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## Ecological Demography: A Synthetic Focus in Evolutionary Anthropology

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The interests of evolutionary anthropologists, behavioral ecologists, and demographers converge on the ecology of human fertility. Ecological conditions influence the optimum pattern of maternal effort. Patterns of abortion, neglect, and infanticide vary with mothers' ability to invest in their children and children's ability to use that investment. As in most other mammals, the ecology of human fertility varies between the sexes: status and resource control are important for males, whereas reproductive value is crucial for females. In pre-industrial societies, and even in monogamous societies in demographic transition, wealthy men had more children than did poorer men. This correlation, often assumed to have disappeared, persists today, with richer men still having more sexual access than others. Sex differences in the ecology of fertility mean that sex of the offspring, as well as birth order, influences parental investment. Because individual fertility varies with environment, it is not surprising that "natural" (uncontrolled) fertility varies across societies or that demographic transitions proceed locally, with occasional reverses, as individuals strive to maximize their lifetime reproductive success in changing, competitive, conditions.

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Anthropologists, biologists, and demographers are all interested in human reproductive patterns, sex differences, and ecological correlates of behavior—in the life histories of humans. The underlying paradigms they use can differ significantly. Classical demographers study population patterns, whereas historical demogra-

phers approach human populations in a manner more like that of anthropologists and biologists, seeking family patterns and population shifts that correlate with external conditions such as economic fluctuations.<sup>1</sup> I agree with Watkins<sup>2</sup> that any "satisfactory theory of fertility change has to explain differences in the onset and pace of fertility declines as well as fluctuations in fertility." (p. 28). Yet classical demographic transition theory has not proved especially helpful. Demographic correlations vary in time and space far more than one would expect them to<sup>3,4</sup> if the correlations represented universal principles. As Schofield and Coleman<sup>5</sup> noted, "Any subject which finds it necessary, or indeed possible, to consider its material divorced from an appropriate body of theory must be in trouble" (p. 5).

Humans, of course, are not the only species in which fertility varies. For other species, the predictive ecologi-

cal rules are relatively clear, although they have not always been quantified. The power and predictive ability of models of fertility onset and fluctuation for other species derive from life history theory in behavioral ecology.<sup>6–10</sup> Ecological demography arises from two facts: that the reproductive behavior of humans, like that of other species, is influenced by natural selection and that current fitness is the product of both genotype and environment.<sup>11–13</sup> Here I review classic atheoretical and recent theoretical studies that contribute to this emerging field, exploring the extent to which human reproductive responses to ecological conditions, considered in their broadest context, follow the same selective rules as other species.

### NEW PERSPECTIVES

Ecological demography begins with the proposition that demographic patterns, observed at the population level, arise from individuals striving to maximize their successful lifetime reproduction. Genetics, cultural transmission, and the environment interact to produce a sometimes changing set of reproductive strategies. Individuals within a population may experience different environments; therefore, optimal reproductive strategies can differ not only over time, but within subgroups of a population as well. Ecological demography primarily differs from classic demography in its focus on ultimate versus proximate “causes,” its focus on individual versus group costs and benefits, and its recognition that the reproductive ecology of males and females frequently differs. As a result of these differences, it uses measures that are based on individuals rather than on populations.

#### Level of Causality

Many demographic analyses involve what evolutionary anthropologists call proximate triggers. For example, we may discover that, in a particular society, men who marry younger women have more children in their lifetimes than do men who marry older women or that younger women command a higher bride price than do older ones. One can ask why such patterns exist at several levels. The ultimate cause of a behavior’s evolution is

always its impact on the persistence of a genetic lineage through survival and reproduction. Many quite different proximate mechanisms may come into play because they enhance survival and reproduction. When we wish

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to understand whether a behavior is a functional evolutionary response, the study of trait-environment correlations—of ultimate function—takes precedence. Elucidating proximate mechanisms can enrich our understanding. What mechanisms are useful depends on salient features in the external environment and on whatever internal devices already exist in the organism. For example, fertility declines are predicted to occur as a functional evolutionary response in humans, as in other species, when parental effort enhances offspring success sufficiently to compensate for the lost numbers.<sup>14</sup> Different proximate

mechanisms can cause fertility to decline: later age at marriage, longer interbirth intervals, earlier “stopping.” When, as in medicine or family planning, our primary concern is intervention,<sup>15</sup> the particular mechanism becomes important.

#### Levels of Selection

Clearly, the only behaviors that can evolve by natural selection are ones that enhance the success of a genetic lineage. Such behaviors are selfish, parental, reciprocal, or helpful to relatives, and therefore enhance inclusive fitness. Genetic altruists—those who, to their cost and others’ benefit, restrict or cease reproduction—decline in the population, being replaced by individuals who, as Darwin himself recognized, behave to their own reproductive benefit.<sup>16</sup> Thus there is no evidence of evolved homeostatic population regulation mechanisms (contra refs. 14,17,18). If the function of fertility shifts were, in fact, to regulate population, pre- and posttransition societies might often seek to achieve this regulation through imposed infertility. From a population point of view, nothing would inhibit enforced infertility to regulate population,<sup>14</sup> yet societies “do not favor childlessness.”<sup>19</sup> Indeed, attempts to regulate individual fertility for the good of the group (for example, China’s recent “one child” policy) engender fierce opposition.

Genetic selfishness still produces apparent population responses to resource levels as an emergent phenomenon. This occurs because many families, differing in their resources, attempt to optimize their fertility in varying conditions, and subgroups impose legal or religious coercion. These two fertility responses are functionally quite different. The extent to which restrictions impose costly constraints on individual optimization may predict the extent to which individuals will resist them. It would be rewarding to explore empirically when fertility shifts arise from “ordinary” selection—when, for example, having fewer children results in more living descendants for individuals, versus coalition-imposed fertility shifts. Recently Hawkes and Charnov<sup>20</sup> have summarized the argu-

ments cogently in anthropology (see also Botkin<sup>21</sup>).

### Sex Differences

When women's and men's lives are compared, some reproductive patterns must, of course, be similar. For example, the average number of children can never be higher for women than for men. Other phenomena, such as age at marriage, variance in reproductive success, and the rate and impact of remarriage, can differ strikingly between men and women.

Some of these differences arise simply from the fact that we are mammals. Other things being equal, male mammals achieve maximum reproductive success by expending their reproductive effort as mating, rather than parental effort, and by making a generalized parental effort<sup>22,23</sup> rather than a truly offspring-specific parental investment.<sup>24</sup> Female mammals, equipped to nurse their young, do best by producing healthy, viable offspring, and apportioning their effort among specific offspring.

The principal difference between these expenditure patterns is that mating effort and parental effort that is not offspring-specific, unlike true parental investment, may have a high fixed cost: much must be spent before any success is realized (Fig. 1A). Furthermore, later successes cost little compared to the cost of the first success. Thus, although many males will fail to reproduce, a successful male may have many times more offspring than the most successful female.<sup>25,26</sup> This has profound implications with regard to risk-taking and survival in males versus females. As a result, within polygynous species (including humans, whose evolutionary background is polygynous), males typically survive less well than females (Fig. 1B). This sex difference has further implications for parents: optimal parental expenditure may not mean equal investment in the two sexes.

### New Measures

Aggregate demographic measures are inappropriate for many behavioral ecologists' questions because they vary with the relative representation of subgroups. Further, intragroup variation is not reflected in aggregate

statistics, making differences between populations or between groups within a population difficult to assess.

Behavioral ecological studies typically measure some form of lifetime success: matings, births, numbers of offspring reaching independence, or numbers of grandchildren. Recent studies on humans<sup>27-40</sup> have measured actual lifetime fertility in the behavioral ecological tradition, using measures analogous to the demographers' net reproductive rate (NRR), which calculates the number of daughters expected if all females have mean age-specific fertility and mortality.<sup>41</sup> However, the new measures are based on individual patterns, carry variances, and consider children of both sexes. Studies may also measure within-family survivorship and the mortality rates of children, as well as the number of children alive at some specified age. Measures of children reaching independence reflect the "net success" for parents resulting from the interaction of other measures: survival to maturity, probability of marrying, age at marriage, age at birth of first child, marital fertility rate, child survival, lactational infecundity, and so forth. Predictions from "biological" and standard demographic measures differ.<sup>37</sup> When lifetime reproductive patterns, sex differences, or variation in behavior are important, these "biological" measures are probably more accurate and yield more information than do standard demographic measures.

### THE ECOLOGY OF FERTILITY

Ecological demography considers relationships that might never interest classical demographers. Because population patterns arise as an incidental side effect of individual patterns, rather than as evolved phenomena themselves, ecological demography examines not only the obvious correlations between population and environment (e.g., marriage rate, marital fertility, and cost of living), but individual reproductive costs and benefits. These can include such considerations as mothers' ability to invest in their children, as affected by these women's age, health, nutritional status, marital status, and the length of time since they last gave birth. At-

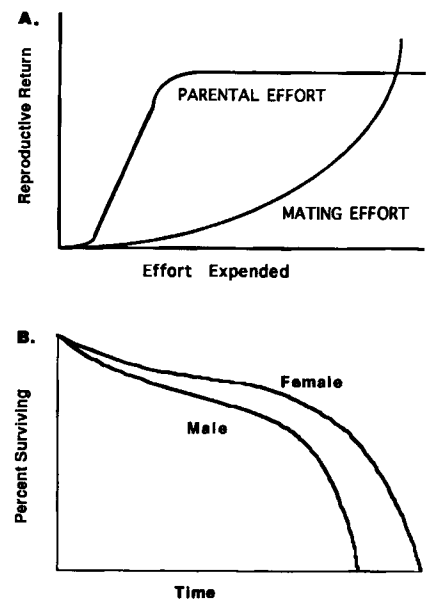


Figure 1. (A) Mating and parental effort have markedly different return curves. Obtaining even a single mate frequently requires great initial effort and expenditure (a high fixed cost). For example, a male red deer may need to wait an extra few years to grow big enough to compete with territorial males, grow antlers, and fight for territory, all to win even a single mate. Investing in offspring (parental effort), however, is typified by a different pattern: there is a level of investment below which the offspring cannot survive and reproduce; above that amount, the offspring's chances improve, but there is a limit on the amount of investment that will improve the offspring's chances.<sup>117</sup> Thus, in any species or in any human society in which males specialize in mating effort and females in parental effort, extremely different behaviors will characterize the two sexes. (B) As a result of these return curves, males will tend to be risk-takers; females will tend to be risk-averse. Reproductive failure will be higher and survival lower among males.

tion might also focus on the desirability of marital partners as influenced, for men, by wealth, land ownership, or occupation and for women, by reproductive value and health. Another subject of interest might be the probable success of a particular child as a consequence of intrinsic factors such as child health and sex, and extrinsic factors such as economics, the worth of other children, and reproductive value.

The costs and benefits of any particular reproductive event differ for men and women of different age, occupation, wealth, and health, and lead to different patterns within populations, depending on the composition of individuals, environmental richness, evenness, and predictability. Let us review, then, individual responses

to ecological conditions that can result in correlations between ecological conditions and fertility patterns. These responses can be physiological or social; those that are social may or may not involve conscious decisions.

### Male Cultural and Reproductive Success: The Importance of Resource Value

When resource-controlling men can have higher fertility than others—for example, through polygyny in bride-price societies—fertility tends to be high, but variable. Such conditions obtain in many traditional societies and some pre- and proto-industrial societies.<sup>42,43</sup> In quite varied societies, wealth or status correlates positively with men's reproductive success.<sup>29</sup> Richer Turkmen were found to have more wives and children than poorer men.<sup>27</sup> In the pastoral Mukogodo of Kenya, wealth also enhances men's reproductive success.<sup>44</sup> Similarly, among the Meru, who use livestock for bridewealth, richer men can marry more wives.<sup>45</sup> In societies as diverse as the Hausa,<sup>46</sup> Trinidadians<sup>47</sup>, and Micronesian islanders,<sup>48</sup> status and wealth correlate with male reproductive success.

In some societies, such as the Ache<sup>49,50</sup> and the Yanomamö,<sup>51–53</sup> few physical resources are owned, but even here, status represents a resource. Among the Ache, not only do men who are good hunters mate more often than other men, but their children survive better.<sup>50</sup> Among the Yanomamö, male kin available for coalitions also represent a resource. The men manipulate kinship terms in ways that make more women available for mating, and render powerful men available as coalition partners,<sup>51,52</sup> so that reproductive success is uneven. In this population, the most successful methods of gaining wives are belonging to a powerful kin group and gaining recognition as a revenge-killer.<sup>53</sup> Among the polyandrous Toda, a man's centrality in the kinship network is related to his reproductive success.<sup>54</sup>

These patterns are consistent with the behavioral ecological hypothesis that resources contribute to reproductive success,<sup>34,35,38</sup> but are not consistent with the demographic hypothesis

regarding children as resources and producers.<sup>55</sup> If parents perceive children as producers in agricultural work, then both land workers and land owners should have high fertility. Yet land owners typically have higher fer-

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tility and, consequently, larger families than land workers no matter what the economic weather. In addition, family size varies, less among owners than workers.<sup>37,42,43,56–60</sup> Land ownership apparently provides a more reliable resource control, a buffer against hard times.

The positive correlation between resources and lifetime reproductive success holds through demographic transition.<sup>38</sup> Results from contemporary societies are mixed.<sup>14</sup> As Low and Clarke<sup>38</sup> note, studies using proxy measures rather than actual resource control often yield negative results. This is true, for example, of a study by Birdsall,<sup>61</sup> which used total fertility rate (TFR) and gross national product (GNP), both population measures, and of a study by Vining,<sup>62</sup> which used individual education and intelligence quotients. Studies that examine lineages,<sup>63</sup> individual patterns,<sup>64</sup> and some census data<sup>65</sup> tend to produce positive results. Today, contraception technology complicates the issue; but when sexual access, rather than fertility, is measured, richer men clearly have more sexual access than do poorer men.<sup>66</sup>

### Bride Age: The Importance of Reproductive Value

Keyfitz<sup>68</sup> used Fisher's<sup>67</sup> concept of *reproductive value* to make predictions about migration, contraception, and

population growth. That concept is also useful in understanding trends in marriage age and remarriage rates. Reproductive value, derived from age-specific fertility and mortality rates, is defined as the probable number of daughters a woman will have during the rest of her life, thus encompassing age-specific fertility and survivorship functions. Thus, in societies with a bride price or other exchange of goods at marriage,<sup>69</sup> young women might be expected to command the highest bride prices. If high reproductive value is seen as desirable, men with great economic resources may be able to command women with high reproductive value. Another way of putting it is that women with high reproductive value are free to choose men with greater resources, although direct female choice is difficult to demonstrate in many societies. Among the agricultural and pastoral Kipsigis, the bride price required for a woman was directly related to her reproductive value.<sup>30,32</sup> With the introduction of western technology and medicine, differentials were reduced.

Poor men might choose to marry older women with greater resources when they can, explicitly trading reproductive value for resource value. Thus in eighteenth and nineteenth century Scandinavia, daughters of upper-middle-class men, who would marry relatively richer men, were considered to be marriageable at the age of eighteen years, whereas daughters of poorer men, who would marry poorer men, were not considered marriageable until they reached their mid-to-late twenties.<sup>36,70</sup> Richer men, in marrying younger women, gained high reproductive value, but also provided resources. Hughes<sup>59</sup> found similar patterns with regard to men's wealth and women's reproductive value in Lancashire, England.

### Remarriage for Widows and Widowers

In most societies, widows commonly remarry far less frequently than widowers, a fact that has no obvious demographic or economic explanation. Further, women remarry at earlier ages than do men, and women's probability of remarriage declines with age. Classical demographers<sup>71,72</sup>

have found such patterns puzzling, for women's economic value, like men's, does not decline with age. Nevertheless, women's reproductive value does decline. Furthermore, the decline from peak reproductive value is a certainty, in contrast to the risk of death, which causes lower-than-peak reproductive value at early ages.

Not surprisingly, when men remarry they tend to marry women who are younger than themselves and have high value. This undoubtedly contributes to the fact that men's second marriages are more fertile than are women's, even in societies with late ages at first marriage and socially imposed monogamy. Although in many societies the pattern can be slightly modified by the operant sex ratio,<sup>73</sup> the patterns are quite strong: widows remarry far less frequently than widowers;<sup>73-79</sup> widows with dependent children remarry at an even lower rate;<sup>74,78-80</sup> and widows commonly do not remarry at all when they are older.<sup>77</sup> In contemporary society these patterns also persist.<sup>81,82</sup>

### Optimization of Maternal Effort

Variation in fertility reflects the fact that maternal investment in one child may occur at the expense of investment in others.<sup>24</sup> Closely spaced pregnancies, when nutrition or other factors are limiting, may result in lowered lifetime reproduction. Today, a clearly negative correlation exists between a mother's job status or education and her lifetime fertility.<sup>15</sup> This implies a conflict: what is invested in work cannot be invested in child care. In traditional societies, too, there exist problems of optimizing maternal effort, even at the physiological level. Bailey et al.<sup>85,86</sup> have found that Efe women's ovarian function and resulting birth schedules follow a seasonal pattern that correlates only with food availability. Clearly, this reflects a physiological response to changing ecological conditions. Even subtle maternal responses during pregnancy, such as adjustment of blood flow to the uterus, fit a life-history model of reproductive optimization.<sup>85,86</sup>

Other investment patterns also respond to ecological conditions. !Kung women have interbirth intervals of about four years.<sup>87</sup> Because predators

are prevalent, !Kung women who depend on bush foods carry a child at least occasionally until it is six years old. Blurton Jones,<sup>88,89</sup> using a model of "backload" (the weight of a child plus foraged material), could predict interbirth intervals and mortality patterns. !Kung women living in compounds, who were not dependent on bush foods, had quite different schedules of births. The number of successful descendants was maximized for

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bush-living women not by maximizing the rate of births, but by responding to the conflict between production of a new child versus the cost of that production in relation to the survival of other children. Again, looking for ecological constraints seems profitable.

Among the Ache<sup>33,90</sup> and the Ye'kwana,<sup>91</sup> nursing women can forage less than others. In some societies, these costs are partially defrayed by having other children assume responsibility for child care. The availability of peers or siblings to serve as caretakers can have an impact on a mother's lifetime fertility. On Ifaluk, for example, women whose first two children were girls had greater lifetime fertility than did others.<sup>92</sup> Because daughters assist in child care on Ifaluk, mothers whose first children are daughters defray some costs.

In other societies, wet nurses were hired to defray these costs. A dramatic example is given by Hrdy,<sup>93</sup> who found that interbirth interval, fertility, and infant mortality all varied with mothers' status. The richest women had

very short interbirth intervals, very high fertility, and low infant mortality. A linear relationship between infant survival and the cost of wet nurses meant that the richest women, who could afford the best wet nurses, fared best. Among the bourgeois, complexities created greater variation in pattern. Poor women had longer interbirth intervals, lower fertility, and high infant mortality. Wet nurses fared worst of all, having long interbirth intervals, very low fertility, and very high infant mortality.

### Abortion, Infanticide, Abandonment, and Neglect

Parental withdrawal of investment in their children seems at first obviously counter-selective. Within other species, including langurs and lions, it typically is not parents, but reproductive competitors (for example, males taking over a harem), who commit infanticide.<sup>94-98</sup> Among primates, the overwhelming majority of infanticides are committed by immigrant males or males who do not belong to the victim's social group.<sup>99</sup> Among humans, step-parents are more likely than parents to abuse or neglect children.<sup>100-102</sup> Yet parents can commit infanticide, abortion, and abandonment. Because each infant requires a great investment, investment biases,<sup>54</sup> even to the extent of infanticide, can be reproductively profitable.<sup>103</sup> Selective reasons for canceling investment in a child include the mother's ability or inability to invest and her access to additional resources such as family or mate, as well as the child's ability to succeed. Other factors are the economic and reproductive value of older children or children who still may be born. Cross-culturally, deformed or seriously ill newborns are at greater risk for infanticide.<sup>103</sup> Similarly, when circumstances such as too-close births, the birth of twins, or the absence of an investing man reduce a mother's chance of successful investment in a child, the likelihood is greater that she will neglect the child or kill it.<sup>103,104</sup> Abortion, too, appears to be more common when the birth of an additional child is likely to reduce the mother's lifetime reproductive success.<sup>82,105</sup> As women age and their reproductive value declines, termina-

tion of investment is less likely. Even attitudes toward abortion in our society are related to the proportion of women in any group who are "at risk" of unwanted pregnancy.<sup>106</sup>

Historical studies of child abandonment indicate that a mother's ability to invest in a child has long been influenced by selective factors such as the mother's health, familial resources, and economic conditions as well as the child's health, legitimacy, and sex. During the eighteenth and nineteenth centuries in France,<sup>107</sup> Spain,<sup>108</sup> and Russia,<sup>109</sup> child abandonment was related to economic factors and mother's abilities. Similarly, although he discerns no pattern, in Boswell's historical overview of child abandonment, 46% (29/63) of the cases he studied were related to maternal ability to invest,<sup>110</sup> despite great variations in time, country, and other circumstances. When one considers resource allocation (16/63; 25.5%) and offspring quality (4/63; 6.3%), selective reasons were apparent in 49/63 cases, or 77%.

### Physiological Sex Biases: Trivers-Willard Effects

In many polygynous species, including humans, male offspring are more expensive to raise than are female offspring:<sup>65,111</sup> they are carried longer in utero, are larger at birth, nurse more and more frequently, and are weaned later. Trivers and Willard<sup>111</sup> argued that in polygynous species under these conditions females in good nutritional condition are more likely to bear sons than daughters. A more broadly applicable statement might be that when the reproductive success of one sex exceeds that of the other (as in elephant seals) or that when parental investment can influence the reproductive success of one sex but not the other (as in baboons), there should be a correlation between parental condition and investment in that sex.<sup>23</sup>

Trivers and Willard assumed that mothers' physiological resources for successfully rearing offspring declines with age. In nonhuman species, as well as in many traditional human societies and developing countries, this is appropriate. Whenever the nutritional condition of mothers does not

decline with age, a male bias in sex ratio may occur in older mothers.<sup>36,112</sup> In polygynous iteroparous species, if a female's condition is good, a bias toward bearing male offspring is predicted to be profitable as a female nears the end of her reproduction, to invest more heavily, with a greater potential reproductive profit if successful (e.g., male-biased sex ratios for older female gorillas<sup>113</sup>). In nineteenth-century Sweden, mothers over the age of 35 years showed a sex-ratio bias toward sons, while mothers under the age of 25 years bore more daughters.<sup>36</sup> Such patterns underlie other influences such as parental sex-preference.<sup>114</sup>

### Other Familial Sex Biases

Because resource control is an effective and widespread strategy for men in acquiring mates,<sup>29,115-117</sup> resource inheritance biases are important; they can influence survivorship and the likelihood of reproduction. Perhaps no other species exhibits the same degree of resource transfer that can take place through inheritance within human families. Inheritance is frequently biased by legitimacy, birth order, and sex.

In societies with heritable goods, the size of a family and the sex of siblings may have somewhat different influences on men's and women's ability to marry at appropriate times. Within polygynous marital systems, inheritance is strikingly male-biased,<sup>118</sup> which is precisely the pattern that would be predicted if reproductive success varies more for men than for women and if male success is influenced by resource control. In many societies, earlier-born sons tend to inherit the greatest proportion of family resources even when, as in nineteenth-century Sweden, more equal distribution is stipulated by law. For Swedish men, only the number of their brothers mattered with regard to their lifetime reproduction, suggesting that brothers compete for resources. In contrast, women's lifetime reproduction decreased as the number of their siblings increased.<sup>36</sup> In many societies, as the total number of women's siblings increases, the more likely it is that the women will be drawn into caring for their siblings, re-

gardless of their sex, at some cost to their own reproduction. Among fifteenth- and sixteenth-century Portuguese nobles, the proportion of never-married men and women decreased with birth order, as did the fertility of married individuals.<sup>119,120</sup>

In contemporary Tennessee, sons in higher-status families fare better than others.<sup>121</sup> Among polygynous Mormons, sex-ratio and parental status are correlated as predicted by Trivers and Willard.<sup>122</sup> Gaulin and Robbins<sup>123</sup> have found a series of other Trivers-Willard effects in contemporary United States society. They examined interbirth intervals, birth weights, and the proportions of children nursed in relation to income and the presence of an adult male in the household. They found that as income increased, so did interbirth intervals and the percent of infants who were breast-fed—for sons, but not daughters. Indeed, on all seven of their measures, patterns differed for sons and daughters. In addition, daughters received relatively more from low-investment mothers, whereas sons received relatively more from high-investment mothers.

In many societies, a sex preference in infanticide exists; this represents a conundrum if it becomes widespread and persistent, for, as Fisher<sup>159</sup> noted, the rare sex comes to be more valuable in any mating market. Dickemann<sup>124,125</sup> found pertinent biases in sex preference in hypergynous societies. Because women may marry "up" and men "down," but the reverse is not allowed, daughters are valuable to lower-class families, but costly to upper-class families. Dickemann found that there was no single within-society sex bias, but that infanticide was female-biased in high-status families and that son preference was less strong in low-status families. These patterns, Dickemann argued, probably also represent a Trivers-Willard effect. It is possible, too, that otherwise rare male-biased infanticide occurred in high-status families.<sup>126</sup>

Voland<sup>127</sup> examined the effect of father's status on children's survival in a nineteenth-century German parish. The overall sex ratio of children born was almost exactly even; the effect of mothers' age was not analyzed. Deaths during the first year of life as a

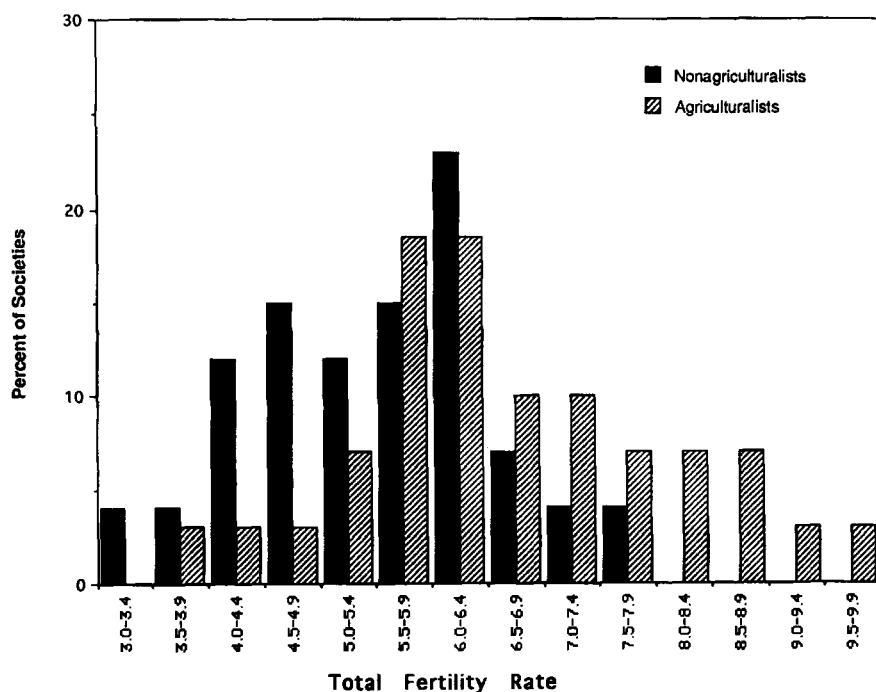


Figure 2 (modified from Bentley et al.<sup>136</sup>). Natural (uncontrolled) fertility varies greatly among societies, with that among agricultural societies being higher than among foragers and horticulturalists ( $n=53$ , Mann-Whitney  $U$ ,  $p=0.005$ ).

result of parental neglect were status-related: for farmers, daughters were likely to be considered less desirable than sons.<sup>40,128</sup> For other classes, the reverse appeared to be true. Voland thus found evidence of uneven parental investment tied to the perceived value of each sex for parents in different classes.

### POPULATION OUTCOMES OF THE ECOLOGY OF FERTILITY

If individual fertility is shaped by natural selection to respond to ecological conditions such as fluctuations in resources, then population patterns should be correlated with external conditions. We should be able to make sense of fertility patterns in noncontraceptive, "natural fertility" societies. We should find that the nineteenth-century European fall in fertility, called "The" demographic transition, is in fact variable, and dependent on local resource conditions.

#### Natural Fertility

"Natural" fertility means simply that there is no evidence, either from historical documents or from starting, spacing, and stopping patterns, of conscious control of fertility within

marriage. As a result of the interactions I have discussed, we can expect natural fertility to vary, perhaps with environment, perhaps with subsistence. Demographers have noted, at least since Henry,<sup>129</sup> that fertility varies across natural fertility societies.<sup>130,131</sup> They have used Coale and Trussell's<sup>132,133</sup>  $m$  to compare the shape of age-specific fertility, identifying cases in which there is no evidence of parity-specific fertility control.<sup>14</sup> Recently, Wilson et al.<sup>134</sup> modeled natural fertility and similarly argued that although the concept is useful, it is important not to construct false dichotomies.

Fertility varies greatly among natural fertility societies, and overlaps considerably with controlled-fertility societies.<sup>135</sup> All of the natural fertility societies showed levels well below the likely physiological maximum and were remarkably heterogeneous. Bentley et al.<sup>136</sup> found significant differences in the fertility rates of traditional societies with subsistence regimes. Intensive agriculturalists had higher fertility than did any other group (Fig. 2). Similarly, Wrigley and Schofield<sup>1</sup> found that marriage rates and age at marriage in pretransition England correlated with various cost-

of-living indices, suggesting that individual fertility decisions responded to economic costs.

### Investment, Production, and Demographic Transitions

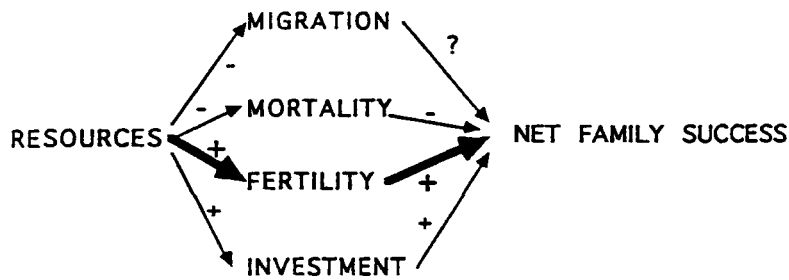
Other things being equal, greater fertility means greater lineage success. But the cost of producing effective, competitive children—who survive, marry, and reproduce—is influenced by ecological conditions. Some conditions favor parents who shift their resources away from having more children and using them to increase their investment in existing children (Fig. 3). Unless there is a net increase in a family's total resources, the available resources must be allocated to fewer children. Under those circumstances, lower fertility fosters higher lifetime success.<sup>137,138</sup> Thus, if parental resources can reduce child mortality or increase the likelihood that children will become well established and marry, the shifts in Figure 3B will be favored. Lower infant mortality, leading to increased population density, increased competitiveness,<sup>139</sup> and industrialization are often cited as "causes" of demographic transition. Neither is necessary<sup>140</sup> or sufficient to produce a decline in fertility. Numerous conditions can make it more expensive to produce effective, competitive children.<sup>14,38</sup>

Perhaps because of the costliness of children, individuals in modern societies make conscious decisions about fertility versus investment. Although accidental pregnancies complicate the picture, parents make deliberate decisions about family size in response to their judgment of available resources.<sup>141,142</sup> When deliberately chosen family sizes are considered, income and family size are positively correlated. When income is judged as favorable relative to others, fertility is increased.<sup>141-143</sup> Women on welfare<sup>64</sup> clearly avoid further pregnancies in order to invest more effectively in their existing children. In fact, as Lancaster and Lancaster<sup>144</sup> have argued, the perception of resources probably has influenced fertility decisions throughout human evolution.

This argument counts children as a net cost economically. What if, as some economic demographers<sup>19,145-147</sup> argue,



## CETERIS PARIBUS



vantage, perhaps, is the insight from ecological demography that such models may, in fact, be very general, affecting all sexually reproducing organisms, and not particular to one or another society, or one or another currency.<sup>14</sup>

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## WHEN COMPETITION IS HARSH:

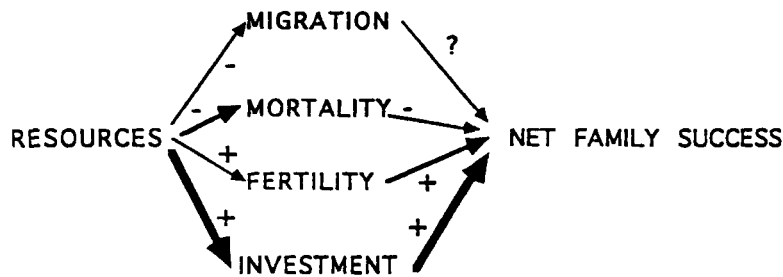


Figure 3. Other conditions equal, putting resources directly into fertility is the winning strategy.<sup>112</sup> Among mammals, this frequently means that males controlling more resources are able to mate with more females; it also means that more offspring can be provisioned. When conspecific competition is intense among offspring, parents may win by producing fewer, but better-invested, offspring.<sup>14,139</sup>

children are a net economic gain for parents in pre-industrial and pre-demographic transition societies? So far, all analyses of actual data suggest that although the situation is complex, children's labor is never sufficient to result in a net economic gain to parents.<sup>143</sup> Parents provide for their children, even in societies in which children work. Even grandparents provide for their grandchildren. Kin help each other, and, as Hamilton<sup>148</sup> predicted,<sup>14,149</sup> kin-helping tends to be preferential according to the degree of relatedness. Nonetheless, in situations in which children can defray some of their cost,<sup>92</sup> families may be larger.

An ecological approach to fertility, although it need not imply any conscious factors, is similar to the demographic models of individual decision and proximate variables,<sup>150-158</sup> to Mosk's<sup>159</sup> "leveraging" approach to fertility, and to Crimmins and Easterlin's<sup>160,161</sup> models of factors favoring a shift to conscious control of fertility. All have two important charac-

teristics: they do not assume that all individuals are uniform and they entail an explicit trade-off between quantity and "quality" of children. The perceived nongenerality of some of these models may not be the consequence of flaws in the postulated relationships but of the difficulty of trying to explain patterns that are based, in part, on reproductive "decisions" by considering only the value of children in monetary (rather than lineage) terms.

Even this brief review suggests that, although there still is much to learn, evidence continues to accumulate that human fertility varies in nonrandom ways with ecological conditions. Recognizing such relationships seems to be the first step toward important functional refinements of the treatment of population patterns. In re-examining demographic models, considering not only monetary, but also reproductive, currencies may help resolve some previously perplexing fertility patterns. An additional ad-

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