

DARWIN AND THE PUZZLE OF PRIMOGENITURE

An Essay on Biases in Parental Investment after Death

Sarah Blaffer Hrdy

University of California, Davis

Debra S. Judge

University of California, Davis

A historical survey of the inheritance practices of farming families in North America and elsewhere indicates that resource allocations among children differed through time and space with regard to sex bias and equality. Tensions between provisioning all children and maintaining a productive economic entity (the farm) were resolved in various ways, depending on population pressures, the family's relative resource level, and the number and sex of children.

Against a backdrop of generalized son preference, parents responded to ecological circumstances by investing in offspring differentially within and between the sexes. Vesting the preponderance of family resources in one heir increased the likelihood of at least one line surviving across several generations, whereas varying degrees of parental investment in emigrating sons or out-marrying daughters might yield boom or bust harvests of grandchildren according to circumstances in more remote locales. Primogeniture (eldest son as primary heir) allowed early identification of heirs and appropriate socialization, as well as more time for parents to contribute to the heir's reproductive success. Son bias and unigeniture decreased as numbers of children per family declined, as land became less critical to economic success, and as legal changes improved the resource-holding potential of females. We suggest that

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Address all correspondence to Sarah Hrdy, Department of Anthropology, University of California, Davis CA 95616.

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changing ecological conditions affected parental decisions regarding resource allocation among children at least as much as did changing ideologies of parent-child relations.

KEY WORDS: Parental investment; Inheritance; Primogeniture; Sex bias; Patriarchy.

“Oh, what a scheme is primogeniture for destroying natural selection!”

Letter from Charles Darwin
to Alfred Russell Wallace,
28 May 1864 (Darwin 1887[III]:91)

INTRODUCTION: DARWIN AND PRIMOGENITURE

Charles Darwin, according to his son Francis, was deeply offended by the “injustice” of primogeniture, the customary British practice of preferentially leaving estates to the eldest son.¹ In England, this preference for oldest sons spread among the gentry in the early sixteenth century. By the eighteenth century, primogeniture among the elites was emulated by the classes below, resulting eventually in some yeoman as well as aristocrats favoring eldest sons (Thirsk 1976:177, 191). Custom became canonized in law; as late as 1925, the land of an Englishman who died without a will went to his eldest surviving son, and if no son survived, to his brother’s eldest son.²

The unfairness of favoring sons over daughters was lost on Darwin; certain things a Victorian simply took for granted. But Darwin was concerned with the issue of fairness as it applied to the treatment of sons. Beyond that, Darwin was alarmed on eugenic grounds by a practice that was so “dreadfully opposed to selection.”

Instead of selecting an heir according to some set of fitness-related criteria, or—as is common in some cultures—letting heirs fight it out among themselves until only the strongest or most motivated son is left (e.g., succession in East African kingdoms: Beattie 1960:27; Oberg 1967:157–158), the choice was arbitrary. “Suppose the first-born bull was necessarily made by each farmer the begetter of his stock!” scoffed Darwin (an animal-breeder in his own right) in a letter to Joseph Hooker in 1862 (Darwin 1887[II]:385).

But in his pique with a custom abhorrent to him, Darwin was not only ignoring the injustice to women but also the inclusive fitness-enhancing

possibilities raised by the differential treatment of offspring by sex and by birth order, one of the primary means by which parents among a variety of species are able to adjust available resources to ecological and social contingencies. In this respect, Darwin was insufficiently "Darwinian." By analyzing these parental strategies, we hope to illuminate not only Darwin's own sexist biases but also the widespread preference for sons that characterizes many more societies than just those with primogeniture.

Primogeniture is after all only an extreme, codified form of differential allocation of resources among offspring. It can be viewed as one extreme along a continuum of hypothetical parental decisions that ranges from channeling all resources toward one offspring to treating all offspring equally (Figure 1). Such differential investment is now commonly analyzed in terms of Darwinian evolutionary theory (e.g., differential parental investment in sons and daughters among primates and other mammals [Clutton-Brock and Albon 1982; Hrdy 1987; Voland 1988] or plants [Shaanker et al. 1988]; parentally facilitated starvation or killing by their siblings of subsequent chicks among asynchronously hatching birds [Mock et al. 1990]).

Although an extreme case, primogeniture developed in different parts of the world, often quite independently, in response to widely recurring dilemmas about how much a parent should allocate to how many, and which, offspring—dilemmas that have confronted parents over the ages in a variety of historical, demographic, and ecological settings. There is considerable agreement that parents often behave like strategists in arranging marriages for their children and in ensuring the succession of family holdings (Bourdieu 1976; Goody 1976), but there is no consensus concerning exactly what it is that these parents are trying to accomplish.³

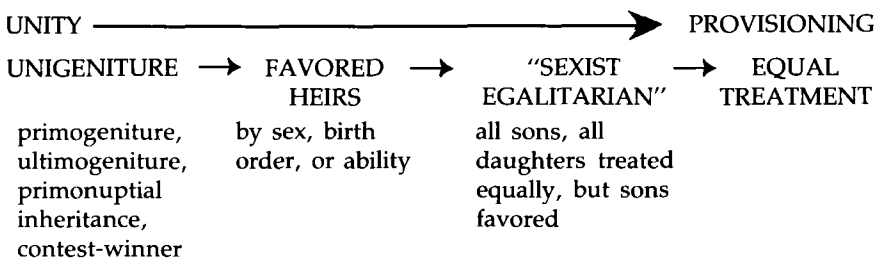


Figure 1. Continuum of parental strategies of heirship, ranging from "unity" (maintaining estate intact) to "provisioning" (providing for each offspring equally). Although strict unigeniture is rare, some degree of preference for a single heir (the oldest son; the youngest son; the first offspring to marry; the most competitive offspring) is common. The preferred category may include more than one heir (e.g., several oldest sons) or all offspring of the preferred sex.

Are these parents conforming to cultural ideals? If so, what shapes the ideals? Why do these ideals change through time? Are parents responding to economic concerns? Reproductive ones? In this "Darwinian" analysis, we seek to examine these questions in a longer time frame than is usual for the historians, economists, and legal scholars who have already done much valuable research on the institutional and cultural background for the practice of primogeniture during specific historical periods.

Consider then the puzzle of primogeniture in its three basic parts: Why channel resources to a single heir? Why prefer males? Why prefer first-borns? By elucidating an extreme case, the analysis of primogeniture may help to illuminate the nature of parental goals as parents pursue what Goody (1976) has termed "strategies of heirship." We will examine each of the questions in order. Let us begin with a brief survey of when parents treat offspring equally and when they channel resources to a favored heir. Why ever practice unigeniture?

"In Massachusetts estates are very rarely divided; the eldest son generally takes the land, and the others go to seek their fortune in the wilderness. The law has abolished the right of primogeniture, but circumstances have concurred to re-establish it."

Alexis de Toqueville, *Democracy in America*,
originally published in French in 1835
(1981:176)

EQUALITY, INEQUALITY AND FAVORED HEIRS

Partible inheritance characterized by egalitarian divisions is the rule throughout most of the United States today (Judge and Hrdy 1992; Menchik 1980; Shamma et al. 1987). At the death of the last parent, his or her resources are divided more or less equally among surviving offspring.

In the United States egalitarian partible inheritance began to emerge during the nineteenth century, proceeding at different rates in different areas (see Ryan 1981 for Oneida County, New York; Gagan 1981 for Ontario, Canada; Ditz 1986 for upland and interior eastern Connecticut), depending on both ethnic origin (e.g., Salamon [1980] found that impartible inheritance prevailed among Irish immigrants to Illinois, partible inheritance among Germans; see also Gjerde 1989) and economic opportunities (Newell 1986).

Glimmerings of equal treatment of offspring were already apparent by

the early nineteenth century in New England (Ditz 1986:76–77). The most detailed documentation of this transition derives from an analysis of 1151 wills filed in Butler County, Ohio, during the 62 years from the formation of the county in 1803 through the end of the Civil War in 1865 (Newell 1986). Newell's midwestern study documents a pattern of increasing equality over this period. Wills exhibiting unigeniture or those in which one or two sons were favored over other offspring declined from 15% in the period 1803–1819 to 5% by the end of the study (1860–1865; Newell 1986:268–269). From this point on, the vast majority of Americans treated sons and daughters equally. For example, by 1890 and for the succeeding 94 years, the majority (70% or higher) of 661 Californian testators who had two or more children treated them all equally. Sixty percent of 475 parents survived by both sons and daughters treated the sexes equally (Judge and Hrdy 1988, 1992).

In colonial America, however, the phrase "egalitarian inheritance" meant something quite different. Egalitarian meant that the primary asset, land, was divided equally among offspring of just one sex, sons. Indeed, in the classic work on inheritance in colonial America, daughters merit no mention (Greven 1970).⁴ (This exclusion of daughters is analyzed below.) Furthermore, historians of colonial America have tended to focus more on the degree to which inheritance was partible than on the variation in the amount and type of shares different sons received, as well as variation in the timing of when they received them (cf. Auwers 1978; Jones 1981).

When rural New England fathers exercised their right to designate who got what, many of them stuck close to the intestate formula that singled out older sons for special treatment. Of a sample of 46 wills in Suffolk County, Massachusetts, in the last decade of the seventeenth century, most (44 of them) were written by men. One-half of these men mentioned more than one son. Of these fathers known to have more than one son, 17 singled out a particular son for special treatment or acknowledged that a particular heir had in the past received land either as an *inter vivos* gift or in exchange for debt or payment.⁵ In six cases, the testator specifically invokes the phrase "double share for eldest son" (Judge, Hrdy, and Vervaeke, unpublished data).

For those fathers who died without making a will, intestate laws varied from colony to colony (summarized in Shammas et al. 1987:32). Generally these laws dictated that a widow was entitled to a life estate in one-third of her husband's property; the remaining two-thirds went to his children. In New Hampshire, Massachusetts, Connecticut, Rhode Island, Pennsylvania, and Delaware colonies, this real and personal property was divided into equal parts equivalent to the number of children plus one. A double share of both the personal property and the

land went to the eldest son; younger sons and daughters received one share apiece. In revolutionary New York, testate law allocated a double share of personal property to the eldest son *in addition to* his right of primogeniture in the land, rendering New York in the period around 1750 more biased in its preferential treatment of eldest sons than it had been earlier, when it had practiced Dutch custom, and even more extreme than Britain, normally thought of as the archetype for primogeniture. In contrast to the situation in New York at this time, British primogeniture only applied to real property (Shammas et al. 1987:33).⁶

Authority for allocating double shares to eldest sons supposedly derived from Mosaic injunctions. Reference to an obscure passage in Deuteronomy 21 can be found scribbled in the margins of an early New England intestacy statute (Shammas et al. 1987:34). In fact, Deuteronomy 21 was written to guide a polygynist Hebrew should he find himself in possession of a captured younger concubine whom he preferred to an older wife (Deuteronomy 21:10–15). Thus, “if the first-born is hers that is disliked, then on the day when he assigns his possessions as an inheritance to his sons, he may not treat the son of the loved as the first-born in preference to the sons of the disliked, who is the first-born, but he shall acknowledge the first-born . . . by giving him a double portion of all that he has” (Deuteronomy 21:15–17). Why would monogamous, primarily Protestant colonists, who were not in the practice of capturing concubines, so unquestioningly follow this precedent unless they were predisposed to do so for other reasons? The Bible recommends many other practices that colonists saw no reason to adopt, so the stated rationale is an unlikely explanation.

Throughout the early colonial period, it is difficult to consider inequality separately from son preference. An analysis of wills from Buck’s County, Pennsylvania, for the period 1685–1756 indicates that testators often attempted to treat sons more equally than did intestate laws, but at the expense of daughters, who received *less* than they would have under intestate law. Similarly, “economies” in the treatment of widows also tended to benefit sons (Shammas et al. 1987:42–47, 55). Daughters tended to do better either when estates were liquidated (Shammas et al. 1987:57) or when merchants left estates whose primary value was in assets other than land (Narrett 1981).

For the most part, the colonial practice of favoring sons generally, and awarding double shares to elder sons, functioned to ensure that at least one son received a substantial portion of land.⁷ What did parents, and the favored heirs, gain from this practice?

“. . . the value of land as a resource may lie not only in the food and shelter it provides, but also with the breeding privileges it confers upon its owner.” (Woolfenden and Fitzpatrick 1978:107)

Partibility in Ecological Context

Impartible inheritance, or in more attenuated form the lumping of assets designated for favored heirs, tends to be practiced when division of assets entails costs. For aristocrats, these costs are often highly symbolic and political as well as economic. Hence, for the moment we confine our discussion to peasants and family farmers. In their case, the main cost of partibility is that it reduces the size of a holding below the minimum needed to support a family, although clearly the desire to maintain social status and local political power still remains a factor.

In those Eurasian and American agrarian societies in which a minimum amount of land has been critical for marriage and reproduction, habitat saturation forced parents to leave the main landholdings to selected offspring, smaller compensation (not necessarily land) to other sons, and dowries or "portions" for daughters. Indeed, the English word for a married man, "husband," bespeaks this history of resource-based reproduction. It derives from the Old English "husbond," in use by the thirteenth century to specify a farmer who owns his own house and land (Homans 1941:72). Among these peasants, plots of land were likely to pass from father to son, although under some circumstances a plot passed to a daughter or, more often, a widow, who was then joined by a male partner (see Haines 1990 for examples among German peasants).

When Hajnal (1965) distinguished non-European marriage patterns (early and nearly universal marriage) from European ones (late marriage and celibacy common for some women as well as men), he was in fact describing one of the consequences of a breeding system in which eligibility to breed depended on a minimal holding of land (cf. Low 1991; Voland 1990; Voland and Engel 1990). Similar land-based breeding systems have been studied for other animals, including cooperatively breeding territorial birds (Koenig and Stacey 1990) and such primates as gibbons and marmosets. Individuals achieve breeding status only after they have acquired or inherited a territory or other resource base and are joined by a mate, who is attracted by the resource that the chosen partner controls. As in humans, nonbreeders either emigrate or opt for a nonbreeding, helper role (Stacey and Koenig 1990).

Most sociobiological models of mating systems have been built upon the assumption that *females* are the limiting resource and that the optimal strategy for males is to inseminate as many females as possible (Bateman 1984; Symons 1979; Trivers 1972). Thus males compete with other males for access to mates, with the result that virtually all females but only some males breed (see Daly and Wilson 1983 for a concise summary). It is clear, however, that a different model, one based on different assumptions, is needed for resource-defense mating systems

where breeding opportunities are not constrained by access to mates but by access to resources, or to mates in possession of resources (essentially, monogamous or serially monogamous versions of the "resource-based polygynous" breeding system modeled by Emlen and Oring [1977]). To produce competitive offspring in a resource-based system (land-based, in the case presented here), parents must find ways to bias intergenerational transfer of holdings (again see comparable examples among cooperatively breeding birds [Stacey and Koenig 1990]).⁸ Favored or successful heirs (typically males, as discussed in the next section) will be in a position to attract more or higher-quality mates (e.g., in terms of youth or fecundity, see Borgerhoff Mulder 1990 for polygynous Kenyan Kipsigis; Voland and Engel 1990:Table IV for German peasants).

Constraints on the partibility of land, whether ecologically imposed by shortage of arable land or politically imposed by feudal landowners hoping to stabilize intergenerational transfers, have shaped family organization throughout history. Unigeniture is typically linked to a "stem-family" system and, some would argue, gives rise to it (Homans 1941:chap. IX; Berkner 1976:95; Smith 1977). Partible inheritance, on the other hand, is associated with joint or nuclear families (Homans 1941:120).⁹ According to the model presented here, both ecological and historical conditions shape inheritance systems, which in turn lead to particular family systems.

How many heirs a father could afford would depend both on how much land he started with and on prevailing ecological conditions. At different times in Eurasian and American history, farmers have found themselves in one phase or another of recurring ecological and demographic cycles. At low population densities, widely available land could be divided among heirs. In more saturated habitats, decreasing land availability and smaller holdings led to general impoverishment or else increased tendencies to channel land to one or a few heirs (who may have had obligations to provide for nonheirs). Depopulation, opening of frontiers, or new employment opportunities would alleviate the pressure on the land.

Conditions that reduce the pressure on landholdings have been documented for widely different geographic areas and times in both the Old and New Worlds (see especially Le Roy Ladurie [1976] for Languedoc, France, at the end of the Middle Ages; the Midlands of England for roughly the same period [Howell 1976:117ff.]; and the first several generations of settlers in colonial New England [Greven 1970]). Continued population growth leads to land shortages and diminished size of individual holdings. Farmers are forced to choose some form of unigeniture (and with it, impoverishment of disadvantaged heirs) or else greater and greater impoverishment for all will occur in each successive generation

until new frontiers in land or occupational opportunities open up, giving parents the luxury of partitioning resources in line with what Thomas Jefferson (a fierce opponent of unigeniture) called "the natural affections of the human mind" (Katz 1977:17).

As British social historian Cicely Howell points out, "partible inheritance is found where there was enough land for all sons, or where land was not especially significant and the distinction between land and chattels not vital to the survival of the family" (Howell 1976:117). Extremes of impartibility are found where a minimum amount of farmland is essential to set up a reproductive unit, and land is scarce (e.g., in eighteenth- and nineteenth-century Japan [Smith 1977; Skinner 1987]).

Howell's generalization applies well to early colonial New England. Ninety-six percent of first-generation fathers who settled in the wilderness of Andover, Massachusetts, in the mid-seventeenth century divided their property among two or more of their sons (Greven 1970).¹⁰ Greven was able to document only one case of primogeniture in the first generation of settlers at Andover. By the third generation, once abundant forests surrounding the community were under cultivation, only 58% of fathers divided their land among two or more sons; the remaining 42% kept the main landholding intact and left it to a single son (Greven 1970:227–228). "About two-thirds of the inheritances of paternal land by will alone involved the paternal homestead, the majority of inheritors being eldest sons" (Greven 1970:228).

After the 1720s, three-fourths of third-generation sons who were able to obtain portions from their fathers (some of them through purchase) were first- or second-born sons (Greven 1970:130–131). In short, primogeniture was abandoned by the earliest settlers from England, reinvented in attenuated form when land became limited, and once more abandoned when conditions again changed.

Ecological fluctuations were marked by differential degrees of discrimination among sons. It would appear from his famous account of primogeniture in America that Alexis de Toqueville must have encountered a section of Massachusetts during a peak in impartibility.¹¹

Specific case studies in colonial New England provide evidence of parents calibrating their strategies of heirship in line with the availability of resources. After a long period of holding steady at low prices, land prices in Massachusetts began to rise steadily between 1710 and 1750. After 1750, however, pressure on Massachusetts agricultural land (still the main means of production) lessened as New Hampshire opened up for settlement. Once again, sons were treated more equally. By the 1820s, in areas of Connecticut where an increasingly commercial economy began to provide opportunities apart from the land, parents with larger estates not only divided property equally among sons but began

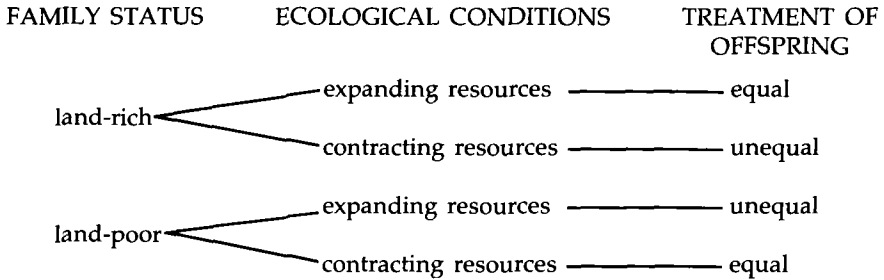


Figure 2. The effects of ecological conditions on equitability in treatment of heirs in families with either abundant or insufficient land.

to include daughters in divisions of real property. Within the smaller landed estates, however, daughters continued to be excluded from inheritance (Ditz 1986:76), possibly so their brothers would be able to remain among the land-rich (see Figure 2 and additional discussion in the next section).

On the surface, it would appear that land scarcity led to inequality, prosperous conditions to equality. In fact this equation is too simple. It is a curious fact that land-rich parents often discriminated among offspring *more*, not less, than did land-poor parents with insufficient resources to provide adequately for each offspring. For example, Ditz found that in the 1770s, when Connecticut land was in short supply, small landholders treated sons more, not less, equally. That is, they were *most* likely to include younger sons (Ditz 1986:Table 4.1, col. 5), though the inclusion of these younger sons tended to be at the expense of their sisters' legacies.

It would appear that parents whose holdings were so small that they could not provide even one son with the minimum holding to support a family (around 20 acres in that area) divided their insufficient resources equally among all sons (Ditz 1986:72, Table 4.3). Similarly, Newell reports that during the period 1803–1865 the Ohio norm was to give each son enough land to farm, but as land became less available, and this tactic became untenable, parents began to bequeath portions of their holdings to all offspring, including daughters, so as much as one-third of the land went to daughters. Thus, the land-rich were less egalitarian in difficult economic times as they acted strategically to maintain standing in the landholding class while those with little land gave unequal bequests during economic prosperity in the hope that favoring one heir might enable him to lift himself into the realms of the land-rich. The richest could afford to be egalitarian when resources were expanding, and the poorest realized no gain from inequality when prospects were poor (Figure 2).

None of the American examples are as pronounced as the unequal

treatment of heirs reported for Eurasian elites (reviewed in Dickemann 1979a; Boone 1986). Political stratification was more extreme, and in Asia at least, ecological conditions were more extreme (in terms of recurring calamities, such as famines; Dickemann 1979b). By contrast, conditions tended to be generally more favorable in New England, and more options existed for new settlements and migration. Rates of infant mortality were usually much lower (especially in the healthier, higher-elevation areas like Andover, where both men and women routinely lived to age 70; Greven 1970:26).¹² Although the data for colonial New England are not as extensive as one might like (in particular we need to know more about the marriage prospects of sons and daughters who migrated; Jones 1981), rates of celibacy and childlessness in general tended to be much lower for rural New England than for comparable areas in the Old World.

Relative differences in well-being were never as extreme in New England as they were in eighteenth-century France or nineteenth-century Japan or India. Whereas in Japan typically only one son per family would marry (Smith 1977),¹³ the situation in New England was more flexible, and many younger sons would eventually marry, although (we speculate) not necessarily at as young an age, or to as young a wife, or in their natal community.

According to the simplified model discussed here and in the next section, we hypothesize that in these land-based breeding systems, parents with relatively large landholdings responded to ecological conditions differently from those with relatively smaller holdings (Figure 2). According to this model, parents with abundant land (as in the first generation of settlement) responded to expanding resources by providing for all sons, but they responded to contraction of resources and pressure on land by providing each son with the minimum necessary (or its cash equivalent), while channeling the bulk of productive land to one or several favored heirs.

Even though most sons were likely to survive and eventually married, those favored with landholdings of at least a minimum size (20 acres in Connecticut, closer to 30 in Andover) would be more likely to marry within their natal community.¹⁴ By contrast, land-poor parents responded to contracting resources in the opposite manner, behaving with *greater equality*, so parents divided legacies in a scatter-shot manner—in Dickemann's words, for an extreme Eurasian case, placing "equal bets on a series of equally uncertain outcomes" (1979b:189, n. 3).

During periods of increased land availability or prosperity, land-poor parents might discriminate among sons to ensure that one or two of them would remain in the landed class; this is admittedly the least well documented portion of the model. Ditz (1986) essentially anticipates this interpretation when she writes for early Connecticut that "The large

majority of colonial families in a position to provide each son with at least twenty acres of land or its cash equivalent chose to concentrate their resources on some sons at the expense of others." During the 1770s, more than half of all testators in a position to bequeath twenty acres to each son gave favored sons property worth at least twice the value of what least-favored sons received (Ditz 1986:72, Table 4.3, col. 4). In the case of land-rich parents, channeling assets to favored heirs allowed selected offspring to maintain a privileged socioeconomic status, but in the case of relatively land-poor parents it provided a means to elevate one or more selected offspring into a more privileged position with increased probability of survival and successful reproduction. To understand unigeniture, we need to ask what parents gain by consolidating resources in the hands of a few offspring.

"... keep your Estate in one Hand; never divide it or cut off any, especially Lands. Let every one who succeeds, make what Additions he can. . . . And by this Means with Frugality & Industry, the Estate will increase vastly in a few descents. 'Tis not good to be upon a Level, or under the Foot of every Scoundrel. . . . As for the other Children, if there are several, give them Trades. . . . This I think is better for every one, than to have a little Scrap of Land to Starve upon, and the Estates ruined, & the Family sink into Obscurity. . . ."

The Reverend Thomas Cheesebrough, eighteenth century,
Stonington, Connecticut¹⁵

A Darwinian Model for Biased Inheritance

Given that parents are linked by both sentiment and genes to each of their offspring, what premium could be attached to membership in the land-rich class to cause parents to discriminate against one offspring in order to ensure that another offspring receives a substantial portion of land? Land-based breeding systems provide part of the answer, but for the rest we need to consider a chronic evolutionary stumbling block.

Whether hunter-gatherers, pastoralists, peasants, or seigneurs, humans have confronted the same threat of lineage extinction that confronts other organisms characterized by limited lifetime production of young. Indeed, for most humans (there will certainly be exceptions among expanding populations with high fertility and high infant survivorship), the actual probability that either a man or a woman will die without leaving surviving offspring is probably far higher than heretofore realized by most evolutionary biologists (but see Goody 1976:87 for an early statement of the problem). We follow the lead of anthropologist Mildred Dickemann (1979b), who specifically calls attention to the

threat of lineage extinction in her writing on Eurasian marriage systems. We believe that the “stumbling block” is more general than even Dickemann realized, and that it will require rethinking of certain basic assumptions.

Dying without offspring is common and occurs under a variety of conditions (e.g., see Goody 1976: app. 2). This point came to our attention when we noticed that of 1538 twentieth-century Sacramento County, California, testators, 40% died without any surviving children. Only a small fraction of those testators not survived by children left surviving grandchildren (Judge and Hrdy 1992). Concerned that our sample might be atypical, we searched for other data sets with information on the proportion of adults who die childless (summarized in Table 1). Data from Rancho Bernardo, near San Diego, California (Friedlander 1992), turned out to be very similar to our data from Sacramento County.

Even data from much more remote and more prolific populations revealed surprisingly high rates of childlessness. Demographic data for a population of !Kung hunter-gatherers characterized by relatively high infant mortality and with births at roughly five-year intervals, during which the mother nurses the preceding offspring, reveal that 36% of 44 women who passed the age of menopause had no surviving children (Draper and Buchanan 1992). Twenty-five percent of 124 women in a sample of Herrero women, from a population sometimes exhibiting higher fertility than the !Kung, had no surviving children when last interviewed. Male rates of childlessness among the Herrero were lower, and reproduction had not necessarily ceased by the age at interview—sixty years or older (Pennington and Harpending, Pennsylvania State University, unpublished data).

In stratified societies, successful male polygynists can reduce the likelihood of dying childless by siring large numbers of progeny (Betzig 1986), but such exceptional fecundity would be accompanied by even larger wifeless segments of the male population who left no progeny at all. Even under the near-optimal conditions that characterized British ducal families (pronatalist sentiments, interbirth intervals shortened by the use of wet nurses, and better than average nutrition resulting in high fertility) roughly twenty percent of married women and twenty percent of married men died without leaving progeny (Table 1). (Note that only information on legitimate offspring was available, so the estimate of male childlessness is likely to be high. For this reason, and also because lineage survival tends to be measured as “patrilineal” survival, rates of lineage extinction are going to be higher than rates of biological or genetic extinction. The question of why lineages are defined as they are—in this culture, in terms of the legitimate patriline—is beyond the scope of this paper.)

Table 1. Proportions of Adults Dying without Surviving Offspring in Populations Spanning Various Times and Conditions

Population	Time Period		Proportion Childless	Average Number of Children	Source
	Predominant Economic Type	and			
!Kung, northwestern Botswana, Africa	1928-1988: A transitional period between gatherer-hunter subsistence and sedentary stockraising		31% of 45 men over age 60	3.6 ever born to men	Draper and Buchanan 1992
			36% of 44 women over age 60	3.5 ever born to women	
Herrero, Nagamiland, Botswana	1921-1986. Between 1909 and 1986 refugees from southwest become prosperous pastoralists		17% of 66 men over 60 years had no child alive when last interviewed	Completed family size ranges from 2.6 among cohort born before 1921 to 4.5 among 1941 cohort ¹	Pennington and Harpending, unpublished data
			25% of 124 women over 60 years had no child alive when last interviewed		
British Ducal Families	1330-1729. Elite landholders		27% of married men (not counting illegitimates) ²	1680-1729	Hollingsworth 1957:20-22
			23% of married women	7.0 (born to married women)	
	1730-1829		19% of married men	1730-1779	
			19% of married women	8.5 (to married men) 9.1 (to married women)	
	1830-1939		17% of married men	1780-1829	
			12% of married women	7.9 (to married men) 10.5 (to married women)	
Krummhörn, Germany	1720-1847			1830-1879	
				6.1 (to married men) 8.0 (to married women)	
			28% of nonemigrant men	1880-1939	E. Voland, personal communication
			21% of nonemigrant women ³	5.2 (to married men) 4.8 (to married women)	

Wethersfield, Connecticut Upland, Connecticut coastal Massachusetts, colonial America	1750s Agriculture with emerging mercantile economy 1690-1700. Subsistence agriculture on small farm holdings, incipient mercantile economy	21% of probates 47% of probates 26% of probates 25% of 44 male testators mention no children ¹	Ditz 1986
Suffolk County, Ohio	1790-1800. Agriculture with emerging mercantile economy	3.5 mentioned in will ²	Judge, Hrdy, and Vervaecke, unpublished data
Rancho Bernardo, southern California	1890-1900. Mercantile economy, many recent immigrants	41% of 176 testators (68% of whom are male) mention no children ³ 44% of 107 male testators 51% of 87 female testators	Newell 1980
Butler County, Ohio	1860s	2.2 mentioned in will ³	Newell 1980
Sacramento County, northern California	1972-1990. White upper middle class community, predominantly professional men and homemakers 1890-1984. Mildly stratified mixed community, primarily mercantile with agriculture of declining importance	38% of 172 testators 32% of 126 dead men 30.1% of 521 women aged 50 or more or dead 40% of 908 male testators 40% of 630 female testators 39.4% of 1073 intestate decedents 1.7 surviving offspring (908 male testators) 1.6 surviving offspring (630 female testators) 1.8 surviving offspring (1073 intestate decedents)	Friedlander 1992 Judge and Hrdy 1992

¹Completed family size increased through time with introduction of antibiotics and decrease in primary sterility.

²These estimates are bound to be low. Proportion of childless elite men would be higher if data for *unmarried* elites were included. Similarly, in the Krummhörn case, rates of childlessness would be higher for emigrants than for those able to remain.

³These estimates are likely to be high. Until the listing of all "heirs of law" was legally mandated, information on family composition is based on names of offspring mentioned in the will itself, and these data are sometimes incomplete.

Throughout human prehistory and history, we believe that the significant likelihood of dying without children provided a chronic challenge to lineage survival. Dread of lineage extinction would only be exacerbated by customary preferences for descent in a particular (typically male) line. We assume that natural selection shaped human reproductive strategies to make them responsive to fluctuating local socioecological conditions at both behavioral (Weinrich 1977) and physiological (Ellison 1991) levels. In addition, we believe that at a conscious level, humans also became aware of local family histories, and this awareness informed mentalities capable of even more fine-grained calculations in matters of marriage and inheritance, and these calculations eventually became reflected in customs (Bourdieu 1976; Goody 1976; Richerson and Boyd 1992).

Although the adoption of agriculture and food storage some six to ten thousand years ago led to population increase, these improvements in subsistence technology did not eliminate the basic challenge to long-term survival of lineages. Using measures of surname survival (which can be viewed as a proxy measure of lineage survival), Howell (1976:131) calculated only an 8% chance of survival for the period between 1280 and 1700 in the heavily agricultural Midlands region of England; comparable statistics are available for other agricultural regions (Hsu 1948: 3–12, 271–276; Le Roy Ladurie 1976; Hammel 1974:343–344, all cited in Dickemann 1979b).

Nevertheless, although agriculture did not ensure long-term lineage survival, agriculture did alter the *prescription* for it. As arable land became saturated, use of productive land became an increasingly important (perhaps the single most important?) feature of a peasant's phenotype in terms of multigenerational lineage persistence.

Land and family posterity became closely identified in cultural traditions; as Smith puts it for Tokugawa, Japan, "ultimately, the competition for land was a competition for family survival" (1977:134). Although people often measure success in symbolic terms having more to do with prestige, wealth, and land ownership than with genetic success, in the case of men the two types of success have been highly correlated over time (Betzig 1986; Low 1991; Voland 1990).

Theoretical population genetic models developed by Alan Rogers demonstrate that *at certain levels of wealth* for parents in saturated habitats, wealth can turn out to be a *better* predictor of long-term fitness than the number of children they produce (see Rogers 1990:Fig. 4). By contrast, in a newly opened, expanding frontier, or in an economy with new opportunities to earn a livelihood, a high reproductive rate can be more advantageous than a high level of wealth. In terms of inheritance, the former set of conditions makes biased inheritance or actual unigeniture more adaptive; the latter favors equal treatment of heirs.

People all over the world are interested in the well-being of their children, although in some cases the well-being and survival of the family, "House," or lineage may take precedence over the well-being of individual children (Dickemann 1979a; Hrdy 1992). The prevalence of a particular one of these variations on the theme of lineal persistence depends on how parents resolve the tension between "unity" of family holdings and "provisioning" for each child (see above, Figure 1). Only where transferable resources or opportunities are either very abundant or virtually absent, or where families are very small, would we expect such tension not to exist.

Nowhere is a congruence between "lineage survival" and "patrilineal survival" more convincingly demonstrated than in Smith's studies of Tokugawa, Japan. Smith's analysis of tax registers for farmers living on the Nobi plain between 1717 and 1830 provide a compelling account of agrarian patrilines in competition with neighboring patrilines. Landholdings were in continuous flux, bought and sold as the fortunes of neighbors rose and fell (Smith 1977:117). Some sixty percent of changes in landholdings were the result of transfer of land between local families in the same village (Smith 1977:118). Typically, any growth in size of holdings was at the expense of families with smaller holdings, who gradually sank into landlessness, resulting in the local "demise" of the family.

Smith followed the fates of families and their holdings from one tax registration period to the next. Of 146 families with large holdings, 76% retained large holdings at the next census. By contrast, only 1% of those with small holdings had substantially increased their holdings, and only 45% still retained any holdings at all by the next registration. Of those families who passed out of existence, 1% had previously held large holdings, 5% medium-sized holdings, 14% small holdings, and 28% had been landless in the earlier census (Table 2; cf. Low 1991 for a European example). Not only was it easier to move down the economic scale than up, but for those who moved down, the demise of the family became an increasingly likely fate. (It is of course not possible to document the genetic consequences of these family histories, but one might reasonably expect a correlation between family demise and lower than average genetic representation in succeeding generations.)

In his summary of eighteenth-century agrarian marriage systems in Nakahara, Smith's explanation for unigeniture goes beyond immediate economic costs of land fragmentation. These Japanese peasants lived in "stem-families" that closely approximated the ideal of unigeniture, and they practiced a form of preferential inheritance far more extreme than anything found in colonial America. Almost invariably only one son inherited the land, and only this son (who succeeded to family headship) married. Typically this heir was the eldest son (for exceptions see

Table 2. Changes in the Status of Peasant Holdings from One Census "Observation" to the Next, Based on Smith's study of records from Nakahara, Japan

Class of holding at next observation	Class of holding at first observation			
	Large	Medium	Small	Landless
Large	76% (111)	14% (19)	5% (3)	0% (0)
Medium	19% (28)	61% (86)	10% (6)	3% (2)
Small	1% (2)	12% (17)	45% (26)	6% (4)
Landless	3% (4)	8% (11)	26% (15)	63% (45)
Demised family	1% (1)	5% (7)	14% (8)	28% (20)
All holdings	100% (146)	100% (140)	100% (58)	100% (71)

NOTE: Figures in parentheses indicate number of cases.

(Reprinted from Table 7.1 in *Nakahara: Family Farming and Population in a Japanese Village, 1717-1830*, with the permission of Stanford University Press, © 1977).

Hayami 1983). "Practice was remarkably consistent—with only the heir remaining in the family and the other sons and daughters leaving" (Smith 1977:134).¹⁶

A clear advantage of this "stem-family" system was to keep the family farm and other property intact from one generation to the next. "Had more than one son stayed at home and married, this rule of impartible inheritance would have been difficult to enforce, since after the father's death the pressure to divide the property would have been intense. Indeed, in most cases where a second son married and stayed in the family, partitioning resulted soon after" (Smith 1977:134), with the attendant consequences of family "obscurity" so feared by Reverend Cheesebrough.

For the disinherited offspring, fates varied. Many migrated out and hence removed themselves from the data base of subsequent demographic studies (Low 1991; Voland 1990). Prospects for younger sons who migrated a short distance away might be very limited, but the prospects in other parts of the world could be even worse. In European and American cases many migrants would die, depending in large part on where they went (Earle 1979; McNeill 1976:55). Some of them, however, (an unknown proportion) would go on to found new dynasties.

Although we often have detailed information about those who left—primarily males, some females; primarily nonfavored heirs of breeding

age (Carr and Menard 1979; Horn 1979; Low 1991; Voland 1990)—we do not yet have good data on the rate of survival or reproductive success of the emigrants.¹⁷ Some contemporaneous information is available in the form of letters, and the fates of nearby family members would be well known. Nevertheless, parents (probably with good reason) did not behave as though they were able to predict the outcomes of different strategies. Their “estate planning” appears to have been very conservative.

There can be little doubt that parents were concerned about the productive capacities of their farms as well as their own maintenance in old age. Considerable space in men’s wills is devoted to provisions for aging widows. Yet there is no indication that parents were attempting to produce as many children as possible and then keep them all on hand as potential laborers and caretakers. Rather, the unequal treatment of offspring appeared to be aimed at preventing eventual disappearance of the family line. Parents (in fact, mostly fathers) treated the family farm like a trust, allocating it to a favored heir who by dint of this inheritance had an increased probability of marrying and producing surviving offspring. Unequal treatment of heirs was a strategy to minimize the probability of dying without surviving grandchildren.

In the Eurasian and American cases discussed here, favored heirs do not actually receive their legacy until they marry, or else heirs marry shortly after receiving it. Specific provisions may be made for replacing a favored heir with another sibling should he die prior to reproduction. And finally, although favored heirs may be obliged to help the widow and their siblings, they retain considerable managerial rights and are expected to favor their own children’s interests (e.g., see Ditz 1986 for early Connecticut). In short, marriage and inheritance customs ensure reproduction in at least this favored branch of the family, guaranteeing a relatively secure resource base to produce and support a maturing family.¹⁸ In reproductive terminology, then, generational variance in the reproductive success of this category of lineal heir would be kept very low. Reproductive success among nonfavored heirs would be more variable: many would not reproduce, a few would be very successful.

Population biologists (Gillespie 1977)¹⁹ were the first to point out that among children in two lines with equal mean numbers of children but different variances (one line *always* produces two children, while others alternate between one and three), the line with lower intergenerational variance in reproductive success will result in higher reproductive success over many generations (see Mueller 1991 for an application of this model to humans). If lineage survival was their goal, parents would be expected to allocate resources in line with multiple facets of economic opportunity, including options for nonfarm-based livelihoods and op-

portunities for migration and settling new habitats. According to Ditz's historical summary of parental goals in early nineteenth century Connecticut, "Preferential partibility suggests that these [landholders] did not intend to supply their children with a mere head start. They wanted to guarantee the status of freeholder (or marriage to a freeholder) to as many children as possible without ruining the chances of all." Although employment in nonfarm activities helped to expand the limits within which the tension between unity and provisioning could be resolved, "neither the still new sources of local employment nor the increased opportunities for emigration and resettlement in the early nineteenth century eradicated this basic tension" (Ditz 1986:77).

From a Darwinian perspective, the tension between unity and provisioning takes on an added dimension. Depending on the extent to which there exists a tradeoff between transmitting genes and transmitting wealth to the next generation (Rogers 1990:480), parents should opt for a few well-endowed offspring virtually certain to produce at least a few surviving children. Generational variance in reproductive success in this favored line would be low; in each generation, at least one offspring and his family would be guaranteed to produce grandchildren. Secondary or unfavored heirs would receive enough of a stake to set off in life, but they would confront a riskier future. Only occasionally would these less-favored lines be marked by success, so intergenerational variance in reproductive success would be much higher. As environments change because of soil depletion, economic development, or expanding frontiers, this mixed strategy—conserving the main body of resources while gambling with the remainder—might well be optimal for long-term preservation of a lineage (cf. Dickemann 1979b).

The answer to "why unigeniture," in Darwinian terms, may be that where wealth or landholdings are correlated with fitness, parents ensure long-term fitness by favoring particular offspring. Disinheriting all but a single heir (absolute unigeniture) is rare, but innumerable milder inequalities can be documented across human history. Theoretically, of course, in a completely monogamous breeding system it should not matter if the favored heir is male or female. Still unanswered then is the question of why these favored heirs are so often male.

"Dryton, son of Pamphilus a Cretan, of the diadochi . . . a hipparch over men, being healthy and of sound mind and sensible, has made the following will. . . . The horse on which I campaign and all my armor [I bequeath] to Esthladas, my son by Sarapias my former wife . . . of the remaining buildings and waste grounds . . . let Esthladas have half and Apollonia and her [four] sisters half."

Abridged excerpt from the Last Will of Dryton, 126 B.C., translated in Pomeroy 1984:104–105

WHY PREFER SONS?

There is a general consensus that patriarchal tendencies have deep roots. One of the earliest wills on record, written on papyrus in 126 B.C. by a Greek soldier living in Egypt, favors an only son at the expense of his sisters (Pomeroy 1984:104ff.). This type of son bias was characteristic of widespread areas of the ancient Near East (Lerner 1986). Nevertheless, scholars tend to examine the *emergence* of social, economic, and symbolic systems that favor male over female interests in different time frames. Hence Gerda Lerner (1986), a feminist historian, seeks the origins of patriarchy in the marriage and legal arrangements of ancient Mesopotamia around the third millennium B.C. Although we concur with Lerner's historical analysis as far as it goes, using an evolutionary framework we push the origins of biases favoring male interests back in time by millions of years.

The Resource-holding and Productive Potential of Sons

Among mammals generally, and among primates at least since the Oligocene 30 million years ago (Fleagle et al. 1980), a long evolutionary history of sexual selection has led to greater muscle mass, strength, and aggressiveness among males in many species (for exceptions see Hrdy 1981; Ralls 1976). Among humans and the hominoid apes (Ghiglieri 1987; Manson and Wrangham 1991; Wrangham 1987) the tendency is for males to remain in their natal place to breed while females migrate to mate or marry (male philopatry). This propensity of hominoid males to remain in their natal territory facilitates male-male bonding and kin-based alliances among males and may in fact derive from the need for such allies to defend against competing "brotherhoods." Whatever the explanation, male philopatry means that females must either leave or breed with close kin. This female dispersal occurs at considerable cost (Part 1991), especially in terms of female autonomy, because females move into social units without the support of close kin (Hrdy 1981:100-106, 184-187).

Among humans, male domination of females is both reinforced and exacerbated by patrilocality.²⁰ Women generally leave their natal families and marry into households where they lack the social and political support offered by kin (Quinn 1977; Hrdy 1981). Both physical capacities (especially those relating to aggressive potential) and prevailing social systems created conditions in which males have traditionally had greater resource-procuring and resource-holding potential than females do. That being so, control of property given to daughters runs a high risk of

being usurped by her husband or his lineage (which typically would be defined in terms of the one-sided calculus of the "patrilineage" rather than in strictly biological terms). Even if a woman could retain control over property inherited from her parents, her legacy would be perpetually in danger of being diverted to serve her husband's patrilineal ends.

Not only have hominoid males long been able to overpower an individual female on a one-to-one level, wresting resources from her (Smuts 1992), but with the exception of one remarkable species of chimpanzee, *Pan paniscus* (Parish 1992), males—surrounded as they are by kin—have also been more likely than females to form durable coalitions. In social settings in which possession is nine-tenths of the law, sons make better prospects for parents seeking not only powerful allies but reliable custodians for the resources under paternal control.

We believe this combination of factors explains in large part why preferential inheritance by males (typically sons) came to characterize the majority of human cultures. Even in matrilineal societies, where descent is calculated through the female line and women tend to have a high degree of personal autonomy, property typically passes from male to male—that is, from mother's brother to her sons (Murdock 1981: Table 11).

In historical times, these rudimentary biases favoring males have led to far more extreme parental preferences for sons over daughters (particularly among those cultures that calculate descent through the male line) than any of the other facultative sex biases found in nature (Clutton-Brock 1991; Hrdy 1987). Patriarchal authority, a uniquely human historical development, renders humans the only primate species in which men can control the productive as well as reproductive capacities of females (Hrdy 1981).

In addition to the males' greater capacity to protect resources, in some economies the labor potential and culturally mediated opportunities open to sons lead to sons having a higher likelihood than daughters of repaying their families for resources expended in rearing them (Cain 1977, 1982). For example, among peasants in Bangladesh, a son will become a net producer of calories by the age of 10–13. By age 15, his cumulative lifetime production will have completely repaid his parents for what it cost them to rear him. By age 21, he will have paid for himself and one sister. In contrast, even though a daughter begins to work hard at an early age, she will never repay her parents before she marries and leaves to join another family's patriline.

These patterns—which are far from universal—may be either ameliorated or exacerbated by various premortem customs, such as marriage payments (Hrdy 1990). Daughters may represent a liability to parents who pay large dowries, but they represent a net gain to those who

receive bride-prices. For example, in different North Indian castes, daughters requiring dowries are regarded as a liability among elites and a costly tool for manipulating social status among the subelites, whereas among the poorest groups daughters may be an asset to families who receive bride-prices for them (Dickemann 1979a; Parry 1979; see Volland et al. 1991 for a mirror image of this case, in which daughters are far more valuable to propertied than to poor families).

Although it is widely acknowledged that males do have greater resource-holding potential, most previous sociobiological efforts to explain male-biased inheritance have focused not on the greater resource-holding or resource-enhancing potential of males (for an exception, see Sieff 1990) but on the reproductive consequences of son preference (Hartung 1976; Trivers and Willard 1973).

The Reproductive Potential of Sons

According to evolutionary theory, parents should bias investment in offspring with reference to expected reproductive returns (Hamilton 1967). That is, they should invest preferentially in the offspring best able to transform that investment into reproductive success.

More specifically, Trivers and Willard (1973:90) propose that "Natural selection should favor parental ability to adjust the sex ratio of offspring produced according to parental ability to invest." As currently interpreted (Clutton-Brock 1991), this proposition leads to the hypothesis that parents will bias investment in offspring towards the sex best able to translate parental investment into reproductive success. Hence, according to this theory, whenever male variance in reproductive success is greater than that for females (as in polygynous species, where successful males may have dozens of offspring, unsuccessful males none), and when maternal or parental condition is correlated with subsequent reproductive success of offspring (as in the case of a well-nourished mother mammal who produces large, competitive sons—e.g., red deer; Clutton-Brock 1991), then parents in good condition should bias parental investment towards the sex for whom it will make the most difference. That sex will typically be male. By contrast, mothers in poor condition whose sons will be less likely to be successful competitors should pursue the conservative course of producing more daughters, who whatever their condition or rank are likely at least to breed.

A recent study of modern testators in Vancouver reports a pattern of parental investment after death in line with that predicted by the Trivers-Willard model. Parents with estates greater than \$110,350 favored sons whereas those with estates smaller than \$20,350 discrimi-

nated against them (Smith et al. 1987). This reversal is in agreement with a general pattern of exaggerated son preference among elites first reported by the British economist Josiah Wedgwood—a relative of Darwin, who shared his dislike of primogeniture. In his analysis of British wills (1928), Wedgwood noted that “It appeared to be usual among the wealthier predecessors in my sample [of 99 twentieth-century British testators], for the sons to receive a larger share than daughters. In the case of the smaller estates, equal division is much more common” (1928:48; also see Wedgwood 1929). This “Wedgwood effect” can be widely documented not only for Britain in historical times (Trumbach 1978:4) but for medieval Portugal (Boone 1986), precolonial northern India (Dickemann 1979a), eighteenth-century German peasants (Volland 1984), and nineteenth-century midwestern Americans (Newell 1986: 271).

Although the Trivers-Willard model focuses on parental manipulation of the sex ratio at birth, the authors clearly anticipate applications of their model to other forms of parental investment, which could include inheritance: “In species with a long period of [parental investment] after birth of young, one might expect biases in parental behavior toward offspring of different sex, according to parental condition: parents in better condition would be expected to show a bias toward male offspring” (Trivers and Willard 1973:91).

Subsequently, Hartung (1981, 1982) applied similar reasoning to the particular case of male-biased inheritance patterns in humans. He argued that where (a) variance in reproductive success for males exceeds that for females, whether in polygynous mating systems or in monogamous contexts in which some men have differential access to concubines or sequential wives, and (b) male success in obtaining mates is enhanced or determined by the resources he controls (as described in the section on partibility), then it follows that parents who differentially channel wealth to sons should have more grandchildren than do parents who dilute the benefits wealth has for their sons’ reproductive success by diverting it to daughters. Furthermore, a “logical extension of the hypothesis suggests that individuals in the lower economic strata of a society should transfer wealth to daughters, or without bias, regardless of the prevalence of polygyny.” For, if “inherited wealth is not sufficient to put a male within reach of the ‘polygyny threshold’ (in the marriage or mating sense) no increase in reproductive success will result” (Hartung 1982:5).

An obvious prediction generated by Hartung’s model is that the greater the degree of difference between male variance in reproductive success and female variance in reproductive success, the greater the intensity of male bias in inheritance patterns. Unfortunately, data at

hand only permitted Hartung to perform an approximation of this test. Using data from Murdock's *Ethnographic Atlas* (1967), Hartung was able to show a significant correlation between the degree of polygyny and the existence of marriage systems in which males pay a "bride-price" to obtain wives (Hartung 1982:fig. 5); he argued that this correlation is evidence supporting the existence of resource-defense polygyny among these people (cf. Borgerhoff Mulder 1988, 1990). Next, Hartung sought to demonstrate that male-biased inheritance patterns are more likely to occur in polygynous compared to monogamous societies (1982:fig. 7; but see also Dickemann's 1982 critique of the limitations of using coded ethnographic data such as that compiled by Murdock).

According to Hartung, then, parents should channel resources to sons because resources will improve the reproductive success of sons more than they can the reproduction of daughters. At present, however, our ability to test Hartung's hypothesis is complicated by the difficulties of teasing apart the relative importance of differential reproductive potentials, different resource-holding abilities, and different productive capacities of sons versus daughters. Furthermore, many of the parents who either invented or chose to adopt customs favoring sons in general, or first-born sons in particular, were already embedded in patriarchal systems with deep-seated traditions disadvantageous to daughters.

Given this prior history, and the difficulty of controlling for it, we may learn more from the *abandonment* of son preference, as parents switch from son preference to equal treatment of sons and daughters. Consider the spread of egalitarian inheritance in the United States, described above. By 1890 egalitarian inheritance was the norm, and between 1890 and 1984 71% of Sacramento County testators were treating all offspring equally (Judge and Hrdy 1992) *even though the reproductive success of male—but not female—testators increased with log wealth* (as measured by size of the estate the testator owned at death; Figure 3). This difference between men and women was apparently due to the greater likelihood that a wealthy man would marry more than once or marry again after divorce or widowhood.

Neither Hartung's model nor the Trivers-Willard hypothesis, as currently articulated, can explain egalitarian treatment of offspring in this population. Both models predict that Sacramento County parents *should* favor sons more often than they do. For this reason, we posit that the ability of women to hold, manage, and defend property improved over the course of the nineteenth century, in part because of their changing legal status (e.g., as a consequence of the Married Women's Property Acts), and we plan to examine the increasingly egalitarian inheritance patterns in the light of increased resource-holding potential of women.

Of the three questions posed by primogeniture (Why channel re-

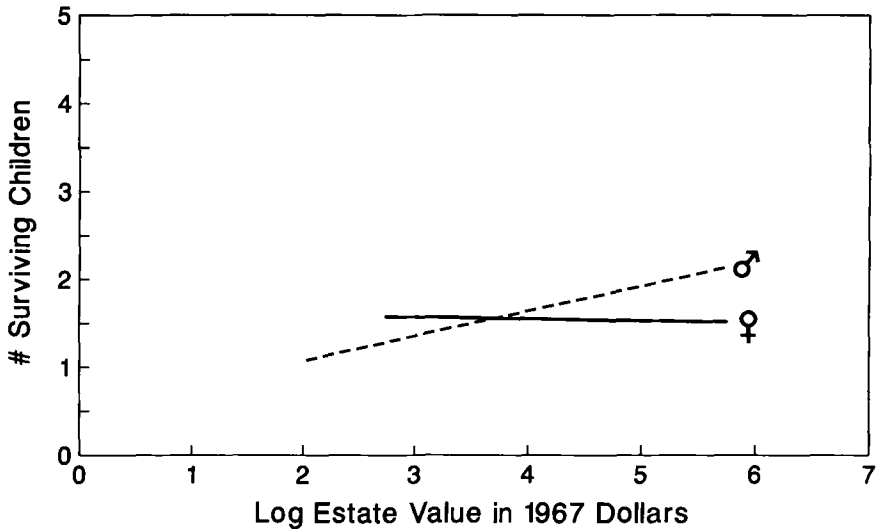


Figure 3. Estate value and number of surviving children for testators in Sacramento County, California, 1890–1984. Data include 908 male and 630 female testators in a primarily mercantile, monogamous population (Judge and Hrdy 1992). The number of offspring surviving at the time of the parent's death increases with estate value in the case of men but remains constant for women.

sources to a single heir? Why a male? Why a first-born?), the question of why parents should prefer sons is easy to answer at the historical level: a generalized preference for sons, and with it an inclination to value male lines over female lines, already existed. It is less easy, however, to explain the prehistoric *origins* of son preference. Furthermore, we still have no convincing explanation for why a preference for sons was retained under some conditions, abandoned in others—although scientifically this area should be the most promising for future research.

Because preference for sons is so entrenched and widespread, it is difficult to formulate a research question that could be answered using the comparative method. In this respect, explaining preferences for first-born sons should be methodologically more straightforward since we can compare societies with and without birth-order preferences and examine the conditions under which different preferences (e.g., last-born versus first-born) emerge.

“As ragged as Lazarus in the painted cloth, where the glutton's dogs licked his sores; and such as indeed were never soldiers, but discarded

unjust serving-men, younger sons to younger brothers . . . the cankers of a calm world and a long peace."

Falstaff, *Henry IV, Part I*: Act IV, scene 2,
by William Shakespeare, seventeenth century

THE IMPORTANCE OF BIRTH ORDER

To describe anyone as a younger son in sixteenth-century England was a "short-hand way of summing up a host of grievances," writes social historian Joan Thirsk. "Younger sons were pitiable enough, but younger sons of younger brothers were plainly the very lowest of the low" (1969:360). For those 10% or so of the world's cultures in which patrilineal primogeniture is practiced, except for appropriate kinship and gender, birth order takes priority over all other qualifications—virtue, innate ability, reproductive attributes, or luck. Why should the selection of primary heir ever depend on order of birth? And why is preferential inheritance by the first-born roughly five times more common than preferential inheritance by the last-born (Murdock 1981)?

First-borns versus Last-borns

Although primogeniture was to become the predominant form of inheritance in Britain, it was scarcely the only form of favoritism practiced. Preferential inheritance by youngest sons, the "Borough English pattern," dotted the village landscape of medieval England, with villages favoring oldest sons existing cheek by jowl with those favoring the youngest. The pattern was seemingly arbitrary (Homans 1941). In parts of Germany, ultimogeniture applied to sons, but if no sons were available, the *oldest* daughter was favored (Haines 1990:66). Among the ancient Maya, kingship descended in the patrilineal line, apparently first to the oldest son, and then if the oldest son died, heirship moved laterally to the youngest brother, whose oldest son, in turn, ruled. Thus, although primogeniture was the primary pattern, there is evidence that primogeniture could be combined with lateral succession from older to younger brother (Schele and Freidel 1990:fig. 6.4, 431*n*).

In contrast to generalized son preference, which tends to be a stable and long-lasting component of many family systems (see above), birth-order preferences generally are more arbitrary, and the preference appears weaker and seemingly less stable through time. Nevertheless, one merit parents might have seen in ultimogeniture—particularly when other economic options were available to older offspring—would be that

by the time the parents died, other progeny would have established themselves already. In areas where the homestead itself was not a very desirable legacy, ultimogeniture might be linked to responsibilities of the last child to remain at home and care for aging parents.

Of a sample of 563 societies examined by Murdock (1981), 43 were characterized by patrilineal descent and primogeniture, only 10 by patrilineal descent and predominant inheritance by the youngest male heir. Although agriculture was the primary subsistence mode for most cultures in both groups, pastoralists as well as hunting, fishing, and gathering peoples were also represented (e.g., the Central Arctic, Ket, and Yukaghir peoples practice ultimogeniture whereas the northeastern California Modoc gatherer-fishing and hunting people practice primogeniture).

Primogeniture emerges as the more common of the two customs, and perhaps also the more durable. A preliminary look at the literature on ultimogeniture suggests that rather special intervening circumstances may be essential for parents to opt for ultimogeniture (e.g., Leach 1954). To date, the most detailed study of ultimogeniture is found in Haines's (1990) research on eight areas of Germany, including Westphalia, lower Silesia and eastern Schleswig-Holstein. Ultimogeniture, and its counterpart primogeniture, developed in Germany during the Middle Ages with the emergence of the *Grundherrschaft* or landlord system. Based on data on inheritance patterns between 1680 and 1770, only a single son or daughter was present at the time of succession in 24% of cases, but in the remaining 75% a choice was made among sons and/or daughters. Youngest sons succeeded in 57.8% of these cases. In only a minority of cases (8.5%) did an oldest or middle son succeed. In other instances, usually because there was no son available to come home, a daughter succeeded (8.4% of the time; Haines 1990:269). As the average number of children born per family declined after 1870, female heirs became (by default) more common.

Haines argues that three sets of special circumstances led to the development of ultimogeniture in these areas. First, the prevalence of an important cottage industry in linen production meant that older children could be set up in occupations other than farming. Involvement in wool and flax production, spinning, and weaving might even permit upward mobility of some older children into the bureaucracy and merchant classes, so inheritance of the farm was not necessarily the most advantageous lot. Second, parents could afford to have older offspring move into other occupations because alternative farm labor was locally available (Haines 1990:260, 348). Third, death duties known as the *sterbfall* were owed the landlord when right of access to the land was transferred to an heir by tenants. This tax could be as high as one-half of all movable wealth. Hence by designating youngest sons (or daughters if there was

no son), parents postponed paying the sterbfall as long as possible, and by lengthening the generation time between taxes, reduced total outlays the family would pay.

In the absence of such external factors as death duties, primogeniture has certain practical advantages over ultimogeniture. Given unigeniture, designating the favored heir in advance (on whatever grounds) has obvious advantages. Especially when different offspring are to be reared preferentially in terms of access to resources and education, it makes sense to identify heirs early on—an awkward task for parents trying to identify the *last* child born.

Early identification of favored heirs may reduce social tension and permit families to prepare children for adult roles. This biased investment during development is facilitated in the case of first-borns, each of whom is by definition “the only child” at least for a time, til the next sib is born. Developmental factors (age, body size, strength, priority of usage) would also tend to favor the oldest offspring relative to sibs. Where the same inheritance custom persists over many generations, as in Tokugawa, Japan, customary socialization of children molds quite different personalities in older versus younger sons (heirs versus non-heirs; Skinner 1987), and the special role of grandmothers in childrearing is facilitated by the generational overlap between the grandparent’s lifespan and those of children born to their eldest son.

Reproductive Value versus Generational Overlap

Beyond the developmental advantages inherent in selecting older offspring as heirs, two major competing hypotheses to explain primogeniture must be considered. The first is linked to population parameters, the second to the amount of generational overlap.

Population ecologists have long known that in an expanding population, early-born offspring have higher reproductive value (see the recent review in Partridge and Harvey 1988; Promislow and Harvey 1990). Even before later-born offspring mature, the early offspring can establish themselves and begin to breed. Early breeding is especially advantageous in populations with high adult mortality rates because it enables more individuals to breed before they die. Furthermore, if a father does die young, the transition of power to the new heir is facilitated if the designated heir is an older offspring.

The second rationale for primogeniture in organisms with overlapping generations derives from the potential for parents to assist the heir, as well as in some cases to scrutinize the heir while they are still able to

adjust inheritance strategies. If necessary, parents can help or, as a last resort if the heir is beyond help, arrange for a replacement.

In social systems with primogeniture, the advantages of being the heir would usually outweigh individual differences. Nevertheless, exceptional cases come to mind. One example of a strategic adjustment of heirs according to circumstances is provided by the life of the French statesman Talleyrand (1754–1838). Talleyrand was the second son of an ancient, powerful, but no longer wealthy Parisian family. With the designated heir in hand, the second son was sent to a wet nurse far from his home, a cheaper alternative than paying a nurse to live in. It was only after the first-born died that the second-born was recalled from his nurse. Unfortunately the poorly attended second son had suffered a crippling injury. When Talleyrand's mother gave birth to yet a third son, it was decided in the interests of the family that the crippled son should forfeit the right of primogeniture. Twice rejected as heir, Talleyrand was educated for a career in the church before abandoning that course to become a diplomat. The rest, of course, is history.

Given that the best-documented cases of primogeniture have developed in saturated habitats with stable populations (e.g., in Japan), the hypothesis invoking greater reproductive value of older offspring in burgeoning populations would not apply. For this reason, we prefer the hypothesis based on "generational overlap" and the attendant "Talleyrand option" for still-living parents to fine tune their own strategies of heirship. Together with the generally accepted "developmental rationales," some combination of these factors could explain the preference for first-borns. For parents to reserve the option to tinker with, or even in rare cases disinherit, the designated heir long after he has been selected would be in line with the basically conservative mentality of propertied parents posited above in the section describing a Darwinian model for biased inheritance.

CONCLUSION

Very early in our heritage, key features of hominoid existence—particularly the fact that males tended to remain among their kin—created conditions that encouraged a cycle of bias favoring sons. Greater resource-holding potential of sons would have contributed to male-biased inheritance (once such resources were transmitted between generations), leading to increased female dependence on resource-holding males, which in turn promoted development of generalized ideologies of male authority. The emergence of formal legal systems can, under some conditions, codify male domination of the means of production (as

they certainly did in many peasant economies where female property ownership was restricted). Under different sociopolitical and ecological conditions, however, legal systems ensuring relatively equal resource-holding potential for sons and daughters make it practical for parents to treat offspring equally.

Against a background of generalized preference for sons, propertied parents are confronted with decisions that range from maintaining the property intact versus providing equally for each appropriate descendant. Parents who decide to direct larger portions of land to one or a few sons are primarily responding to ecological conditions.

The custom of limiting the number of heirs is more widespread and stable than the particular rules for designating *which* son or sons to choose. In spite of considerable variability, for several reasons involving developmental factors favoring easily identified and older competitors, as well as helping to insure suitability and success of the heir, first-born offspring are preferred over later-born offspring under most circumstances.

“When I think of the future I often ardently wish I was settled in one of the Colonies, for I have now four sons (seven children in all, and more coming) and what on earth to bring them up to I do not know. . .”

Letter from Charles Darwin
to Syms Covington, 1850
(Cited in Bowlby 1990:300)

AFTERWORD: ON DARWIN’S “SEXIST EGALITARIAN” WILL

Darwin saw in primogeniture a scheme for “destroying natural selection” because the choice of heir ignored criteria related to genetic fitness. It was not until a century later that inclusive fitness theory would pave the way for analyzing parental investment decisions in terms of costs and benefits to groups of relatives (Hamilton 1964), and biologists would begin to think in terms of long-term reproductive success of lineages. Under certain circumstances, channeling resources to selected male heirs turns out to be an expedient route for avoiding lineage extinction.

Since females in saturated habitats with land-based breeding systems choose husbands on the basis of resources controlled by the male rather than on the basis of his genotype, landholding becomes the most critical feature of a male’s phenotype. In the case of human inheritance patterns, then, custom and parental decisions determine these phenotypes and directly influence attractiveness to potential mates and hence reproductive success.

Far from "destroying natural selection," primogeniture in land-based breeding systems appears to be a uniquely elaborate human invention for promoting inclusive fitness and long-term perpetuation of a family line (meaning, for most cultures, a patrilineal line). Analyzed a century later, Darwin's own view of primogeniture was insufficiently Darwinian. We are tempted then to ask a somewhat personal question about Darwin's life: Was there anything Darwinian (rather than just Victorian) in the decisions he made about his own heirs?

At his death in 1882, Darwin left an estate of £331,000, a legacy far larger than the worried father of "seven children . . . and more coming" had expected. Darwin's astute investment of his paternal legacy had made him a rich man. Much of this wealth derived from Darwin's purchase of shares in some twenty different railroad companies (Atkins 1974:96). By virtue of the size and source of his income, Darwin belonged to the upper middle class, although through his family he was linked both to England's traditional landed gentry and to men successful in professions and commerce.

In no sense did Darwin depend on the land, and on economic grounds he had no incentive to practice unigeniture. His aversion to primogeniture was not contradicted by self-interest or by the inclusive fitness of his family. By the middle of the nineteenth century, the majority of Britain's mercantile middle class practiced partible inheritance, and many were beginning to treat all offspring equally. On the order of 48% of lower middle class wills and 55% of upper middle class wills showed evidence of partible inheritance. Even when they inherited different kinds of property, daughters and sons were treated "as if they might have the right to inherit equally in terms of value" (Davidoff and Hall 1987:206).

Yet Darwin, perhaps best described as an ambivalent liberal, was selective in terms of which of the inheritance practices he adopted from this emerging mercantile class. Surprisingly liberal in some respects, in other matters he followed the received wisdom of the country gentry (Bowlby 1990; Frank Sulloway, personal communication).

Though Darwin's ancestors had benefited from bequests to first-born sons, Darwin himself (a second son but the only male progenitor in his family) declined to favor his eldest son in any significant material way, and he made elaborate use of partible inheritance to treat each of his sons and each of his daughters equally. At the same time, Darwin gave far more to sons than to daughters, producing a classic "sexist egalitarian" will (Newell 1986).

Whatever the reason, Darwin was scrupulously fair in his treatment of his five sons. He did leave William Erasmus Darwin, his oldest surviving son (who in turn did not have any children), the family portraits,

papers, manuscripts, medals, and the silver candlesticks inscribed by the Royal Society. Even the money Darwin spent to set William up in legal practice and the special legacy he received (as oldest son) from Darwin's more conservative sisters were subtracted from William's shares to equalize what each son received (Darwin 1881).

The same attention to fair play was not extended to Darwin's two daughters. Darwin calculated what it would take to insure that each daughter had roughly the same to live on as he and his bride Emma lived on when they first set up housekeeping (before any children were born), and then made sure each daughter could expect that much income after adjusting for the intervening inflation. Emma was well-off in her own right; she was to remain at Down House for as long as she lived and to have his watches and jewelry. The bulk of the assets (nearly 80% of it) was divided among his five sons. Each daughter received just over half of what each son received (a $7/74$ th share, whereas the five brothers each received a $12/74$ th share; see 1881 letter from William Darwin to his father confirming his intentions, on display in the dining room at Down House).

Darwin had seven grandchildren, born to three sons. Only one of his daughters (Henrietta) ever married, and neither daughter bore a child. Did Darwin anticipate this or did he, by his treatment of his daughters (valuing them less than sons), in some way contribute to their childlessness?

That Darwin did in general value daughters less than sons is well documented in many odd, and occasionally inconsistent, corners of his writings. He was convinced that men on average had "mental power" superior to women (Darwin 1874:564) and that a man can be expected to attain "a higher eminence in whatever he takes up" (see Darwin 1874:563–566).

As we attempt to explain Darwin's views on primogeniture, we return to the same challenging problems that confront all evolutionists interested in human nature: how to sort out and weigh biological self-interest, economic self-interest, and the medley of accumulated cultural prejudices. Some combination of these factors constrains the vision of even the most brilliant members of a bright species, as well as the ordinary conspecifics who seek to analyze them.

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Sarah Blaffer Hrdy and Debra S. Judge have been using archival data to study allocation of resources at death by residents of Sacramento and Yolo counties in California from 1890 through 1984 and of Suffolk County, Massachusetts, during the seventeenth, eighteenth, and nineteenth centuries. Hrdy is Professor of Anthropology at the University of California, Davis, and the author of *The Langurs of Abu: Female and Male Strategies of Reproduction* and *The Woman That Never Evolved*. Judge is a graduate student at UC Davis and has published articles on primate, avian, and human behavioral ecology. They share interests in evolutionary biology, behavioral ecology, and the biology and culture of gender relations.

NOTES

1. "My father had a strong feeling as to the injustice of primogeniture, and in a similar spirit was often indignant over the unfair wills that appear from time to time. He would declare energetically that if he were law-giver no will should be valid that was not published in the testator's lifetime; and this he maintained would prevent much of the monstrous injustice and meanness apparent in so many wills." From Francis Darwin's editorial note to *The Life and Letters of Charles Darwin* (Darwin 1887[II]:385).

2. The Administration of Estates Act abolished primogeniture in 1925 and enacted a single, uniform table for intestate succession of all property—real estate and personal. Previously land had been governed by common law, whereas personal property was in the domain of church courts and, in the case of intestacies, was divided equally among a man's children (Atkinson 1953:29).

3. To simplify matters, we assume in this paper that parents control the resources and are responsible for allocating them. The actual situation may sometimes be more complicated than this. For example, offspring may be differentially motivated to compete for resources (according to what their other options are, etc.) and manipulation by offspring may affect parental choices (James Boone, personal communication). Unfortunately the primary source of data in this area is probate documents, which do not record such stratagems.

4. For example, whereas sons, their education, degree of independence, property, and wealth take up a half-page-long column in the index, daughters are not listed. The author's "oversight" faithfully reflects the viewpoint of colonial fathers and the dearth of available information on daughters.

5. Obligations imposed on favored heirs to pay off their siblings pose a problem in this analysis, since these payments could in fact constitute a form of

equalization. Unfortunately, although the practice was common, there are few quantitative data that would enable us to discover if payments for land (in cash, or in terms of other obligations) were equal to the value of the land that favored heirs received. Certainly if we examine the New York case (Dutch-influenced and more mercantile than rural) these obligations are very heavy indeed (Narrett 1981). Our preliminary interpretation for rural New England, however (based in part on reading a sample of seventeenth-century wills and inventories describing very disparate types of land, with quite different anticipated productivity), is that the land allocated to eldest sons represented a superior commodity—i.e., the best portions of a father's estate—not readily available at the price paid on the open market.

Consider the case for "purchases" of land while the father was still alive. One must ask why eldest sons would pay good money for the land designated to them since they had good reason to expect they would inherit double shares of the total anyway. (If the fathers died intestate, all eldest sons—and if they wrote wills, most of them—could expect double shares.) One obvious answer is that the land designated for older sons was desirable and the brothers competed for it. Moreover, we are not aware of favored heirs renouncing their inheritances because they found the obligations (in terms of payments to sibs) too onerous. Tentatively, then, we assume that favored heirs do indeed receive more value.

It is of course possible that dowries were a form of equalization (what Goody calls a "premortem legacy"), but we simply do not have data with which to examine relative values of dowries versus legacies. Klapisch-Zuber's (1985) assessment for European cases indicates that dowries worked to "exclude [their beneficiaries] from inheritance." It is possible that American dowries also gave short shrift to daughters, but this remains to be shown.

6. English common law (and hence the rule of primogeniture) governed the descent of land only. Church courts controlled the distribution of personal property, which in the case of intestacies was divided equally among children (Friedman 1985:29). In 1683 when British legal customs were imposed on the former Dutch colony of New York, primogeniture replaced the more egalitarian inheritance system that was practiced in Holland. Of the Manhattanites who actually left wills, however, these increasingly urban, primarily mercantile parents circumvented the intestate rules and left their possessions more equally (Narrett 1981:40, 224, 341).

7. Land and other assets were transferred during the lifetime of fathers, as well as by legacies after his death. In some cases, property designated by the wills was already in possession of sons at the time their fathers died. These lifetime transfers are more difficult to document, and we do not deal with this problem here. We should be explicit about our working assumption, however, namely that *inter vivos* transfers do not alter the pattern of preference for first-born sons; this remains to be proven.

8. In the literature on cooperatively breeding birds, habitat saturation refers to a condition in which all, or nearly all, of the suitable habitat is occupied, so a dispersing individual has little opportunity to set up a breeding territory. As a consequence, young birds remain in their natal area, available to serve as "nonbreeding helpers" while waiting either to inherit the natal territory or for a suitable territory to open up elsewhere. Because of such hazards as predation and starvation, animals enhance their probability of surviving until a breeding opportunity arises by remaining in their natal group. In food-storing species, such as acorn woodpeckers, survival of both individuals and lineages is correlated with size of the storage facility (Koenig and Stacey 1990).

9. Causal relationships between inheritance patterns and family organization remain obscure, but we follow Berkner (1976) in assuming that ecological circumstances tend to prevail eventually, though cultural inertia in the form of custom is certainly influential in the short-run (Homans 1941:24-25) in determining which inheritance customs persist. Hence, when Berkner writes that "partible inheritance and nuclear family households are more likely to be found together when the options are open, impartible inheritance and stem family households are more likely to be found together when many options are closed" (1976:95), we assume that by "closed options" he means, in ecological parlance, saturated habitats near carrying capacity.

10. On average, 8.4 children were born to wives during this period; 7.2 of them would survive to age 21 (Greven 1970:30).

11. It was during the late eighteenth century that, one by one, the states began to abolish primogeniture for intestacies. Possibly as late the 1750s, New York still allocated eldest sons right of primogeniture in the land, plus a double share of personalty (Shammas et al. 1986:33).

12. In areas of Europe with very high mortality rates, Le Roy Ladurie argued that parents treated sons more equally because it would have been imprudent to do otherwise; the favored son might so easily die (cited in Dickemann 1979b). One must look to the southeastern North American colonies, or South America, to find comparably poor survivorship in the New World. A seventeenth-century man in his twenties who migrated to Maryland could expect to live only to his early forties (Jordan 1979), a sharp contrast with areas like Andover.

13. Critics of Smith argue that he overstates the extent to which Tokugawa Japanese actually conform to the stem-family ideal (e.g., Hayami 1983). Even in his critique, however, Hayami (1983:15) notes that eldest sons were the heirs two-thirds of the time, and that primogeniture was most pronounced in elites and least often followed in families with less property, which were also the families most liable to extinction (1983:28). What interests us here are these *general patterns* that emerge in response to demographic and ecological realities (Berkner 1976).

14. Greven writes for Andover that "without the means to support a wife, marriage was virtually impossible" (1970:37). For a conflicting opinion, see Auwers, who writes that "private ownership of land and capital were not considered essential for marriage" (1978:142-143). The difference here is that Greven takes into account birth order, and differential access to father's wealth by first-born sons, whereas Auwers is examining marriage age of all sons relative to father's economic position without taking into account the fact (documented elsewhere in her work) that later-born sons may not have the same access to that wealth that their older brothers do.

15. From Dexter 1916:1, cited in Ditz 1986:46-47. Interestingly, Reverend Cheesebrough, the archadvocate of primogeniture, appears to have been the younger son of a younger son (Mary Towner, Graduate Group in Animal Behavior, University of California, Davis, personal communication 1992).

16. Various customs enhanced the probability of parents having at least one son married to a fertile wife (Smith 1977; Skinner 1987), but failing that, parents had the option to bring in a son-in-law, adopt a relative, or bring in an outsider. This last option, if commonly pursued, would represent a challenge to socio-biological interpretations.

17. Data on differential survival and fertility of migrants, depending on which sex remains on the natal territory and which sex migrates, and so forth (e.g., see Walters 1990 for red-cockaded woodpeckers) are essential for understanding human mating systems.

18. In parts of the world where marriage itself is problematic, the same end can be accomplished by channeling property to the first offspring who marries ("primonuptial inheritance"), as is done in parts of Portugal (Douglas 1988).

19. We are indebted to H. Kaplan and J. Lancaster for calling this work and its application to our attention (see Lancaster and Kaplan 1991).

20. Of 179 gathering-hunting societies, 62% have patrilocal residence patterns, 16% bilocal, and 16% matrilocal (Murdock 1967; Ember 1978). Using a much larger sample of 563 cultures with all types of subsistence, "virilocal residence" prevails in every region of the world except South America, where matrilocal residence is more common (Murdock 1981:133).

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