PREFERENTIAL PARENTAL INVESTMENT IN DAUGHTERS OVER SONS

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Female-biased parental investment is unusual but not unknown in human societies. Relevant explanatory models include Fisher's principle, the Trivers-Willard model, local mate and resource competition and enhancement, and economic rational actor models. Possible evidence of female-biased parental investment includes sex ratios, mortality rates, parents' stated preferences for offspring of one sex, and direct and indirect measurements of actual parental behavior. Possible examples of female-biased parental investment include the Mukogodo of Kenya, the Ifalukese of Micronesia, the Cheyenne of North America, the Herero of southern Africa, the Kanjar of south Asia, the Mundugumor of New Guinea, contemporary North America, and historical Germany, Portugal, and the United States.

KEY WORDS: **Parental Investment; Parental Behavior; Sex Ratios; Reproductive Strategies; Child Neglect; Evolutionary Theory.**

Societies in which sons receive better treatment than daughters are commonplace in ethnographic and demographic research, whereas societies in which daughters are favored are relatively rare. This article focuses on evolutionary biological explanations of female-biased paren-

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tal investment. The major theories involved are introduced first, followed by a discussion of the evidence for sex-biased parental investment and some illustrative examples.

Research on sex-biased parental investment is closely related to studies of biased sex ratios, but the two topics are distinct. This article is concerned with parental investment; sex ratios are discussed only when they are used as evidence of sex-biased parental investment.

THEORETICAL OVERVIEW

Two complementary questions have motivated the large and growing body of recent biosocial research on sex-biased parental investment. First, what might be the adaptive advantages of parental preference for children of one sex? Second, what are the physiological and behavioral mechanisms involved in sex-biased parental investment?

The Evolutionary Biology of Sex-Biased Parental Investment

Fisher's Principle. Charles Darwin was the first to attempt an evolutionary biological explanation of the sex ratio. Although at first he considered the balanced population sex ratios that are common in nature to be examples of a trait that evolved because of its advantages to the species, he later decided that "the whole problem is so intricate that it is safer to leave its solution for the future" (Darwin 1874:293). An explanation based on the reproductive advantages to individual parents was offered by R.A. Fisher (1958:158–160; see also Charnov 1982; Daly and Wilson 1984:224–226; Shaw and Mohler 1953), who began with the observation that because every individual in a sexually reproducing, diploid species gets half of its genetic material from its father and half from its mother, selection should favor parents who invest equally in daughters and sons. The idea is that a single unit of investment in an individual of one sex will have the same effect on a parent's fitness (measured in terms of grandchildren) as a unit invested in the other sex. If daughters and sons cost the same to produce, then equal numbers of sons and daughters would be expected. On the other hand, if daughters and sons do not cost the same, selection would favor greater production of the cheaper sex so the overall parental investment in the sexes is equal. For example, if sons cost half as much to rear as daughters, the equilibrium sex ratio for the population will be 200 males for every 100 females. Although an average male will leave only half as many offspring as an average female, males also cost only half as much to

Table 1. Predictions Based on Fisher's Principle

Relative Costs of Daughters and Sons	*Sex Ratio at Birth*	*Amount of Parental Investment in Each Individual Born*	*Overall Ratio of Parental Investment in the Two Sexes*
Daughters cheaper to produce	Female-biased	Male-biased	Equal
Sons cheaper to produce	Male-biased	Female-biased	Equal
Daughters and sons cost the same to produce	Equal	Equal	Equal

produce, so one unit of investment in sons will yield the same number of grandchildren as one unit of investment in daughters.

Because Fisher's principle is an explanation of why the overall ratio of parental investment in the two sexes in a population should be equal, strictly speaking it does not contribute much to a discussion of female-biased parental investment. Although Fisher's principle would predict female-biased offspring sex ratios in certain circumstances and greater parental investment in individual daughters than sons in others, depending on how one measures parental investment, almost any species or society could be interpreted as having "female-biased parental investment" (Table 1). If one uses the sex ratio as one's yardstick, then Fisher's principle predicts that, when daughters cost less to produce than sons, parents would have more daughters, which might be interpreted as female-biased parental investment. If instead one uses the amount parents invest in each individual offspring as a measurement of parental investment, then societies in which sons are cheaper would be defined as having "female-biased parental investment." The important thing to note is that, if Fisher was correct, in *all* of these situations selection should favor an overall equal ratio of parental investment in the two sexes, and in none of them would we be justified in labeling the population as having female-biased parental investment.

Fisher's principle may, however, help to explain why so few examples of female-biased childhood sex ratios are found in human societies. If males tend to die at a higher rate than females before the end of the period of parental investment, then males would be, on average, cheaper to rear because the period of parental investment would be cut short for many of them. Because parents should produce more of the cheaper sex, they should produce more sons. This pattern is precisely the one we see in most human societies. With some exceptions, in most human

societies male children tend to suffer from higher mortality rates than females, and slightly more male children are usually born.

The Trivers-Willard Model. Fisher's prediction of overall equal parental investment in the sexes applies to the population average, and in certain circumstances natural selection may favor deviations from equal parental investment by individual parents (Clutton-Brock and Albon 1982). Trivers and Willard (1973) identify one set of conditions that could lead to sex-biased parental investment. In its broadest formulation, the Trivers-Willard model predicts that if the condition of mothers during the period of parental investment correlates with the probable reproductive success of their offspring, natural selection should favor the ability of parents to adjust their investment in the sexes to favor the sex with the best reproductive prospects. More specifically, Trivers and Willard predict that, when the reproductive success of males is more variable than that of females and males benefit more than females from good maternal condition and suffer more than females from poor maternal condition, males should be favored by mothers in good condition and females by mothers in poor condition. Among humans, Trivers and Willard suggest that socioeconomic status may be a good predictor of parental investment patterns if reproductive success of males is greater than that of females at the upper end of the hierarchy and lower than that of females at the lower end (Table 2).

The Trivers-Willard hypothesis has had a controversial but generally successful history of application to nonhuman species (see Clutton-Brock and Iason 1986; Gray 1985; Hrdy 1987, 1988). Among humans, the model has been applied to data from feudal north India, imperial China, medieval Europe (Dickemann 1979), historical Germany (Voland 1984, 1988; Voland et al. 1991), medieval Portugual (Boone 1986, 1988), the Micronesian atoll of Ifaluk (Betzig and Turke 1986), nineteenth-century Mormons (Mealey and Mackey 1990), contemporary North America (Gaulin and Robbins 1991), and the Mukogodo of Kenya (Cronk 1989a, 1989b; see also Sieff 1990 for a review). Five cases that may involve female-biased parental investment (Germany, Portugal, the Mukogodo, Ifaluk, and the Cheyenne) will be discussed below.

Kin, Mates, and Resources. Natural selection may also favor sex biases in parental investment if offspring compete among themselves or with their parents for access to resources or mates, or if one sex of offspring tends to enhance the reproductive success of its parents or siblings by providing either resources or mates (Clark 1978; Hamilton 1967). If siblings of one sex tend to compete with one another or their parents for mates or resources, this competition may increase the costs of rearing offspring of that sex, and natural selection will favor greater production of the less competitive sex (Table 3). This situation is referred to either as

Table 2. The Trivers-Willard Model

Maternal Condition/ Socioeconomic Status	*Reproductive Prospects of Offspring*	*Predicted Bias in Parental Investment*
Poor/Low	Daughters higher	In favor of daughters
Good/High	Sons higher	In favor of sons

Table 3. Local Mate and Resource Competition and Enhancement

Model	*Preconditions*	*Predicted Bias in Voluntary Parental Investment*	*Overall Parental Investment (Both Involuntary and Voluntary)*
Local mate competition	One sex of offspring more expensive because it competes with parents or siblings for mates	In favor of the less competitive sex	Equal
Local resource competition	One sex of offspring more expensive because it competes with parents or siblings for resources	In favor of the less competitive sex	Equal
Local mate enhancement	One sex of offspring cheaper because it enhances the mating success of parents or siblings	In favor of the cheaper sex	Equal
Local resource enhancement	One sex of offspring cheaper because it enhances resource base of parents or siblings	In favor of the cheaper sex	Equal

local mate competition (Hamilton 1967) or *local resource competition* (Clark 1978), depending on the object of competition. On the other hand, if offspring of one sex tend to help their parents or siblings by attracting or obtaining mates or resources, this assistance may decrease the costs of rearing offspring of that sex, and natural selection should favor greater production of the cheaper, more helpful sex. This situation is referred to as either *local mate enhancement* or *local resource enhancement* (Sieff 1990; see also Toro 1982; Trivers and Willard 1973).

The essence of these ideas is the same as that of Fisher's principle: when offspring of one sex cost more than offspring of the other, parents should produce more offspring of the cheaper sex (see Hoogland 1981).

The contribution of the local mate/resource competition/enhancement model is to point out that in some circumstances male and female offspring will impose different costs on parents regardless of the wishes of the parents themselves, and that this difference will lead the parents to direct more of their voluntary and deliberate investment toward the cheaper sex. For example, competition between sons and parents for resources will increase the amount parents must invest in a son. The fact that much of the increased investment will be the involuntary result of their competition with sons for resources does not take it out of the category of parental investment (Trivers 1972:139), and Fisher's principle still applies. Most research on sex-biased parental investment is primarily concerned with voluntary and deliberate parental investment, however, and local mate/resource competition/enhancement is still helpful as a guide to circumstances in which parents may prefer to direct their voluntary parental investment toward either daughters or sons.

Local mate competition has been most successfully applied to a variety of insect species (Griffiths and Godfray 1988; Hamilton 1967; Werren 1980) and may also explain sex ratio biases in wood lemmings (*Myopus schisticolor*) (Trivers 1985:277–278; Williams 1979). Local resource competition was first identified among African galagos. Whereas male galagos range widely, females remain near their mothers' home ranges and are therefore more costly because they compete with their mothers for food. Galago mothers accordingly produce fewer competitive, costly daughters and more sons (Clark 1978; for other nonhuman examples, see Caley and Nudds 1987; Clutton-Brock et al. 1982; Cockburn et al. 1985). Red-cockaded woodpeckers provide a possible example of local resource enhancement (Gowaty and Lennartz 1985). In this cooperatively breeding species helpers-at-the-nest are almost always males, and the offspring sex ratio is significantly biased toward males.

Although these ideas have only rarely been tested on data from human societies (e.g., Cronk 1989a, 1990), circumstances that may make offspring of one sex cheaper or more expensive to rear are common in our species. For example, in societies with bridewealth, competition among brothers and between fathers and sons for access to and control of resources with which to pay for wives might lead to a parental preference for daughters. Daughters in these societies would also have the added benefit of attracting bridewealth payments from other men. Similarly, daughters may be favored in societies with direct exchange of women, rather than bridewealth, if fathers, sons, and brothers compete with one another for the right to negotiate their daughters' and sisters' marriages. And finally, one sex or the other might make itself cheaper by doing more work. For example, on the Micronesian island of Ifaluk daughters are generally more helpful to their parents than sons, and

women whose first two children are daughters have higher reproductive success than women whose oldest children are sons (Turke 1988). However, there is no evidence of any tendency among Ifalukese to have more firstborn daughters than firstborn sons. Other possible examples of local mate and resource competition and enhancement are discussed below.

Other Explanations of Sex-Biased Parental Investment

Alternatives to the evolutionary biological approach to sex-biased parental investment come in two major varieties, idealist and materialist (Hrdy 1990:26). The idealist approach rests on the idea that parents' valuations of sons and daughters are essentially cultural constructs and as such are not reducible to either reproductive or economic costs and benefits. The fact that, as will be shown below, there is often surprisingly little fit between parents' actual behavior and their stated, culturally determined preferences gives little support to this point of view.

The nonevolutionary materialist approach holds that parents are rational actors, favoring sons or daughters according to the costs and benefits associated with offspring of each sex. These costs and benefits are usually conceived of in economic terms, although occasionally such benefits as group defense by males, the role of one sex or the other in descent group formation, and alliance formation through marriage may enter into the analysis (Hrdy 1990). Das Gupta's study of parental behavior in rural Punjab is a good example of this approach (Das Gupta 1987). Rural Punjabi sons in general are favored and usually have lower mortality rates than daughters, which Das Gupta attributes to a complex of cultural, social, and economic factors. It is interesting to note, however, that firstborn daughters in the rural Punjab actually have lower mortality rates than firstborn sons (95.7 vs. 126.8 deaths per 1000 live births), possibly because mothers favor firstborn daughters for the help they provide in caring for their younger siblings (Sieff 1990:33). Bambara women in Mali also say that although they have no overall preference for sons or daughters, they prefer daughters to be born first so they can benefit from their daughters' help (K. Dettwyler, personal communication; see Johansson 1984 for an economic explanation of a case of male-biased parental investment).

These materialistic, rational-actor models are very similar to the local resource enhancement and competition models described above. The fundamental difference between the two approaches is the level of

explanation sought. Local resource enhancement and competition models, like other evolutionary biological models, attempt to explain behaviors in terms of their consequences for reproductive success. In order to demonstrate that a model is relevant to a particular case, one must demonstrate not only that parents favor the cheaper sex, but that parents benefit reproductively as well as economically or socially from the modeled behavior. If reproductive benefits cannot be demonstrated, then the behavior is explained only on the proximate level of rational economic decision-making. In only one case (Cronk 1990 and below) has a demonstration been attempted for a human example, and the results were negative, but many other opportunities exist for these tests, some of which will be discussed below. It is important to note that because they are concerned with different levels of explanation, the rational actor and local resource enhancement/competition models are complementary, not contradictory.

Sources of Evidence of Sex-Biased Parental Investment

Given that in some circumstances it may be adaptive for parents to favor children of one sex over children of the other, how is sex-biased parental investment accomplished, and what sorts of evidence have been used to identify it? One way to bias one's investment in favor of one sex is simply to give birth to more of that sex. In general, human sex ratios at birth are slightly male biased, although a number of factors, including the timing of fertilization, smoking, and a variety of diseases, may be able to lower the ratio (see James 1987a for a review). The main difficulty with using the sex ratio at birth as evidence of sex-biased parental investment is that good data are often hard to come by, especially in traditional societies. As explained above (Table 1), even when the sex ratio at birth is strongly biased, overall parental investment is not necessarily biased in the same direction.

It is also unclear how responsive the sex ratio at birth is to conditions experienced by the parents. The main evidence of responsiveness is that males appear to be more vulnerable to maternal condition during pregnancy both pre- and postnatally (Stinson 1985). For example, in one study of pregnancies among 140 female former anorexia nervosa patients, the sex ratio at birth was even (n = 86), but the death rate during the first week of life was highly biased (six males and only one female died; Brinch et al. 1988). This greater male vulnerability to conditions during pregnancy may fit the prediction of the Trivers-Willard model that mothers in poor condition should produce more daughters. On the other hand, greater male vulnerability could be an effect of a develop-

mental process that has nothing to do with the Trivers-Willard model. To test the validity of this prediction, we need studies of sex biases in vulnerability to maternal condition during pregnancy in species in which the reproductive success of female offspring is typically affected more by maternal condition than is the reproductive success of males. If in these cases we find greater female vulnerability to maternal condition during pregnancy, it would strengthen the argument that greater male vulnerability to conditions during pregnancy in our species is a product of the Trivers-Willard scenario and not just happenstance.

Sex biases in parental investment may also be reflected in birth-spacing patterns (Gaulin and Robbins 1991). For example, longer intervals following the births of girls than those following boys may reflect a desire by parents to devote more attention to the rearing of daughters. Alternatively, intervals may be longer before the births of the favored sex if the in utero death rates of the other sex are increased (Jane Lancaster, personal communication).

After birth, parents have a wide variety of ways to bias their investment in favor of children of one sex, ranging from infanticide to neglect to differential solicitude. The difficulty is not in imagining the methods parents use, but in detecting them. One way is to look for the possible effects of sex-biased parental investment on childhood sex ratios and associated childhood mortality rates. The main problem with this approach is that many other things besides parental behavior can affect these variables. For example, males may be more vulnerable to environmental stresses than females (Stinson 1985), or work patterns may expose children of one sex to greater risks.

Another way to detect parental sex biases is by asking them their preferences. In most societies, parents express either no preference or a preference for sons, but preferences for daughters have been noted in Jamaica and Venezuela (Cleland et al. 1983) and among Colombian women (Turner and Simmons 1975 [cited in Coombs 1977:265]), some Filipinos (Coombs 1977; Stinner and Mader 1975), American women of Hispanic origin (Coombs 1977), and Australian women of Greek and Italian origin (Callan and Kee 1981). The difficulty with these data is that informants' statements about their own behavior are likely to be better guides to their beliefs and traditions than to their actual behavior, and the two may not necessarily coincide (Cronk 1991a; Harpending and Pennington 1991; Hrdy 1990; see also the Mukogodo, Ifalukese, and Herero examples, below).

Finally, one can look at the actual behavior of parents. This approach is clearly the best way to detect sex-biased parental investment, but it is by no means the easiest or most clear-cut. Infanticide can provide some of the most dramatic evidence of sex-biased parental investment. Infanticide among humans is most often female-biased. A notable exception

are the Ayoreo Indians of Bolivia; however, the sex ratio of infanticide deaths (194:100) is not significantly different than the sex ratio of births (137:100; $\chi^2 = 2.20$; $p > .10$; Bugos and McCarthy 1984; see also Pérez Diez and Salzano 1978). Thus, even sex biases in infanticide are not necessarily good evidence of sex-biased parental investment.

Another approach is to observe parental behavior for signs of greater solicitude toward one sex. This observation may be done either directly, through the use of behavioral scan techniques (Altmann 1974; Borgerhoff Mulder and Caro 1985; Gross 1984), or indirectly through the use of other indicators of investment patterns. Betzig and Turke (1986), for example, used behavioral scans to study association patterns between parents and offspring on Ifaluk. One of the main advantages of this method is that it can be replicated almost anywhere, making systematic comparisons possible. One difficulty with this method is that "association" may be a weak guide to parental investment patterns, and it may be hard to say whether the benefits of association are flowing from parents to offspring or vice versa (Betzig and Turke 1986; Sieff 1990:32). Breast-feeding patterns provide a much less ambiguous guide to parental investment patterns. Frequency and length of nursing bouts, length of the nursing period in a child's life, and, in societies with alternatives to breast milk, the proportions of children of each sex that are breast fed can all be good guides to parental investment patterns (Cronk 1989a; Gaulin and Robbins 1991).

Indirect measurements of parental investment patterns can be obtained from a number of sources. For example, the records of a dispensary and a clinic suggest that Mukogodo parents are more solicitous of daughters than of sons (Cronk 1989a, 1989b, and below), and marriage records and dowry customs suggest that lower-status Portuguese nobility were more willing to invest in daughters than sons (Boone 1986). The disadvantages of using records are that they reveal only a small slice of total parental investment and that this method is not easily replicated elsewhere because comparable records may not be available for other societies.

Anthropometry provides another very promising but infrequently used way to assess parental investment in the sexes. For example, analysis of body fat through skinfold measurements can reveal differences in the health and nutritional status of boys and girls that may be the result of differential parental investment (Harpending and Kurland 1991). Other possibilities include the use of hormonal assays to assess stress levels among children and parents (Ellison 1988; Harpending and Kurland 1991) and the employment of theory-blind medical practitioners to assess children's health and nutritional status. Like sex ratios and mortality rates, however, sex differences in health status may be produced by factors other than parental behavior.

EXAMPLES

The Mukogodo

The Mukogodo are a small group of impoverished Maa-speaking pastoralists in Kenya. Until the 1920s and 1930s, they lived in caves as hunter-gatherers and beekeepers. Other Maa-speaking pastoralists generally despise foragers, and the Mukogodo are still stigmatized by their past. As a result of both their low status and their poverty, Mukogodo men are less successful than men from neighboring groups in obtaining wives and have relatively poor reproductive prospects. Mukogodo women, on the other hand, can always find a husband, either among the Mukogodo themselves or among one of the wealthier neighboring groups, and they have good reproductive prospects. As a result, the reproductive success of Mukogodo females is significantly higher than that of males. According to the Trivers-Willard hypothesis, Mukogodo parents should favor daughters since they have better reproductive prospects than sons, and the available evidence indicates that they do just that. The childhood sex ratio (ages 0–4) is significantly female-biased (67:100). Because the sex ratio at birth is probably about equal or even slightly male-biased, the sex ratio bias is most likely the result of better treatment given daughters. Support for this interpretation comes from data on the use of local health facilities: Mukogodo parents are more likely to take daughters than sons to a local dispensary and to enroll them in a child care clinic (Tables 4 and 5). Furthermore, they may nurse daughters longer than sons ($0.5 < p < 0.10$; see Cronk 1989a, 1989b).

Another possibility is that, in accordance with the local resource enhancement hypothesis, Mukogodo parents favor daughters because they attract bridewealth payments that may help their fathers or brothers to obtain more wives. If this expectation were true, then men with more daughters or more sisters should have more wives, but no such relationship can be found in the data. A regression of total number of wives and number of daughters from men's first marriages who survived to age 15 reveals no significant relationship between these variables ($N = 220$, Pearson correlation coefficient = 0.111, regression coefficient = 0.041, $t = 1.652$, p[two-tailed] = 0.100). Similarly, the mean number of wives for men with daughters from their first marriage who survived to age 15 is actually slightly less than the number of wives for men with no such daughters, although the difference is not statistically significant (mean [no daughters] = 1.333; mean [some daughters] = 1.320; $t = 0.13$; p[two-tailed] > 0.25). Nor do women enhance the marital success of their brothers. No statistically significant relationship was found between men's numbers of full sisters surviving to age 15 and

Table 4. Visits by Children Ages 0–4 to the Don Dol Roman Catholic Mission Dispensary in 1986, by Ethnic Group, Sex, and Type of Visit

	Mukogodo				*Non-Mukogodo*			
	Males		*Females*		*Males*		*Females*	
	New Visit	*Repeat Visit*	*New Visit*	*Repeat Visit*	*New Visit*	*Repeat Visit*	*New Visit*	*Repeat Visit*
n	74	35	113	78	153	76	116	69
N	109		191		229		185	
	(36.3%)		(63.7%)		(55.3%)		(44.7%)	
Population percentage[a]	42.2%		57.8%		51%		49%	

[a] The Mukogodo figures are based on the numbers of person-years lived by children of each sex in the 0–4 age group in 1986. The non-Mukogodo figures are based on the 1979 Kenyan census (Central Bureau of Statistics 1982:122).

The female bias in visits to the dispensary is significantly different than the pattern shown by the non-Mukogodo dispensary visitors ($\chi^2 = 13.4369$, $p < .001$).

Table 5. Enrollment and Attendance at an Underweight Baby Clinic Run by the Don Dol Roman Catholic Mission, by Ethnic Group, in 1986

	Mukogodo		*Non-Mukogodo*	
	Males	*Females*	*Males*	*Females*
Officially enrolled	12 (34.3%)	23 (65.7%)	206 (49.1%)	214 (50.9%)
Population percentage[a]	42.2%	57.8%	51%	49%
Actual monthly attendance	121 (38.5%)	193 (61.5%)	NA	NA
Person-months lived[b]	768 (44.4%)	960 (55.6%)	NA	NA

[a] The Mukogodo figures are based on the numbers of person-years lived by children of each sex in the 0–4 age group in 1986. The non-Mukogodo figures are based on the 1979 Kenyan census (Central Bureau of Statistics 1981:122).

[b] Total numbers of months lived during 1986 by Mukogodo children of each sex.

The female bias in actual monthly attendance among the Mukogodo is statistically significant ($\chi^2 = 4.441$, $p < .05$).

their numbers of wives ($N = 330$, Pearson's correlation coefficient = 0.095, regression coefficient = -0.045, $t = -1.731$, p[two-tailed] = 0.084). The lack of any relationship between men's numbers of daughters and sisters and their numbers of wives may be due to the poverty of the Mukogodo. Mukogodo herds are so small that it is probably unusual for a Mukogodo man to be able to take livestock given to him as

Table 6. Stated Offspring Sex Preferences of Mukogodo Women

Stated Preference	*Sex of Current Offspring*				
	More Boys	*More Girls*	*Even*	*None*	*Total*
More boys	8	3	2	1	14
More girls	0	3	0	6	9
Even	11	16	8	9	44
No preference	18	24	8	4	54
Total	37	46	18	20	121

bridewealth and immediately use it to pay for another wife for himself or one of his sons. Most men would probably have to use animals received as bridewealth to pay off debts and to maintain reciprocal livestock sharing arrangements, to sell for cash, and simply to support their families.

Interestingly, the stated sex preferences of Mukogodo women do not match their behavior (Table 6; Cronk 1991a). Although their behavior and the childhood sex ratio suggest a strong tendency to favor daughters, many mothers express a preference for sons, and their overall stated sex preference is roughly equal. This finding demonstrates the importance of coupling studies of parents' stated sex preferences with measurements of actual parental behavior, since the two do not necessarily correspond.

Ifaluk

Ifaluk is an atoll in Micronesia inhabited by about 450 people who subsist mainly on fish, taro, breadfruit, and coconut (Betzig and Turke 1986). Ifalukese society is mildly stratified, with five clan chiefs, two local village chiefs, two chiefly advisors, and ten likely adult successors to these positions. Chiefs enjoy a variety of perquisites, including tribute, advantages in food-sharing arrangements, extra fish from cooperative catches, and less work than other men of their age group (Betzig 1988). Furthermore, Ifalukese chiefs have higher reproductive success than commoners (Turke and Betzig 1985). Since World War II there have also been a few job opportunities on Ifaluk, and the 25 Ifalukese men who have worked for a salary also have greater reproductive success than other Ifalukese men (Turke and Betzig 1985). Following Trivers and Willard (1973), Betzig and Turke (1986) predicted that high-status men and men who had worked for wages would invest more in sons than in daughters and that lower-status Ifalukese would invest more in daughters. They measured parental investment by recording association patterns between parents and children on an Ifalukese islet during 48 days

in 1983. Whereas about two-thirds of the time that high-status and wage-earning men spent associating with their children was spent with sons, low-status men spent nearly the same proportion of time with daughters (the difference is statistically significant). The time mothers spent with their children was similarly distributed; the wives of high-status and salaried men spent between 49% and 62% of their time with sons, and the wives of low-status men spent 65.7% of their time with daughters. Although Betzig and Turke's analysis exhibits a number of problems (e.g., failure to separate observations into parent–child dyads; see Sieff 1990:32), these data do appear to support the Trivers-Willard model, and perhaps similar behavioral scans will be used more often to gauge parental behavior. Finally, it is interesting to note that Ifalukese parental behavior does not correspond with earlier findings that the Ifalukese express a preference for daughters over sons (Burrows and Spiro 1957:246), which again demonstrates the danger of assuming that stated sex preferences reflect actual behavior.

The Cheyenne

Among the Cheyenne Indians in the late nineteenth century, young men had two possible roads to success (Moore 1990). The more prestigious path, followed mainly by young men born to the most prestigious polygynous families, was to become a trader, priest, or "peace chief." This goal was an expensive proposition since becoming such a leader required a young man's father and his agnates and allies to pay gifts to instructors and sponsors. The other path was to try to become a "war chief" by bravery in battle. This less expensive but more dangerous route was followed mainly by young men born to poor, fragmented, and marginal families. Peace chiefs not only tended to survive longer than war chiefs, they also tended to be more polygynous. Cheyenne society at the time was also divided along these same lines into "peace bands" and "war bands," with peace bands being generally wealthier and of higher status than war bands.

Records from a census in 1892 suggest that the Cheyenne may have been adjusting their sex ratio, and thus perhaps their parental investment patterns, in accordance with the Trivers-Willard hypothesis. The sex ratio for children aged 0–4 was 27 males to 39 females (69:100) in the war bands and 33:34 (97:100) in the peace bands (Moore 1990). Although the female sex ratio bias in the low-status war bands is not statistically significant ($\chi^2 = 2.182$, $p > .10$), the data's fit with the expectations of the Trivers-Willard model is intriguing enough to justify further analysis, which is currently being conducted by Diana Robinette of the Uni-

versity of Tennessee. One factor that complicates this case is the use of adoption among Cheyenne to form same-sex play groups (Moore and Campbell 1989). Adoption occurred mainly within band types rather than between them, however, and thus may have had little or no effect on the sex ratios (see also Moore 1980, 1987).

Historical Germany

Eckart Voland and his colleagues have found evidence of female-biased parental investment in historical demographic data from three different regions in Germany: Schleswig-Holstein, Ostfriesland, and the Krummhörn (Voland 1984, 1988; Voland and Siegelkow 1990; Voland et al. 1991). In a sample from Schleswig-Holstein between 1720 and 1869, the daughters of smallholders had better survivorship rates than sons (10.9% vs. 15.8% mortality during the first year of life), which may be due to their low status compared with an upper class of wealthier farmers, in accordance with the Trivers-Willard hypothesis (Voland 1984; cf. Brittain et al. 1988:688). The Trivers-Willard model also received some support from data from Ostfriesland between 1668 to 1879, where mortality rates suggest that widows may have favored daughters over sons (Voland 1988).

Data from the Krummhörn in the eighteenth and nineteenth centuries offer some of the most interesting evidence of female-biased parental investment (Voland and Siegelkow 1990; Voland et al. 1991). Infant mortality rates suggest that high- rather than low-status families biased their investment in favor of daughters, a pattern that corresponds with both the relative reproductive prospects and the parental investment costs of sons and daughters. Owing to land scarcity, only the youngest son of a farmer inherited any land, and as a result sons of wealthy farmers were more likely to remain lifelong celibates than those of smallholders and landless families. Furthermore, additional sons had to be paid their share of the inheritance, which weakened the economic power of the farm.

The daughters of landed farmers were cheaper to raise than their brothers because they inherited only half as much capital as their brothers. Moreover, the daughters of landed farmers were less likely to remain celibate than either their brothers or the daughters of smallholders and landless families. Both the Trivers-Willard and local resource competition models seem to be relevant to this case: high-status Krummhörn parents may have been more solicitous of daughters because of their better reproductive prospects, their lower costs, and the damaging effects brothers may have had on one another's fitness owing to the scarcity of land.

Table 7. Neonatal Sex Ratios in Good, Bad, and All Harvest Years, 1671–1720, in Turcifal Parish, Portugal

	Males Born	*Females Born*	*Males per 100 Females*	*Annual Mean*	*Total*
Bad years ($n=14$)	283	312	90.71	42.50	595
Good years ($n=36$)	741	661	112.10	38.94	1402
All years ($N=50$)	1024	973	105.24	39.94	1997

For sex-ratio difference between bad years and all years, $\chi^2 = 6.10$; $p < 0.025$
For sex-ratio difference between good and bad years, $\chi^2 = 17.40$; $p < 0.0005$
Source: Cowgill and Johnson 1971:325

Historical Portugal

Nobility. Historical demographic data on the Portuguese nobility between 1380 and 1580 reveals another possible example of female-biased parental investment (Boone 1986, 1988). The Portuguese nobility was divided into four strata. Those with primary titles were on top of the hierarchy, followed by members of the royal bureaucracy, a landed aristocracy called the senhorial class, and untitled and military specialists. Among the upper nobility, male offspring had better marital prospects than their sisters, whereas the reverse was true among the lower nobility. Furthermore, women needed dowries to marry, and the fact that lower-status women had better marital success than higher-status women suggests that the parents in the lower nobility were more willing than those of the upper nobility to invest in daughters. Boone argues that because patrimonies among lower-status nobles were often incapable of supporting a noble household, the dowries paid by these households for their daughters' marriages may well have been larger than the amounts of property they passed on to their sons. No quantitative data is available to compare dowries and patrimonies, however, and thus it is not clear whether the greater willingness of lower-status parents to invest in daughters led to truly female-biased parental investment.

Peasants. Female-biased parental investment is also suggested by data on peasants in the Portuguese parish of Turcifal between 1671 and 1720 (Cowgill and Johnson 1971). Grain prices can be used as a rough guide to harvest quality: high prices may have been the result of poor harvests and short supplies of grain, whereas low prices may have been the result of good harvests and abundant grain supplies. Although the birth rate did not change with harvest quality, the sex ratio at birth did. When prices were high (and harvest presumably poor), more girls were born, but when prices were low (and harvest presumably good), more boys were born (Table 7). Cowgill and Johnson (1971:325) conclude, "there is little doubt that the annual standard of living, as estimated by

Table 8. Correlations Between Wheat and Barley Prices and Male and Female Deaths, 1671–1720, in Turcifal Parish, Portugal

	Male Deaths	*Female Deaths*	*All Deaths*
Wheat	0.1201	0.2830*	0.2189
Barley	0.0770	0.4096**	0.2703

*$p < .05$
**$p < .005$
Source: Cowgill and Johnson 1971:323

the price of grain, had a significant association with the sex of a child." Females seem to have suffered more than males from food stress during poor harvest years, judging from correlations between grain prices and mortality rates (Table 8). This difference may have been due to the custom in which food was usually first served to male family members, and women received only leftovers (Cowgill and Johnson 1971:325–326).

The obvious conclusion from these data is that maternal food stress during pregnancy led to a female-biased sex ratio at birth, but exactly how and why this bias happened remains unclear. Cowgill and Johnson suggest that the proximate cause of the sex ratio variations was likely to have been male-biased stillbirths during poor harvest years. Unless the additional male fetal deaths occurred soon after conception and mothers were able to reconceive soon thereafter, however, the increased stillbirths postulated by Cowgill and Johnson would have reduced the overall number of births during poor harvest years. Another possibility is that the sex ratio at conception was sensitive to maternal nutritional stress, but most available evidence indicates that famine has little effect on the sex ratio at conception (see James 1987b:887). The ultimate reasons for the variations in sex ratios in Turcifal are no clearer. Perhaps investment in sons was avoided during bad harvest years because they are more sensitive both pre- and postnatally to maternal food stress during pregnancy (Stinson 1985). Given all of the questions that remain about the data from Turcifal, a detailed reanalysis of Cowgill and Johnson's original data might prove worthwhile, especially in light of the progress that has been made in the past 20 years in research on sex ratios and parental investment patterns.

Contemporary North America

Gaulin and Robbins (1991) have suggested that the ability of mothers in modern American society to invest in their offspring may be influenced by both annual household income and the presence or absence of

an adult male in the household, and that, in accordance with the Trivers-Willard model, women who are poor or who do not have the help of an adult male may invest more in daughters than in sons. The responses of several hundred women to a questionnaire about their socioeconomic circumstances and reproductive histories give limited support to this prediction. The most convincing supporting evidence comes from data on nursing: women with annual household incomes of less than $10,000 or without an adult male present were more likely to breast-feed their daughters than their sons. In addition, women without an adult male present tended to breast-feed their daughters 5.5 months longer than their sons. Gaulin and Robbins also argue that a female bias in parental investment among poor women and those without coresident adult males is shown by longer intervals before the birth of daughters than before sons, but their reasoning is unclear. It is widely accepted that the intervals *following* the birth of a child of a certain sex may reflect parental investment patterns, but it is not clear why the intervals *before* that child's birth would be subject to manipulation since it is not obvious how parents could reliably predict a child's sex before its conception, even if the prediction is not conscious. One possibility is that the intervals before girls would be longer among women in worse condition since they would experience higher in utero death rates of male fetuses (Jane Lancaster, personal communication 1991), but Gaulin and Robbins do not make this argument themselves. Also, not all of the preconditions of the Trivers-Willard may be present among modern Americans. Specifically, Gaulin and Robbins give no evidence that the reproductive prospects of the daughters of women who are poor or who do not have an adult male present are better than the prospects of these women's sons. If no difference exists, then the Trivers-Willard effect, if present, would have to be seen as a sort of vestigial response to a situation that in the human past would have made greater investment in daughters than in sons advantageous to parents.

Nineteenth-Century United States

United States census records have provided circumstantial evidence of shifts in parental investment in favor of daughters during the nineteenth century. The general pattern indicates that treatment of daughters may have been worst in rural areas and best in urban areas. The reason appears to have been economic. Sons were more valuable in rural farming areas, whereas industrialization presented daughters with new economic opportunities and increased their value to their parents. Hammel, Johansson, and Ginsberg (1983) have shown that, in the United States as a whole, between 1800 and 1860 the childhood sex ratio in

nonurbanized regions was male-biased, whereas in more urbanized regions, such as New England, it was female-biased. These results match earlier findings from Massachusetts in 1860 that life expectancy was higher for male children in rural areas and in towns smaller than 10,000 and higher for female children in towns of 10,000 people or more (Vinovskis 1972). In a more detailed study of sex ratios and mortality patterns in Massachusetts between 1860 and 1899, Ginsberg and Swedlund (1986) found that although the survivorship of males aged 10–19 was much better than that of females in areas dominated by agriculture, fishing, forestry, and mining, the difference between male and female survivorship was much smaller in more industrialized areas. This example demonstrates dramatically how changes in the economic value of daughters can affect the amount of parental investment they receive. It is important to note that although these studies suggest that parental investment toward females increased with industrialization, the conclusion that parental investment ever became truly female-biased, even in industrialized areas in nineteenth-century America, is not justified.

The Herero

The Herero are prosperous pastoralists in the northern Kalahari desert. Several types of evidence indicate that Herero daughters are favored over sons. First, the infant and childhood death rates of Herero boys are between two and three times those of Herero girls, which is far beyond what would be expected from greater male vulnerability alone. The effects of the high male mortality can be seen on sex ratios. The sex ratio at birth is estimated to be 105 males to 100 females, but it drops to 97:100 by the end of the first year of life and to 94:100 by the end of the fourth year. Second, some !Kung neighbors of the Herero have noticed the vulnerability of Herero sons and explain that Herero mothers take "their daughters to their hearts" but refuse their sons (Harpending and Kurland 1991). Finally, preliminary analysis of skinfold measurements show the effects of greater investment in daughters: by age 2, girls have almost 40% more triceps fat than boys.

The reasons for this sex bias are not clear. Harpending and Pennington (1991) tested a local resource enhancement model, with mixed results. The idea is that daughters may make themselves cheaper to raise by attracting wealth not only in the form of bridewealth payments, which are small, but also in the form of seduction and child fees paid by fathers of children of unmarried women. One prediction of Harpending and Pennington's model is that newborns should have better chances of surviving if they have older siblings of the opposite sex. A newborn boy may have better reproductive prospects if he has an older sister to attract

wealth to the family, while a newborn girl will be more valuable if she has an older brother to help by attracting wealth to the family. The available data only half-support this prediction. Although an older sister does have a significant positive effect on the survivorship of a newborn boy until age two, having an older brother does not enhance the survival chances of a newborn girl. Another possibility is that Herero parental behavior is affected by their child fostering customs. Many Herero children are fostered, and fostering by maternal grandmothers is especially common. Thus, having many daughters may provide women with more opportunities for indirect reproduction in the future (Harpening and Kurland 1991). This idea remains to be tested, but it does receive support from some women's statements that their daughters' children are "of their own blood" while those of their sons are of "unknown blood."

The Herero themselves attribute the high death rate among boys to witchcraft motivated by jealousy, which is inspired by births of sons but not daughters. This jealousy may endanger both baby boys and their mothers, so an added risk is involved in having a boy. Harpending and Kurland (1991) predict that, if true, mothers of male infants should be more stressed than mothers of females, and they suggest that these stresses may be detectable through salivary or urinal assays of adrenal hormones.

As in the Mukogodo case, Herero parents do not admit to any sex bias in parental investment. This finding reinforces the case for treating informants' stated sex preferences as potential guides to cultural traditions and beliefs but poor guides to actual behavior (Cronk 1991a, 1991b; Harpending and Pennington 1991).

The Kanjar

The Kanjar are a peripatetic people in South Asia who specialize in prostitution and production and sale of clay and papier-mâché toys and other household items. They also give public performances of music and dance, beg, and occasionally offer carnival-type rides (Berland 1982, 1987; Gautam 1983). Kanjar society is remarkable for the degree to which the usual positions of the sexes have been reversed. Males are said to live "like drones" (Tandon 1968:80), tending to be passive, cooperative, and subordinate to females, whereas females dominate public and private affairs and are socialized to be aggressive and independent. Although their parental behavior has never been studied in detail, Kanjar parents express a strong preference for daughters. This preference is reflected in the fact that celebrations are held at the birth of a girl, whereas the birth of a boy is received without fanfare (Berland 1982:131).

Both economic and reproductive factors may play a role in explaining the Kanjars' preference for daughters. First, Kanjar females are more economically productive than males. Activities that are exclusively or primarily done by females, such as prostitution, dancing and singing, the sale of toys and other items, and begging, account for about 51% of the income to Kanjar households in rural areas and about 73% in urban areas (Berland 1987:253). Especially attractive and talented Kanjar girls may also be sold into professional groups of prostitutes and dancers in urban centers, which further increases their economic value to their families. The effect of girls' economic productivity on parental investment patterns became especially clear in 1986–1987 when Pakistan underwent a period of Islamization. The Kanjar stopped dancing and the prostitution market was depressed, and there was a slight shift towards more equal treatment of sons and daughters (Joseph Berland, personal communication).

Second, Kanjar females help their brothers to get married. Bridewealth among the Kanjar is very expensive, ranging from two to ten times their annual income (Gautam 1983:22), so many marriages instead involve exchanges of one woman for another. Usually the children of siblings are exchanged. One of Berland's female informants explained it this way: " . . . the only way I can avoid paying a fortune for my son's bride is to make his marriage with my brother's daughter and to give my daughter to my brother's son. We call this *wady de shadi* or exchange marriage" (Berland 1982:128, 1987:259). Berland's informants also pointed out that exchange marriage makes it easier for a household to save cash to pay bridewealth for other marriages. Of course, when Kanjar daughters do marry for bridewealth they bring a great deal of wealth to their households. Thus the Kanjar appear to favor their daughters both because of the wealth they bring to their households and because of their ability to help their brothers to marry.

The Mundugumor

The Mundugumor of Papua New Guinea were studied by Margaret Mead and Reo Fortune in the 1930s (McDowell 1991; Mead 1935, 1949). The Mundugumor lived near the confluence of the Yuat and Sepik rivers and subsisted on horticulture and fishing. A difference of opinion existed between Mundugumor fathers and mothers about the values of daughters and sons: fathers tended to favor daughters, whereas mothers tended to favor sons. Relationships between fathers and daughters were close, and fathers tried to favor their daughters over their sons in inheritance and tried to allocate more property to them. The reverse was true of Mundugumor mothers, who had closer relationships with their

adult sons than with their daughters, and who attempted to allocate more goods and property to sons than to daughters.

The reason for Mundugumor fathers' preference for daughters seems to be related to their marriage system, which, like that of the Kanjar, involved direct exchange of women. Ideally, girls were to be used to obtain wives for their brothers, but fathers also sometimes used their daughters to obtain additional wives for themselves. This situation put fathers and sons in direct competition for the resources—daughters and sisters—needed to obtain mates and thus increased the costs of sons to fathers. The tension between fathers and sons is reflected in their relationships, which were characterized by formality, respect, and avoidance, and by the fact that sons "had to be vigilant to ensure that their sisters were not used to acquire more wives for their fathers" (McDowell 1991). Relationships between brothers were also distant and formal, whereas those between brothers and sisters were close and cooperative.

It is less clear why mothers favored sons over daughters. Perhaps women sided with their sons in the competition between fathers and sons because a women's inclusive fitness is enhanced if her son obtains a wife but not if her husband obtains one, or perhaps women's favoritism toward sons was simply an attempt to balance their husband's favoritism toward daughters, or perhaps both factors contributed. Although Mundugumor society has changed so much since the time of Mead and Fortune's fieldwork that it may no longer be possible to determine which factors most affected their parental investment patterns, many other societies with direct exchange mating systems offer similar opportunities to study the effects on parental behavior of mating competition between fathers and sons.

CONCLUSION

Table 9 summarizes the examples presented above. In almost all cases the evidence of female-biased parental investment is indirect. The Trivers-Willard model has been suggested as an ultimate, evolutionary explanation of more than half of the cases, but the set of ideas known as local mate/resource enhancement/competition and the nonevolutionary rational actor model may help to explain five of the examples. This finding provides support for Sieff's (1990) contention that models other than Trivers-Willard deserve more attention in evolutionary biological studies of sex-biased parental investment among humans. The examples of the Kanjar, nineteenth-century America, the Mundugumor, and possibly the Herero suggest that researchers should look for female biases in parental investment wherever females are more economically produc-

tive than males, attract large bridewealth payments, are used in direct exchange mating systems, or where fathers, sons, and brothers are the main competitors for the resources required for mating. In most of these cases, the evidence is sufficient only to support the rational actor model. In order for the local resource enhancement/competition model to be supported as well, the observed female bias must be shown to lead to reproductive advantages for the parents in terms of either their own reproductive success or that of their other offspring.

Many opportunities exist for improvement and expansion of research on sex-biased parental investment. For example, none of the studies discussed here address the issue of the proximate psychological mechanisms involved in parental behavior (cf. Mackey and Coney 1987). This analysis is a necessary step toward a full, vertically integrated explanation of any behavioral pattern (Barkow 1989; Cronk 1991b). The discrepancies between informants' stated sex preferences and their actual behavior are relevant to the issue of proximate psychological mechanisms. In none of the cases discussed above for which there are data on both parental investment and parents' stated sex preferences do the two correspond. This finding suggests not only that parents' statements should not be used as proxies for actual parental behavior but also that the proximate psychological mechanisms involved in parenting may be subtle and are often difficult for informants to articulate. These examples also demonstrate the need for better methods of measuring parental investment, including more direct behavioral observations and more measurements of children's health and nutritional status. A systematic comparison of several different methods of assessing parental investment patterns in a society thought to have sex-biased parental investment would be particularly useful.

The main benefit of more research on sex-biased parental investment would be a more complete understanding of why parental investment patterns vary from society to society, from parent to parent, and from child to child, which may help us to predict and prevent child neglect. For example, one obvious implication of the local resource enhancement model is that development efforts aimed at improving the economic productivity of females may have the unplanned benefit of encouraging parents to treat their daughters better. These projects would also provide new and interesting opportunities for research into why and how parental behavior changes with changing conditions.

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Table 9. Summary of Examples of Female-Biased Parental Investment

Case	*Evidence of Female-biased Parental Investment*	*Possible Explanatory Model*	*Do Stated Sex Preferences and Parental Behavior Correspond?*	*Sources*
Mukogodo	Childhood sex ratio, dispensary and clinic records, nursing	Trivers-Willard	No	Cronk 1989a, 1989b, 1990, 1991a
Ifaluk	Parent–child association patterns	Trivers-Willard	No	Betzig and Turke 1986; Burrows and Spiro 1957
Cheyenne	Childhood sex ratios	Trivers-Willard	No statements available	Moore 1980, 1987, 1990; Moore and Campbell 1989
Schleswig-Holstein	Mortality rates	Trivers-Willard	No statements available	Voland 1984
Ostfriesland	Mortality rates	Trivers-Willard	No statements available	Voland 1988
Krummhörn	Mortality rates	Trivers-Willard/ Local resource competition	No statements available	Voland and Siegelkow 1990; Voland et al. 1991
Portuguese nobles	Dowry payments as indicated by marriage rates	Trivers-Willard	No statements available	Boone 1986, 1988

Portuguese peasants	Correlation between harvest quality and sex ratio at birth	Unknown	No statements available	Cowgill and Johnson 1971
Contemporary North America	Nursing and birth-spacing patterns	Trivers-Willard	No statements available	Gaulin and Robbins 1991
Nineteenth-century United States	Mortality rates	Rational actor, local resource enhancement	No statements available	Ginsberg and Swedlund 1986; Hammel et al. 1983; Vinovskis 1972
Herero	!Kung opinions	Enhancement of opportunities for indirect reproduction?	No	Harpending and Kurland 1991
	Mortality rates, skinfold measurements	Local resource enhancement?		Harpending and Pennington 1991
Kanjar	Participant observation	Rational actor, local mate and resource enhancement	No statements available	Berland 1982, 1987; see also Gautam 1983; Tandon 1968
Mundugumor	Participant observation	Local mate and resource enhancement and competition	No statements available	McDowell 1991; Mead 1935, 1949

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