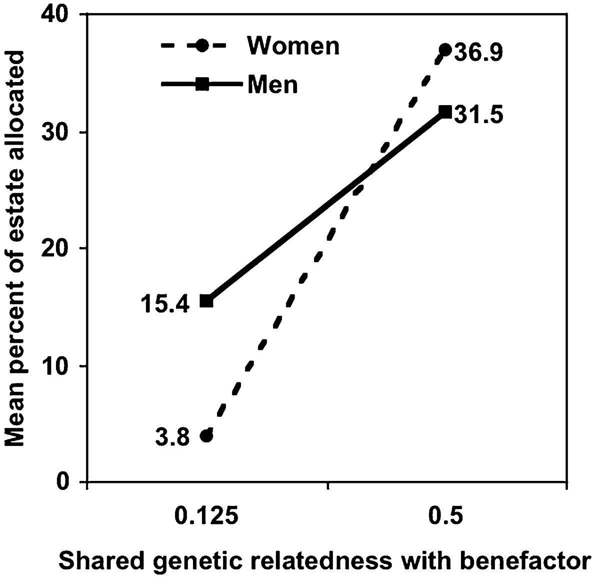


Fig. 5 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex, generation, lineage, and benefactor's wealth (log estate value), as a function of beneficiaries' shared genetic relatedness with benefactor and benefactor's sex

with the lineage variable. Thus, third-, second-, and first-order relatives had r values of −0.25, −0.125, and 0.125, respectively. Note that this re-centering adjusted only the lineage coefficient in the analysis, such that it now compared the difference between second- and first-order relatives, whereas the default 0.3125 centering would have compared the difference between third- and first-order relatives. This was done to be consistent with previous research (Webster 2004) and because there were comparatively too few direct third-order relatives (i.e., great grandchildren), which may have resulted in a less reliable regression estimate for the lineage effect.

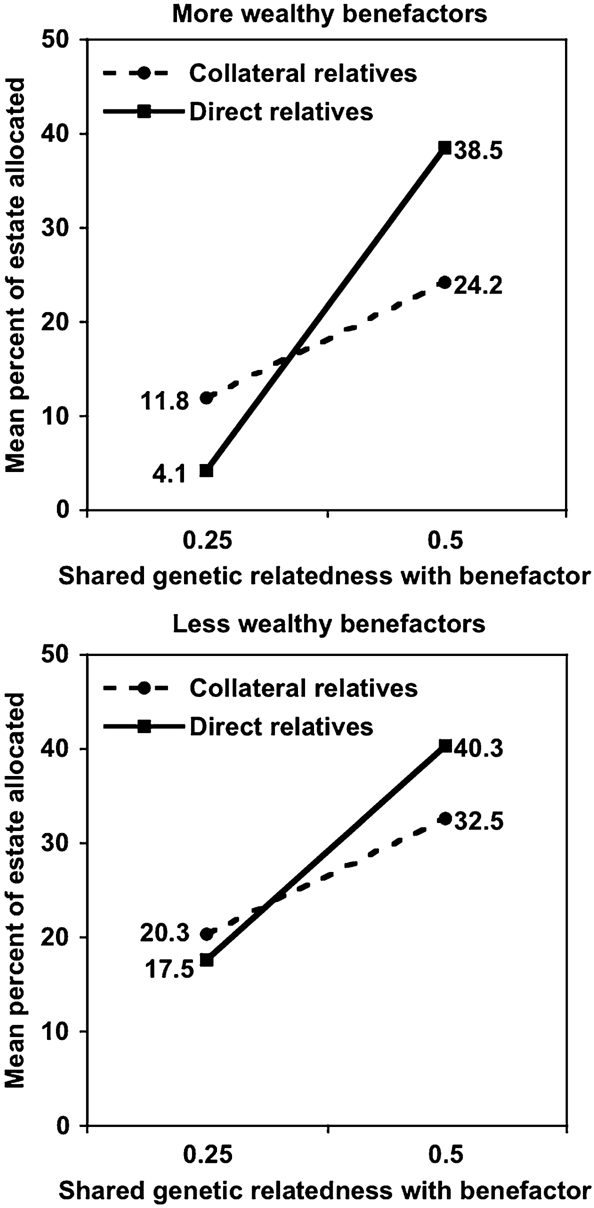
Controlling for relatives' sex and generation, the effects of lineage ($\gamma_{30}=0.0078$, $t_{1150}=0.19$, $p=0.85$, $pr^2<0.001$) and genetic relatedness ($\gamma_{10}=1.20$, $t_{1150}=7.19$, $p<0.001$, $pr^2=0.043$) were qualified by a significant lineage by genetic relatedness interaction ($\gamma_{50}=0.46$, $t_{1150}=7.09$, $p<0.001$, $pr^2=0.042$). Among direct relatives, the genetic relatedness effect ($\gamma_{10}=1.66$, $t_{1150}=9.06$, $p<0.001$, $pr^2=0.067$) was substantially stronger than it was among collateral relatives ($\gamma_{10}=0.74$, $t_{1150}=4.23$, $p<0.001$, $pr^2=0.015$).

Log estate value moderated the genetic relatedness effect (Table 3, right columns). Among more wealthy benefactors, the genetic relatedness effect for relatives of average lineage (that is, at the mean of direct and collateral relatives) was stronger ($\gamma_{10}=1.26$, $t_{1149}=7.78$, $p<0.001$, $pr^2=0.050$) than it was among less wealthy benefactors ($\gamma_{10}=0.79$, $t_{1149}=3.17$, $p=0.002$, $pr^2=0.009$).

Log estate values also moderated the lineage by genetic relatedness interaction (Table 3, right columns; Fig. 6). Among more wealthy benefactors, the lineage by genetic relatedness interaction was comparatively strong ($\gamma_{50}=0.60$, $t_{1149}=8.67$, $p<0.001$, $pr^2=0.061$), such that the genetic effect was markedly stronger among direct relatives ($\gamma_{10}=1.86$, $t_{1149}=10.22$, $p<0.001$, $pr^2=0.083$) than it was among collateral relatives ($\gamma_{10}=0.66$, $t_{1149}=3.87$, $p<0.001$, $pr^2=0.013$). Among less wealthy families, the lineage by genetic relatedness interaction was comparatively less strong ($\gamma_{50}=0.24$, $t_{1149}=2.34$, $p=0.020$, $pr^2=0.005$), but the genetic effect remained stronger among direct relatives ($\gamma_{10}=1.03$, $t_{1149}=3.85$, $p<0.001$, $pr^2=0.013$) than it did among collateral relatives ($\gamma_{10}=0.55$, $t_{1149}=2.03$, $p=0.042$, $pr^2=0.004$). Lastly, benefactors' sex moderated neither the effect of lineage ($p=0.60$) nor its interaction with genetic relatedness ($p=0.36$).

Discussion

Genetic relatedness was a robust correlate of estate allocations within families. This finding was consistent with previous research on wills (Judge 1995; Judge and Hrdy 1992; Smith et al. 1987) and surveys (Webster 2003, 2004, 2006). Interestingly, older people's allocations to their younger kin in wills closely resemble younger undergraduates' allocations to their older and same-aged kin in classroom experiments. It is important to note, however, that wills may include contingencies. For example, a benefactor's grandchildren might only inherit after their parent (the benefactor's child) is deceased. Unfortunately, detailed information about contingencies in the archival probate records was not recorded. In Webster's (2003, 2004, 2006) classroom experiments, no such contingencies were imposed on the undergraduate participants. Thus, it may be difficult to compare the



More wealthy benefactors

Less wealthy benefactors

Fig. 6 Mean percent of benefactors' estate value (log Can$) allocated to beneficiaries, controlling for beneficiaries' sex and generation, as a function of (a) beneficiaries' shared genetic relatedness with benefactor (i.e., r=0.25 vs. r=0.5), (b) beneficiaries' lineage (i.e., collateral vs. direct), and (c) benefactor's wealth (i.e., log estate value), where "more wealthy benefactors" corresponds to 1 SD above the mean estate value (*top panel*), and "less wealthy benefactors" corresponds to 1 SD below the mean estate value (*bottom panel*) findings of the present study with those of classroom experiments based on their different methodological approaches (i.e., archival vs. laboratory). Nevertheless, despite these differences, closer genetic relatives were consistently favored over more distant ones in both probated wills and classroom resource allocation experiments.

Inclusive fitness theory relies in part on an individual's ability to accurately recognize or identify their kin. According to evolutionary theory, humans (and other animals) should have an adaptive psychological mechanism (Tooby and Cosmides 1992) for recognizing kin in order to avoid incest and promote inclusive fitness. For example, Lieberman et al. (2003, 2007) have shown that children who grow up with siblings are more likely to possess strict moral sentiments about incest, whereas children who grow up without siblings possess comparatively more lax attitudes about incest. In a series of related studies, DeBruine (2002, 2004a, b, 2005) has shown that, when strangers' faces are morphed with participants' faces, participants are more likely to respond to the morphed faces as they would to their own kin. Recently, Park and Schaller (2005) have also shown that attitude similarity may serve as a heuristic cue for kinship.

In addition to kin recognition, other proximal variables may mediate the relationship between genetic relatedness and kin-based resource allocation. Recent research by Webster (2006) has suggested that the strength of the relationship between genetic relatedness and kin-based allocations of wealth is partially mediated by such proximal variables as emotional closeness (Korchmaros and Kenny 2001), duration of cohabitation, and amount of social interaction. From a larger theoretical standpoint, such a relationship may suggest that the observed genetic relatedness effect may act through a more proximal, evolved psychological mechanism such as acceptance (Webster 2008) and human attachment (Bowlby 1969). Humans (and other animals that require a substantial amount of parental investment) often become attached to their caretakers (e.g., parents) and to those for whom they care (e.g., children); they also typically form emotional bonds with others through extended cohabitation (e.g., siblings). These caretakers and cohabitants are typically—but not always—close genetic relatives of the target individual. Thus, attachment may serve as a key psychological mechanism of inclusive fitness insofar as kin-based resource sharing is concerned. Although there is some evidence that the genetic relatedness effect may be mediated by emotional closeness (Korchmaros and Kenny 2001; Webster 2006), it is important to note that such a mediation model could not be empirically tested using our sample of wills since emotional closeness between benefactor and beneficiaries was not measured.

The lineage by genetic relatedness interaction successfully replicated Webster's (2004) three studies using a sample more than 15 times larger than that of the previous investigation of archived wills (Study 3). Clearly, lineage played an important role in determining resource allocations within families, not only as a main effect, but also in interacting with genetic relatedness, such that the genetic relatedness effect on kin investment was stronger for direct relatives than it was for collateral relatives. Also important is the fact that the lineage effects were significant when controlling for relatives' generation differences. Controlling for generation as a proxy for age in these analyses is key because, within levels of genetic relatedness, direct relatives tend to be younger—and thus have more reproductive potential—

than collateral relatives (Webster 2004). In contrast to Webster's (2004) three studies, in which the lineage by genetic relatedness interactions were not moderated by wealth, the present study showed that this interaction became stronger as benefactors' wealth increased. Note that the absence of significant wealth moderation in Webster's (2004) studies may have been due to a comparative lack of statistical power, since each of those studies had samples less than one-eighth the size of the present study.

Why should the genetic relatedness effect be stronger for direct lineages than it is for collateral lineages? There are at least five plausible explanations. First, in many families, the number of potential collateral beneficiaries increases with generational distance. For instance, it is often the case that benefactors with more than one sibling will have more nephews and nieces than sons and daughters. Thus, even if benefactors wish to give equal amounts to both their direct and collateral descendents, the amount given to any one of the latter may be lessened if they outnumber the former. This genealogical artifact may contribute to the strength of the observed interaction.

Second, no detailed information about inheritance contingencies was recorded for our sample of probated wills. When people die intestate, it is not uncommon for collateral relatives to inherit only if direct relatives are nonexistent or deceased. Wills may sometimes stipulate similar contingencies. Thus, the legal traditions established for those who die intestate may influence the contingencies that people write into their wills. Such contingencies may in turn contribute indirectly to the strength of the observed lineage by genetic relatedness interaction.

Third, strong cultural and historical norms may influence people's inheritance decisions. In many modern Western cultures, people traditionally will a larger percentage of their estates to their direct descendants than to their collateral relatives (e.g., Cooper 1976; Goody 1983; Le Roy Ladurie 1976). For example, in the present study, direct relatives were given significantly larger percentages of estates on average (23.8%) than were collateral kin (13.0%).

Fourth, it is possible that the parent-child and child-parent patterns of attachment are stronger than sibling-sibling attachment patterns (Bowlby 1969). It is also possible that sibling-sibling conflict is stronger than parent-offspring conflict when children compete for limited resources (Trivers 1974).

Fifth, the lineage by genetic relatedness interaction may be associated with 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 women, who are certain that their child is their own. For instance, equating relatives on age (or generation) 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, owing to paternal uncertainty. Given this fact, over evolutionary time, a resource sharing preference that favored relatives of direct lineage over those of collateral lineage could be beneficial in the context of an individual's inclusive fitness. If such an evolved preference existed, however, one might expect it to be stronger among women than men, given that the latter must contend with paternal uncertainty. Recall, however, that benefactor's sex did not significantly moderate the lineage by genetic relatedness interaction ($p=0.36$). Despite being non-significant, the effect *was* in a direction that favors such an explanation: The lineage by genetic relatedness interaction was slightly stronger on average for female benefactors than it was for male benefactors. Given this lineage difference, it is possible that people pay closer attention to the gradations of relatedness among their direct descendents than they do among their collateral kin, which could lead to a stronger genetic relatedness effect for direct relatives than for collateral ones. It is also possible, however, that this interaction is driven simply by the fact that, on a psychological level, the direct-versus-collateral difference matters most for allocating resources to first-order ($r=0.5$) relatives, and comparatively less for other relatives (r values<0.5).

It is also important to note, however, that collateral kin have an additional genetic distinction from direct kin: Direct relatives share *exact* relatedness coefficients with their benefactor (e.g., r values$=0.5, 0.25, 0.125$), whereas collateral relatives share these coefficients with their benefactors *on average*, since each represents a unique, independent assortment of genetic material (e.g., for siblings, $r=0.5 \pm$ a small amount of genetic sampling error). Moreover, direct and collateral kin also typically differ in their reproductive value. For example, among first-order relatives, one's children (direct kin) are typically younger than one's siblings (collateral kin), which suggests that one should invest more in one's children because they have comparatively more reproductive value owing to their younger age. This is why we statistically controlled for generation as a proxy for age in all of our analyses involving lineage and its interaction with genetic relatedness. Nevertheless, further research on the interactive effects of lineage and genetic relatedness will be necessarily before any concrete conclusions can be drawn.

Our exploratory analyses revealed that benefactors' wealth and sex also moderated the effect of genetic relatedness on estate allocations. First, as benefactors' estate values increased, so too did the strength of the genetic relatedness effect; it became more positive. Second, the genetic relatedness effect was significantly stronger for female benefactors than it was for male benefactors. These exploratory findings from an archival analysis of wills are particularly interesting when contrasted with a related classroom experiment (Webster 2003). Webster (2003) had college students allocate varying lottery amounts to their blood relatives. The effect of genetic relatedness on lottery allocations to blood relatives was moderated by lottery amount, such that students in the small lottery condition showed a stronger genetic relatedness pattern in their allocations than did students in the large lottery condition. Thus, scarcer resources were associated with more evolutionarily conservative kin investment strategies, whereas greater resources were associated with more egalitarian kin investment strategies. Female students also showed a stronger genetic relatedness effect than males.

In contrast to the findings of Webster's (2003) classroom experiment, the present archival analysis showed that the effect of genetic relatedness was positively moderated by wealth. Note that Webster's (2003) experiment had younger students allocating fictional lottery winnings primarily "upward" to older relatives, whereas, in the present study, older will-writers allocated their actual estates primarily "downward" to younger relatives. Thus, the two studies may not be directly comparable. Nevertheless, further investigation of the possible moderating role of available resources on kin investment is clearly warranted. The results of the present study do, however, raise the possibility that human reproductive and kin investment strategies depend on resources such as wealth. For example, modern humans (especially women) often have to trade off the reproductive benefits of passing on their genes with the reproductive costs of parental investment (Trivers 1972). Moreover, wealthier benefactors may have accumulated more wealth over their lifetime by having fewer offspring, compared with less wealthy benefactors who spent their fortunes raising a greater number of offspring. Such a discrepancy could have contributed to the observed positive covariation between steeper genetic relatedness allocation slopes and estate value. Alternatively, it is also possible that wealth (i.e., estate values) is confounded with one or more unmeasured variables (e.g., education, age at marriage, likelihood of divorce) that may be more directly responsible for the observed moderation of the genetic relatedness effect.

Consistent with Webster's (2003) findings was that the genetic relatedness effect was significantly stronger (i.e., more positive) for female benefactors than for male benefactors. For female benefactors, relatives' genetic relatedness was significantly associated with resource allocation, whereas relatives' generation was not. For male benefactors, relatives' generation was significant, whereas genetic relatedness was not, although it was nearly marginally significant ($p=0.11$). This sex difference supports Judge's (1995) finding that, at least among unmarried benefactors, men were more equitable in their estate allocations to beneficiaries than were women. One possible explanation for this effect is that, owing in part to sex differences in parental investment in offspring (Trivers 1972), women may pay closer attention to the structure of their kinship system than men, and women's more conservative kin investment strategies reflect this awareness. Indeed, women tend to recall and list more of their relatives than men in both wills (Judge 1995) and surveys, even when paired with their brothers, who have the same set of relatives (Salmon and Daly 1996).

Limitations and Implications

One limitation of the present research is that it could not address the proximal mechanisms (e.g., socio-developmental factors) that likely mediate the relationship between genetic relatedness and kin investment. In previous research, cohabitation has had a substantial influence on students' allocation decisions (Webster 2003, 2006), while emotional closeness has been shown to partially mediate the relationship between genetic relatedness and students' willingness to provide life-saving assistance to their relatives (Korchmaros and Kenny 2001). Future research should strive to accurately tease apart the effects of genetic relatedness from those of cohabitation and emotional closeness in analyses of inheritance patterns.

A second limitation of the present research is that it could not address empirical questions regarding paternal uncertainty and related issues. For instance, previous studies have found that people invest more in relatives of greater certainty than those of lesser certainty, which is largely a function of paternal uncertainty (DeKay 1995; Euler and Weitzel 1996; Gaulin et al. 1997; McBurney et al. 2002; Michalski and Shackelford 2005; Pashos 2000; Webster 2003). Unfortunately, these intriguing possibilities could not be tested in the present study because the listed relationships between beneficiaries and benefactors were not specific enough in the archived records to allow for such detailed examinations.

A third limitation of the present research is the generalizability of its findings. Our sample of wills, although large, appears to represent a relatively upper middle class cross-section of British Columbians in the mid-to-late twentieth century who happened to write wills. Moreover, nearly two-thirds of the sample was based on female benefactors, and virtually none of the sample listed any spouses. We suspect that this sample of wills represents a specific demographic: those whose spouses have already died. Since wives tend to outlive their husbands, this may explain the nearly 2:1 female-to-male benefactor ration in our sample. Moreover, in British Columbia (and many other North American states and provinces), for people who die without wills (i.e., intestate), their spouse often inherits their entire estate. When people do write wills, many choose to give their estates to their living spouse first and to other relatives only if the spouse is already deceased. Thus, there may be an incentive for widows and widowers to draft wills, whereas spouses can afford to die intestate, knowing that inheritance laws often mirror their own wishes of allocating their estates to their living spouse. It is also noteworthy that sex and age differences in fertility and mortality may contribute to benefactor-level sex difference in estate allocations. For example, women who outlive their husbands typically will their estates to their offspring rather than to their husbands, because their husbands are typically still capable of producing other offspring with other women, which might jeopardize resource allocation to their original offspring. In contrast, men who outlive their wives typically will their estates to their wives rather than their offspring, because their wives are typically postmenopausal, which lessens the probability that resource allocation to their original offspring will be jeopardized (Judge and Hrdy 1992).

Another limitation to the generalizability of our study is that, although it *does* include some disinherited individuals (i.e., those relatives who were listed, but were allocated Can$0), it cannot tell how many disinherited individuals were excluded from wills altogether (via omission) without detailed interviews or accurate genealogical records. Thus, our findings cannot accurately speak to kin investment (or lack thereof) among the disinherited. We do suspect, however, that disinherited kin are more likely to be collateral relatives than direct descendants; therefore, the observed proportions given to collateral kin may be artificially inflated compared with estimates for direct kin. A similar inflation of the lineage effect may happen in families in which there are no direct descendants and a large number of collateral ones; however, classroom experiments in which the numbers of direct and collateral relatives are kept constant support both the main effect of lineage and its interaction with genetic relatedness (Webster 2006). Nevertheless, a clearer understanding of these processes might have been attained through a detailed examination of the inheritance contingencies from the original wills, which were not recorded.

It should also be noted that the present research assumes that wills reflect customary and normal inheritance processes from which we can infer evolved human psychology. This may not be the case. Indeed, many people die intestate, and those who *do* write wills typically have not only the resources to do so, but also the motivation to make sure their estates are allocated in a way that may be contrary to what may have been prescribed by law had they died intestate. From this angle, it is possible that analyses of wills may reveal more about the *exceptions* to the norms of kin-based resource sharing rather than the norms themselves. Thus, the results of this study should be generalized only to the extent that the benefactor (*a*) has actually written a will and (*b*) has probably outlived his or her spouse.

A fourth limitation of the present research is that inclusive fitness typically cannot be directly observed in inheritance patterns. According to inclusive fitness theory (Hamilton 1964), the benefactor must incur a cost when benefiting his or her relatives. In the case of wills, the cost is unclear: Although the benefactor may be giving away his or her estate, he or she is recently deceased and hence has no use for an estate. Alternatively, from the perspective of parental investment theory (Trivers 1972), parents (or typically in this case, benefactors) *do* incur a cost to themselves by investing valuable resources in their offspring. Thus, inheritance decisions can be seen as containing elements of both inclusive fitness and parental investment theories. It may, however, be difficult to infer a reproductive advantage by examining inheritances, especially when benefactors in their eighties are allocating resources to their post-reproductive offspring, who themselves may be in their fifties.

There are, however, at least two possible ways in which inclusive fitness may be acting indirectly upon will-writing behavior. First, many people choose to write their wills years before they die as a means of having some say in how their estates are allocated in the event of an untimely death. Thus, although a will may not be enacted until the benefactor's death, the behavior of will-writing itself may occur when the benefactor's offspring (who typically inherit the majority of the estate's value) are at or near their peak reproductive potential. Indeed, childbearing is often regarded as a critical event that necessitates the writing of a will. Second, even if wills are written when a benefactor's children have passed their reproductive potential, indirect benefits to the reproductive fitness of his or her grandchildren are still possible. For example, a grandmother (i.e., the benefactor) may indirectly improve the social and financial status of a grandson by willing money to his mother (i.e., her daughter), who may then help pay for his college education, which may in turn indirectly improve his ability to attract a mate, increasing his reproductive fitness, and thus increasing the inclusive fitness of the family.

A fifth limitation of the present research is its relatively small effect sizes (i.e., pr^2 values). It is important to note, however, that effect sizes from archival studies (which stress external validity) are often smaller than those from experiments (which stress internal validity; McClelland and Judd 1993). Thus, it is not unusual for archival studies to have comparatively small effect sizes.

Summary and Conclusions

The present research demonstrates the importance of accounting for differences in beneficiaries' lineages and benefactors' resources when examining the effects of genetic relatedness on kin investment. The current investigation replicated the lineage and lineage by genetic relatedness effects observed in previous studies (Judge 1995; Webster 2004) with a far larger sample and increased external validity. Exploratory analyses revealed that the genetic relatedness effect was stronger for female and wealthier benefactors. This sex moderation was consistent with a classroom experiment in which wealth was manipulated (Webster 2003), but the direction of the wealth moderation was not. It is hoped that these findings will encourage researchers to consider the importance of examining differences in lineage, sex, and wealth in their future investigations of human kin investment.

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