Low, Bobbi S., Carl P. Simon, and Kermyt G. Anderson. 2003. The biodemography of modern women: Tradeoffs when resources become limiting. In *The Biodemography of Human Reproduction and Fertility*, J. Rodgers and H.P. Kohler, eds., pp. 105-134. Boston: Kluwer Academic Publishers.

Chapter 6

The Biodemography of Modern Women: Tradeoffs When Resources Become Limiting

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Keywords: age at first birth, age-specific fertility, behavioral ecology, carrying capacity, contemporary United States, life history theory, reproductive histories, resource limitation, social support networks, women's education, women's work

Overview: Life history theory postulates tradeoffs of current versus future reproduction; in both developed and developing nations today, women face evolutionarily novel versions of these tradeoffs. Here we use a nonlinear dynamic model to explore: [1] the general issues of tradeoffs of education, work, and current fertility; [2] some specific examples (e.g., what increase in fertility will compensate for particular delays of age at first birth under given conditions). Finally, we model a largely unrecognized issue. Demographic transitions of the past have been characterized by decreases in fertility accompanied by (sometimes quite large) increases in per capita investment in offspring. The Rio Conference and its follow-up highlighted the conflicts between low-fertility, high-consumption, versus high-fertility, lower consumption strategies -- yet we have few ways to make testable predictions about future conflicts. We explore outcomes when impending resource constraints differentially affect short-generation-time-strategists, versus delayed-reproduction-resource-acquirers. The conditions favoring delayed fertility with resource accumulation are highly constrained; under almost all conditions reproduction in the early 20s leads to the greatest lineage success for women in the models.

1. Introduction

Over 130 years ago, Charles Darwin noted that: "The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of more power and the greater risks run by the parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size, or less vigorous, or subsequently not so well nurtured" (Darwin, 1871, I, p. 319). This life history tradeoff, between offspring quantity and offspring quality, occurs across species, and is quite possibly the driving force in initiating demographic transitions (Low et al., 1992; Low, 1993, 2000a, 2000b). Its importance has been recognized by several disciplines: demography (e.g., Easterlin and Crimmins, 1985; Tilly 1978), biology (Stearns, 1992; Roff, 1992; Lessells, 1991; Smith, 1974; MacArthur & Wilson, 1967), anthropology (Hill, 1993; Hill & Hurtado, 1996; Kaplan, 1997; Low, 1998), economics (Becker, 1981; Becker & Lewis, 1974; Willis, 1973), and sociology (Powell & Steelman, 1989).

But have we overshot the reduction of quantity in favor of quality? In some parts of the world today, fertility has fallen below replacement levels. Further, a growing proportion of modern fertility, in low-fertility settings, is late – and generation time is a powerful force in lineage increase (e.g., Low et al., 2002).

What drives this apparently maladaptive extreme? Post-transition societies appear to have fertility that is lower and later than any calculated optimum (e.g., Hill, 1993; Kaplan et al., 1998; Low et al., 2002). Women's education and women's work are associated with delayed and lowered fertility, as if women were shifting from "reproductive value" to "reproductive plus resource" value in modern mate markets (e.g., Low, 2000b). The characteristic positive association between resource control, including wealth, and fertility (traditional and historical review, Low, 2000a; modern review, Macunovich, 1998) seems to be absent or reversed in many societies (e.g., Borgerhoff Mulder, 1998; see Low, 2000a & 2000b for analytic difficulties).

Interpretation is difficult. Many studies inappropriately lump as a single "population" groups whose members face very different constraints (see Low, 2000b). This is incompatible with studies of resource-reproduction correlations in other species, which typically make comparisons within population and within sex. Studies of modern populations seldom measure variables in ways parallel to those of other species, traditional societies, and transition societies; frequently variables such as education are used as proxies for unmeasured variables (see Low 2000a, Chapter 15 for review). So elucidating the constraints can be difficult. Finally, in some cases empirical data are lacking in the form we need them.

Part of the constellation of behaviors we see today in developed nations is a shift in women's tradeoffs: in low-fertility settings, a woman's relative reproductive value is not such a major issue as in traditional societies, for example. However, the parental value of resources garnered is much greater. In fact, demographic transitions have a precise parallel in other species, called r- and K-selection (MacArthur & Wilson, 1967; Low, et al., 1992; Low, 1993, 2000a): When only extremely well-invested offspring can gain independence, establish themselves and find mates, fertility is lowered and per-capita investment is raised. Human demographic transitions exhibit these same traits. The specific forces are often issues of labor markets (Becker, 1981; Becker & Lewis, 1974; Becker & Barro, 1988; Kaplan et al., 1995a, 1995b) or education (Knodel et al., 1990). When employers require more highly trained employees and education is expensive, investment in the "human capital" of education can be economically profitable, even when it carries some biological cost of delayed and lowered fertility.

Earlier (Low et al., 2002) we explored the conditions under which, in a non-resource-limited population, resource acquisition could compensate biologically (in terms of comparative lineage growth and persistence) for delayed fertility. Not surprisingly, these conditions were extremely limited. First, in declining populations, late-reproducers' lineages declined more slowly than did others (cf. Fisher, 1958). Second, when poorer sub-groups of the population experienced severe mortality, and investment in education could "spring" individuals into a sufficiently safer group, the net lineage increase was greater for those who invested in human capital at the expense of some (but not great) delay in fertility, compared to those who remained in the poor, early-fertility, high-mortality group.

As we noted above, in Western societies today, women who delay reproduction to gain education and high-paying jobs typically suffer relative declines in their lineages – in classic biological terms, they lose. Here we ask: what will happen when resources affect lineage persistence in new ways? How much does it matter, when resources become limiting, whether resource access is egalitarian, or the wealthy have preferential access to (limited) resources? These issues, we suspect, lie behind such conflicts as the confrontations between developed and developing nations, sponsored by the United Nations to think about issues of sustainability at the Rio Conference in 1992 (UNEP 2000). They also may inform debates about the "carrying capacity" of the earth, and concepts of sustainability (e.g., Cohen, 1995; Daily and Ehrlich, 1992, 1996).

To model women's tradeoffs of education, wealth, and fertility, we use a dynamic Leslie-like model (e.g., Caswell, 2001), including education and wealth as well as the usual demographic measures. To begin, there are 9 socioeconomic levels of agents in the model; they have probabilities of following varying life paths. The per capita consumption of women in the 9 levels varies 14-fold. Thus, the model, while simplified, has multiple currencies and multiple actors, to capture some of the complexity of modern women's decisions. It also can be used to explore problems at several levels: within-population variations in strategies, or multiple-population comparisons.

2. Resources and Reproductive Success: Why Biologists Count Genes

In most mammals, and in the majority of traditional human societies for which data exist, status, power, or resource control enhance lifetime reproductive success, especially for males. Variation in men's reproduction in traditional societies arises mostly through differential polygyny — higher-status men can marry earlier and more often than other men, and often they can marry younger women, of higher reproductive value (Low, 2000a). In quite varied societies, wealth or status and reproductive success are positively correlated for men (e.g., Hill, 1984; Low, 2000a, Chapter 7). Richer Turkmen had more wives and more children than did poorer men (Irons, 1979). In the pastoral Mukogodo of Kenya, wealth enhances men's reproductive success (Cronk, 1991). Similarly, the Meru use livestock for bridewealth, and richer men can marry more wives (Fadiman, 1982). In societies as diverse as the Hausa (Barkow, 1977), Trinidadians (Flinn, 1986), and Micronesian islanders (Turke and Betzig, 1985), status and wealth correlate with male reproductive success. Even in foraging societies such as the Ache (Kaplan and Hill, 1985; Hill and Kaplan, 1988) and the Yanomamö (Chagnon, 1979, 1982, 1988), in which few physical resources are owned, status represents a resource. Among the Ache, men who are good hunters not only get more matings than other men, but their children survive better (Hill and Hurtado, 1996). In the Yanomamö, male kin available for coalitions also represent a resource, and men manipulate kinship terms in ways that make more women available for mates, and render powerful men available as coalition partners (Chagnon, 1982, 1988), so that reproductive success is uneven. In Yanomamö, the most successful methods of gaining wives are being a member of a powerful kin group, and gaining recognition as a revenge-killer (Chagnon, 1988). Among the polyandrous Toda, a man's centrality in the kinship network is related to his reproductive success (Hughes, 1988). There is no doubt that resources contribute to reproductive success for men in traditional societies. In modern societies,

the issues of quantity-versus-quality (Easterlin, 1978; Macunovich, 1998, Chu 1998) mean that outcomes are more variable for men than in traditional societies. In some cases wealthier or more powerful men do have more children than others; in some cases they have the same number or fewer but better-invested ones; and in some cases they have more sexual access but no more children (e.g., Easterlin, 1978; Macunivich, 1998; Kaplan, 1996; Pérusse, 1994).

Women typically face more severe tradeoffs than do men in the requirements for garnering resources versus producing and investing in children. The activities that a man performs to gain resources, power, or status typically increase his fertility. Women seldom show differential reproductive gain with resources or status, above some level required for well-nourished children (e.g., Low, 2000a, Chapters 4, 11-15). And because women do most of the primary child care, typically the effort to gain resources conflicts with investment in children. Among hunter-gatherers, nursing women gather food less effectively than other women (Hurtado et al., 1992). Today, few employers have free extensive childcare facilities that allow women to work without loss of income or safe childcare. Across societies, for women, work conflicts with childcare. So professional women today are likely to have fewer children than others.

In all of these approaches, some proxy for "genes identical by descent" (IBD; Hamilton, 1964) is used. Biologists measure eggs laid, offspring born, offspring fledged or weaned, even (if they are lucky) number of grandchildren. For modern human populations, measuring genes IBD and lineage size may no longer be the best predictor of the likely persistence of a lineage. A new wrinkle in the ecology of demography may have been introduced. Once, for humans as for other species, the sheer number of children was the best predictor of a human lineage's success; this may have begun to change in the demographic transition. Biologists' use of demographics has typically been to predict the "success" of different lineages. Throughout most of evolutionary history, this has probably been the best predictor of future persistence (but see Williams, 1966 for the difficulties). Most of the variance has typically been in the number of genes identical by descent (number of relatives, relative size of the lineage); and biologists have chosen some reflection of this (number of matings, number of offspring, number of adult offspring, number of grandchildren; Williams, 1966, 1992).

Biologists try to measure genes because in most species number of genes varies more than proportion of the available resources per gene. Thus, when resources became limiting, the largest lineages have the best chance of having some members survive the resource crunch. However, in modern human populations -- for the first time -- *variance in resources* *controlled, and the ability of resources to provide protection from environmental crashes, may well exceed fertility differentials.* If that is true, then the best predictors of lineage persistence will be some form of resources allocated per offspring, not some reflection of offspring numbers.

That is, if wealth ensures first access to limiting resources, very small, but wealthy or powerful, lineages might in fact persist better than larger – but vulnerable – lineages. If this is true, then it is not surprising that even careful and locally-appropriate studies (e.g., Kaplan, et al. 1995a) find that *biological* fitness is not maximized for many modern populations. The question remains: how advantageous would wealth have to be in the face of resource "crunches" to compensate for varying degrees of delayed and lowered fertility?

Certainly, developing nations at the Rio Conference were concerned about the possibility that wealth might allow protection of small lineages in new ways. What if the power of resource control meant that developed nations could, even with low fertility, protect access to resources, and consume them at a rate that precluded populations of less developed nations attaining the same standard of living? Cohen (1995) raised part of this issue when he noted that any theoretical carrying capacity calculated for any population (including that of the entire earth) would differ, depending on per capita resource consumption. The *I=PAT* calculation (Impact = Population * Affluence * Technology; Ehrlich and Holdren, 1971) is designed to ask about the sustainability of wealthy versus poor lifestyles. Thus, there is an additional set of questions of interest to planners and policy makers: How will the interplay of resource consumption and fertility affect long-term sustainability of resources?

Here we will ask about the outcomes, in terms of population composition, of the protection and privilege afforded by wealth. What will happen when, as Lee (1990) described, fertility becomes a commons problem -- when the children you have are children I therefore cannot therefore afford to have? How much protection by wealth is required to compensate (in biological terms) for differences in age at first birth?

3. Models and Data

People today face more complex reproductive tradeoffs than individuals in other species or people in traditional societies. It is not unreasonable to expect individuals to use heuristic "rules of thumb" in their choices, and to expect that such choices will sometimes, but not always, be optimizing. Here we examine some aspects of the relationships between resources (and education to get those resources) and (1) completed lifetime fertility and (2) timing of fertility (age-specific fertility) for women under different circumstances. We use dynamic modeling to simulate conditions

reflected by the literature on such populations, and to ask whether delayed fertility can, when resources are limiting, result in longer lineage persistence than early fertility. As always, we make simplifying assumptions, and hope that they are not so simple they destroy the utility of the model.

The Model

In this set of Leslie-like models (e.g., Caswell, 2001), we begin with 1000 women at age level 0 in each of 9 socioeconomic levels (Figure 1). Women in each group have some probability of dying, or surviving into the next older age group. At age levels above level 0, females in each group have also some probability of going to school, working, or having a child. We thus construct life paths for women starting life under different socioeconomic conditions, and facing different constraints and tradeoffs, depending on exigencies and past decisions. Women in different socioeconomic groups experience different age-specific rates of mortality (Figure 2a) and fertility (Figure 2b). We calculate not only these usual biological measures, but follow the tradeoffs of these with education, and with earned and inherited wealth. We track not only population size, but also the resources controlled or consumed by different categories of women in each time period. When we come to questions of sustainability, these measures are crucial.

Figure 1 depicts an example pathway a woman's life course can follow in our model. Each compartment in Figure 1 is a state a woman can occupy. Each has a five-digit description (Table 1). The first digit signifies *age* (in roughly five- to six-year intervals for all but the oldest level), the second, *social capital level* (in all cases here assumed to be 2, representing an intact family). The third digit indicates *human capital* (level of schooling); the fourth indicates *physical capital* (SES, wealth and resources); the fifth indicates *parental status* (0 or 1). In the highlighted path in Figure 1, a girl is born into an intact family in wealth class 3 (02030); so her age=0, social capital=2, human capital=0 (no school), physical capital=3, and parental status=0. She goes to school from elementary school (12130) through college (42420), which costs some physical capital (note that she has decreased to wealth level 2). After college, she gives birth, which incurs an additional cost (52411). Then, she works, gaining wealth each period: (624[2.5]1), (72441).

Sometimes a woman can reach a particular status through different routes, and when different paths have different payoffs, we report the either the average (which generates half-units) or in the Figures, both values. A

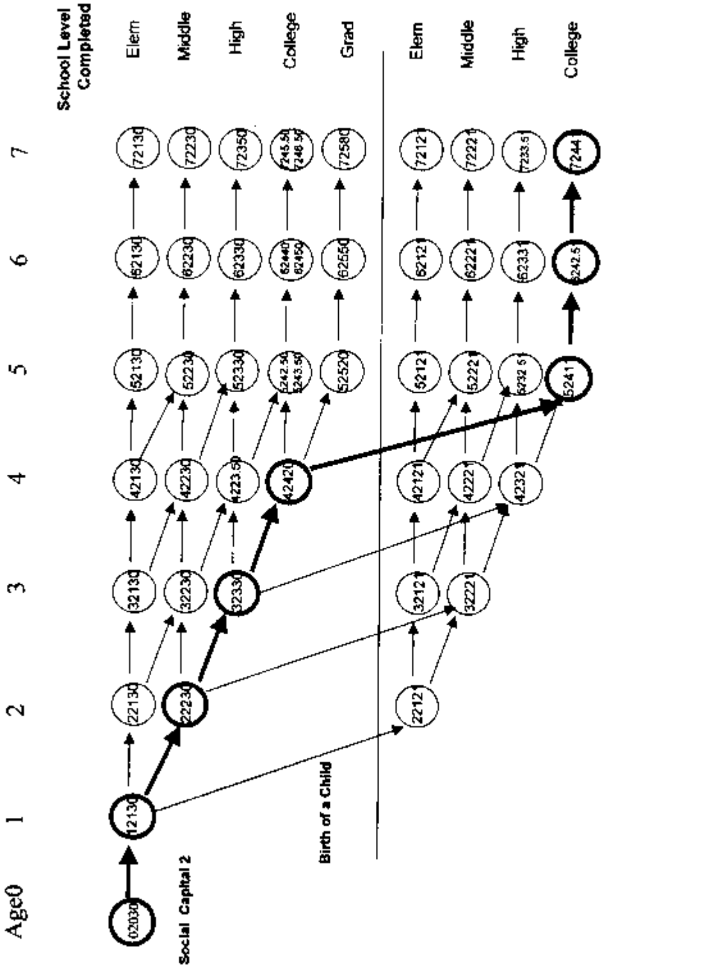

Figure 1. In this model, there are nine levels of physical capital (K_x; treated here as roughly equivalent to socioeconomic status). One level is shown (level 3). There are five human capital levels (H_x ,education: elementary, middle school, high school, college, and post-college); and seven ages, the first six approximately five to six years long (0= birth through early elementary school; 1=elementary; 2= junior high and high school; 3=college, 4=post college, late 20s; 5=early 30s; 6=late 30s; 7=over 40). Thus a woman may occupy over 450 states. One life path is shown: a woman born into SES level 3, who completes college, then has a child, shown as a 5-digit string in which positions represent: 1=age, 2=social capital (here invariant; see Low et al. 2002), 3=human capital level, 4=physical capital (1-9), and 5=fertility (0=no child, 1=child). Although she enters other SES levels, to conserve space we have reflected changes only in the 5-digit string, rather than replicating this diagram nine times and showing transition across diagrams. In some states, either two values exist (e.g., for physical capital) in a string, or two strings of similar values exist, but one contains a new condition (reflected by bold/ underlined type). These result when a woman's condition differs depending on the path she followed (e.g., giving birth, then returning to school, versus continuing to school and giving birth later).

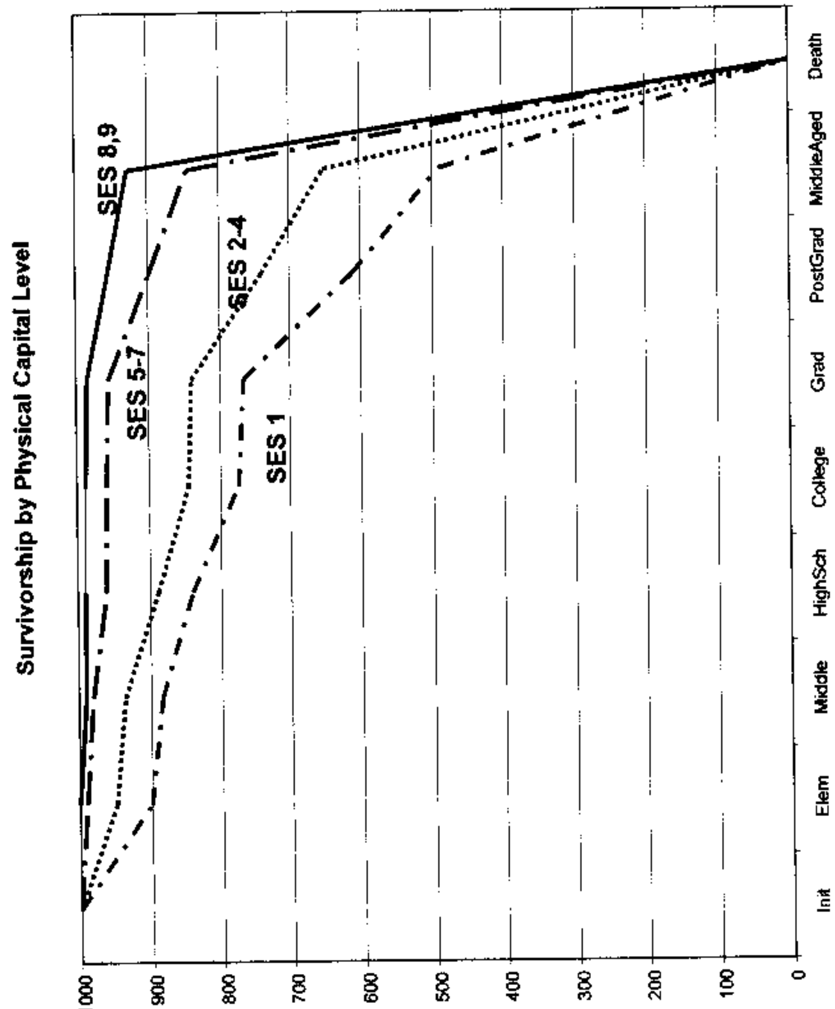

Figure 2a: Women in different socioeconomic levels demonstrate [a] different survivorship probabilities, and [b] different age-specific fertility. See text.

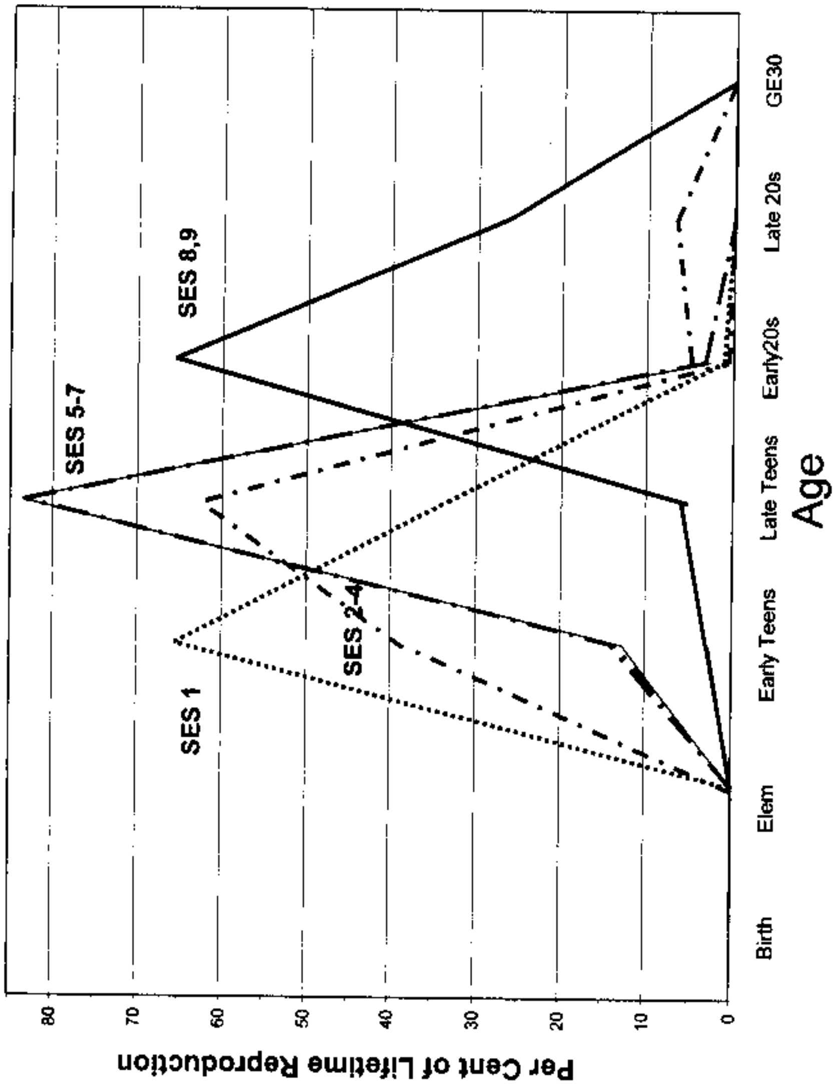

Figure 2b: Women in different socioeconomic levels demonstrate [a] different survivorship probabilities, and [b] different age-specific fertility. See text.

Table 1. Variables represented by each place-holding digit in the model. See text for further explanation.

Digit	Variable	Level	Range	Comment
1	Age	8	0 – 7	Approximates birth to middle age
2	Social Capital	1	2	Not varied in this model
3	Human Capital (H_x)	5	1 – 5	Level of education
4	Physical Capital (K_x)	9	1 – 14	Wealth
5	Parental Status	2	0 – 1	0=no child; 1=has given birth

woman who finishes college and works but never has a child, by the time she is in age group 7, has more physical capital (724[6.5]0, if she goes straight through school). A woman who completes high school and then has a child will, at age level 7, have less physical capital than either of the two previous women (7233.51). These endpoints are highlighted in Figure 1 along with the principal path discussed above.

The Currencies. Because we are interested in tradeoffs for women facing different conditions, we begin by holding the fertility of all women roughly equal, removing total fertility as a variable; only age-specific fertility varies. In this model, women without existing children have some probability of having just over one daughter in one age period (Figure 2b).

In an earlier set of models (Low et al., 2002), we used three currencies: social, human, and physical capital. We focus here on the importance of physical capital (resources, in part attained through human capital, education) when extrinsic resource fluctuations become limiting; we do not consider the effects of social capital. Women are born into one of nine socioeconomic strata. In each round, they die or move to the next older age level. At each age level, we assign some probability determined from the sociological literature, of going to school, having a child, or working (Figure 1). For each currency, the subscript x denotes the age group. In most age levels (below) women cannot simultaneously work, go to school, and have a child.

Human capital, H_x (investment in education and skills at age level x) exists at five levels (elementary, middle school, high school, college, and graduate work). College incurs a current cost, with a delayed payoff of increased physical capital. That is, a woman may lose a level of SES in order to go to college (unless she comes from a very wealthy family: SES levels 8 and 9), but when she later works, she will move up the SES levels more quickly than a woman who works with less education. Post-college education, in this model, mimics typical graduate work, in which the physical capital level is unlikely to change, rather than professional school, in which significant debt can be incurred. Everyone reaches H_x levels 0 and 1 at age-levels 0 and 1 respectively, but not everyone finishes high school (reaches H_x level 3, either in age 3 or later) (Figure 1).

Physical capital, K_x (one's monetary and other physical resources, roughly socioeconomic status: nine levels) increases the probability of gaining human capital, and thus, in time, further physical capital. There is evidence in the literature that social and resource capitals are traded off in some circumstances, and that social and human capital can influence reproductive decisions (above). They certainly affect resource consumption decisions. The nine levels of K_x reflect consumption levels of 1, 2, 3, 4, 6, 8, 10, 12, and 14. That is, per capita consumption by the wealthiest socioeconomic group is 14 times that of the poorest group.

We are thus using wealth to reflect consumption. (Note, unfortunately we have here a conflict between two standard usages; later we will employ K – with no subscript – to denote carrying capacity, or resource potential, of our universe.) We use this range to reflect the estimation by scholars that raising a successful child in the developed world today consumes approximately 15 times the resources consumed by raising a child in extremely poor countries. Even within the US, widely considered to have a moderate GINI coefficient (0.45 in 1999, reflecting wealth variance) the wealthiest five per cent of the population has a median financial base 8.26 times greater than the median of the poorest 20% (US Census Bureau, 2000).

The Women. There are approximately 450 states in which a woman can exist as defined by the above variables. Each state describes her age, wealth, educational, and parental status. There are eight age groups, each of the first seven approximately five years long: 0= birth through early elementary school; 1=elementary school; 2= junior high school and high school; 3=college age, 4=post college age (late 20s); 5=early 30s; 6=late 30s; 7=over 40.

Women have some probability of moving from one state to another state in a time period: for example, the probability of gaining H_x or of surviving to the next age group increases with level of K_x. Giving birth or going to college in a period decreases physical capital, K_x; otherwise women work (and increase K_x unless they have dropped out before

finishing high school). Higher education (Hx levels 4 and 5) leads to comparatively larger physical capital, K_x, at later ages. Women who work after attaining H_x level 3 (high school), 4 (college), or 5 (graduate work) gain 0.5, 1.5, or 3 levels of K_x per round. We estimate the transition probabilities in this model guided by published data. (Copies of the probabilities used are available from the authors.) In this model we consider women's own resources, and do not track relative wealth gains from different kinds of marriages; we leave that for future models.

We here consider four populations. First, the poor: imagine the homeless in the United States. These women are in K_x=1. They have lower survivorship both as children and adults than others (Figure 2a). For example, in one empirical study, 13% of women on welfare died before age 45 (Geronimus, 1996a, 1996b, 1997; Geronimus et al., 2001). These women tend to have early fertility (Figure 2b; cf. Stearns, 1992; Roff, 1992), and tend to remain poor (Corcoran and Kunz, 1997). Rarely do they transfer up more than one level of physical capital. When a pregnancy occurs early, schooling is typically terminated or disrupted (in the model, there is a low probability of return to school at later ages), and future physical capital acquisition is limited.

Lower middle class women (Rank, 1989; Geronimus, 1996a, 1996b; Wilson & Daly, 1997) would, in this exploration of the model, be in K_x=2, 3, 4. Upper middle class women occupy K_x=5, 6, 7. These women survive very well throughout life, and are likely to invest in acquiring both human and physical capital. In the model we give a very slight edge in lineage growth rate to the lower middle class women through slightly earlier fertility (Figure 2b), and a slight educational advantage to upper middle class women. By holding their fertility very close to 1 daughter (and by extension, one son), we reflect modern developed-nation fertility, in which $r \approx 0$. Finally, women with inherited wealth, and professional women, the glass-ceiling breakers, occupy K_x=8, 9. Such professional women appear to be becoming increasingly common (e.g., Sellers, 1998). These women's fertility is typically late and low; their human and physical capital levels are high.

Within each of these three broad categories, we construct a range of reasonable values, using the literature as a guide (e.g., survivorship is lower for K_x=1 than K_x=3; above K_x=4 it is uniformly high). However, we are undoubtedly overestimating the total fertility of these women by beginning with a lifetime fertility equivalent to that of the other three groups. That is, we are underestimating the proportion of women who never have children (cf. Low, Simon, & Anderson, 2002; Anderson and Low, 2002 -- this volume -- for empirical data).

Although we used empirical data to shape age-specific fertility and mortality, had we kept fully realistic figures, the intrinsic rates of increase for the sub-populations would have varied greatly. For example, we limited the fertility of all groups of women to approximately one daughter – not realistic; otherwise, early reproducers would swamp the model (Low et al., 2002). Similarly, while we have modeled "late" (in the 20s) reproduction for wealthy women (Figure 2b), and this means that the existence of any mortality makes r (the "intrinsic rate of increase," defined for each population as the growth rate as a function of age-specific fertility and mortality, under unconstrained conditions) likely to be negative. That is, the population will decrease. We have nonetheless not included women who do not reproduce at all until after age 30. Although such women are increasingly common in the US (e.g., Luker, 1996), they simply go extinct in our model. All these things mean that we underestimate the fertility of low-SES groups, and overestimate the fertility of the very wealthy women. Our results will therefore be less striking than a fully empirically-guided model.

The Questions. Earlier (Low et al., 2002), we explored the relative growth and age structure of non-limited populations for 18 groups: 9 socioeconomic strata and two social capital levels. Here, for four groups, we focus on the relative advantages of different wealth/education/age-specific fertility strategies when resources become limiting. When the carrying capacity is approached, what will happen?

The standard equations for population growth is, in its simplest form,

$$dN/dt = rN\,([K-N]/K) \qquad [1]$$

Roughly translated, this means that the rate of population increase (dN/dt) is a function of the number of individuals (N), times r, the "intrinsic rate of increase" (under unconstrained conditions), multiplied by the term ([K-N]/K), a multiplier used to decrease the rate of population increase as N, the number of individuals alive, approaches K, the carrying capacity (Figure 3; see Cohen, 1995 for definitions). When N is very small, this term approaches unity, and the population increases linearly at a rate r. When N=K, of course, the rate of population growth is zero, and when N>K, the population will decline. Here we adapt the concept but apply it directly to actors, for as Wilbur, Tinkle, and Collins (1974) noted long ago, and as demographers know, selection is not "r- and K-" but "b and d" – it is operationalized through births and deaths. When resources become limiting in any population, the typical response is reduced birth rates and increased death rates.

What happens if shifts in birth and death rates are not equivalent across sub-groups (e.g., socioeconomic levels)? Here, we calculate the

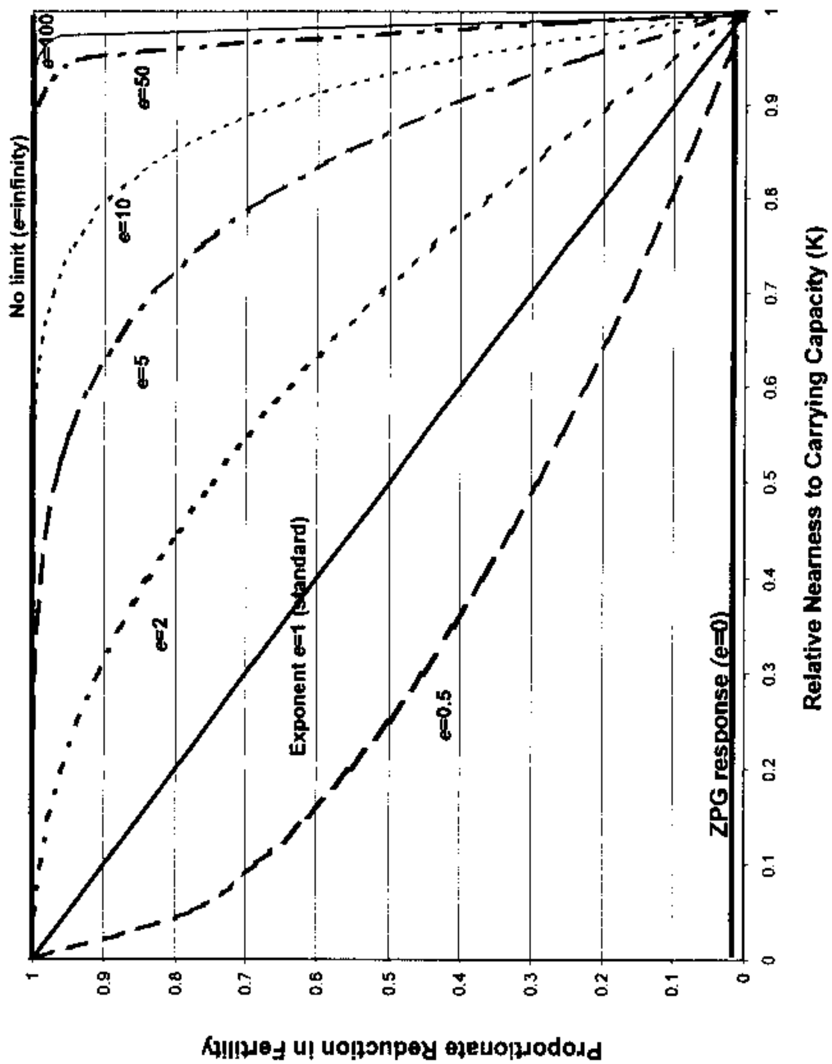

Figure 3: In standard population growth models, the term ([K-N]/K) is used to cause the rate of population growth to slow as numbers (really number of individuals times per capita consumption) approach K, the carrying capacity. The solid diagonal (E=1) represents that trajectory. In this model, we allow SES sub-groups to respond differentially, using exponents for the ([K-N]/K) term of 1, 10, 50, and 100. A group with exponent 100 will show no fertility or mortality response to the approach to resource limits until the limits are actually imposed.

carrying capacity as a resource issue, with responses in fertility and mortality. Each woman in socioeconomic level 1 consumes 1 unit per round; each woman in level 9 consumes 14 units (above). In any run, the total level of resource units is set: for example, perhaps 1,000 women in level 9 can be sustained, or 14,000 women in level 1 – or some intermediate mix. Next, we assign an exponent to the ([K-N]/K) term to create different functions for the slowing of growth for each subgroup (Figure 3). Thus, we calculate differential consumption and differential response to resource limitation for each subgroup separately as limits are reached:

$$dn/dt = rN\,([K-N]/K)^{e} \qquad [2]$$

The Limits. We model the following conditions. The carrying capacity for our universe is 150,000 units, enough to sustain 150,000 women of SES 1, or 10,714 women of SES 8 and 9. Here we are interested in the effects of differential reductions of fertility by the different groups of women as resource limitations are reached. To model such differing impacts of the carrying capacity on the different SES groups in our population, we assigned an exponent to the factor ([K-N]/K) in [1]. The usual assumption is e=1, so that the carrying capacity reduces the growth rate linearly as N approaches K (Figure 3). For a higher exponent, response is non-linear. The effect of carrying capacity is not felt until immediately before the carrying capacity is reached, r becomes 0, and the population no longer increases (Figure 3).

Here we model two scenarios. In Condition 1 (Figure 4a,b), the exponent for the poor is 1 (standard response in Figure 3); for the lower middle class, 10; for the upper middle class, 50; and for the wealthiest, 100 (Figure 3). This means that wealthier individuals do not respond as early or rapidly as poorer individuals to impending resource constraints. In Condition 2 the order of exponents is reversed: the exponent of the wealthiest is 1, of the poorest, 100. Runs continued for time periods equivalent to roughly 220 years.

4. Results and Discussion

In all cases the model began with equal numbers of women in each of the 9 SES categories. The population reached and stabilized near the carrying capacity, defined as 150,000 resource units (Figure 4 a-d). In Condition 1 (exponent for poor = 1, responding soonest to constraint), the disadvantage of delayed reproduction by the wealthy is muted; wealthy women's lineage rate of increase only declines below their natural r when resource consumption is very close to K.

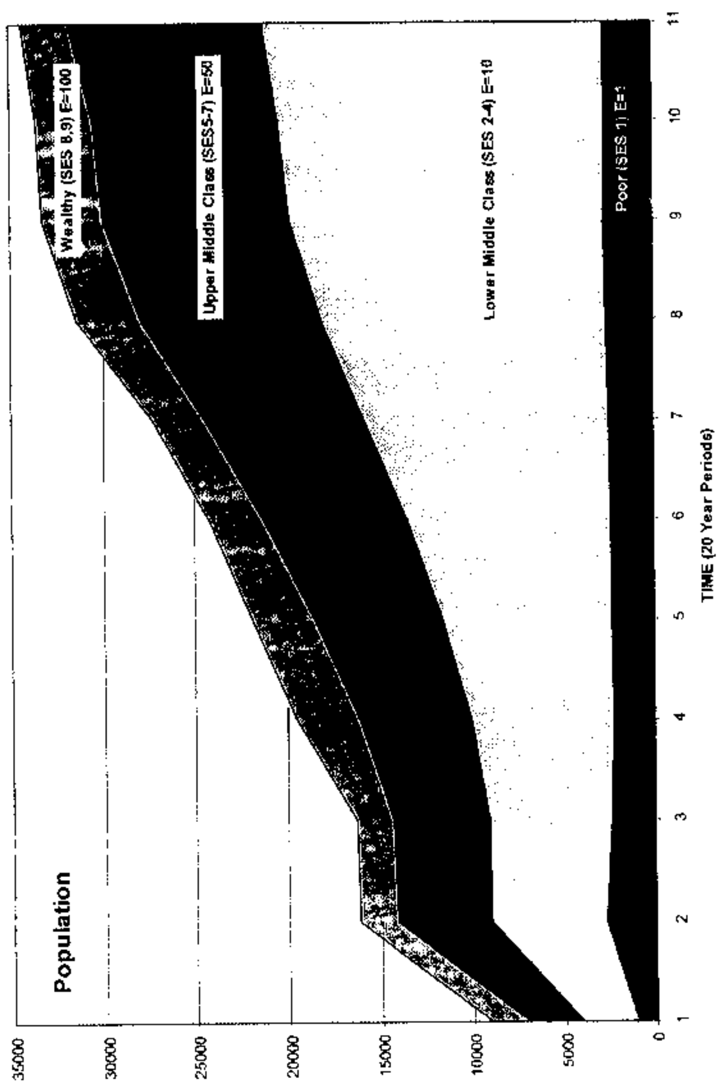

Figure 4a: When the poor are hardest hit by impending resource crunches (exponent=1) while the lower middle class (E=10), upper middle class (E=50) and the wealthy (E=100) are correspondingly less affected, then population numbers [a] and wealth [b] distribution are as shown. When the wealthy respond earliest to impending resource crunches (exponent=1), while the upper middle class (E=10), lower middle class (E=50) and the poor (E=100) respond correspondingly more slowly, population numbers [c] and wealth distribution [d] are as shown.

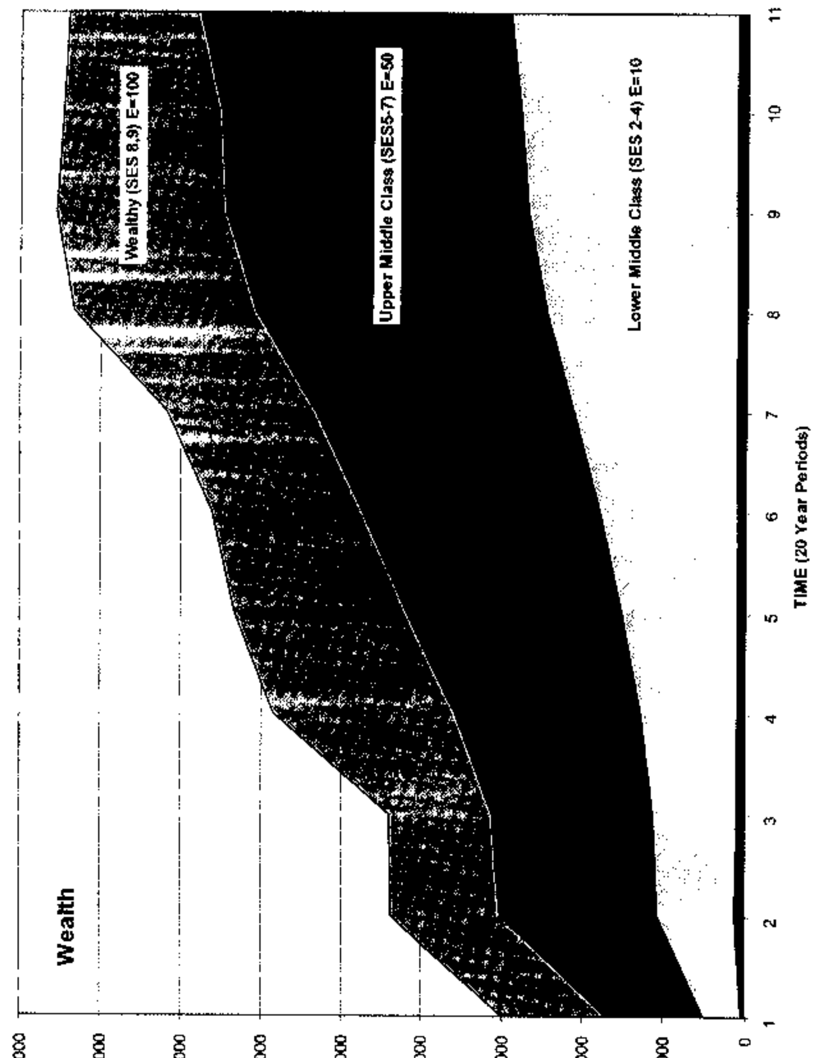

Figure 4b: When the poor are hardest hit by impending resource crunches (exponent=1) while the lower middle class (E=10), upper middle class (E=50) and the wealthy (E=100) are correspondingly less affected, then population numbers [a] and wealth [b] distribution are as shown. When the wealthy respond earliest to impending resource crunches (exponent=1), while the upper middle class (E=10), lower middle class (E=50) and the poor (E=100) respond correspondingly more slowly, population numbers [c] and wealth distribution [d] are as shown.

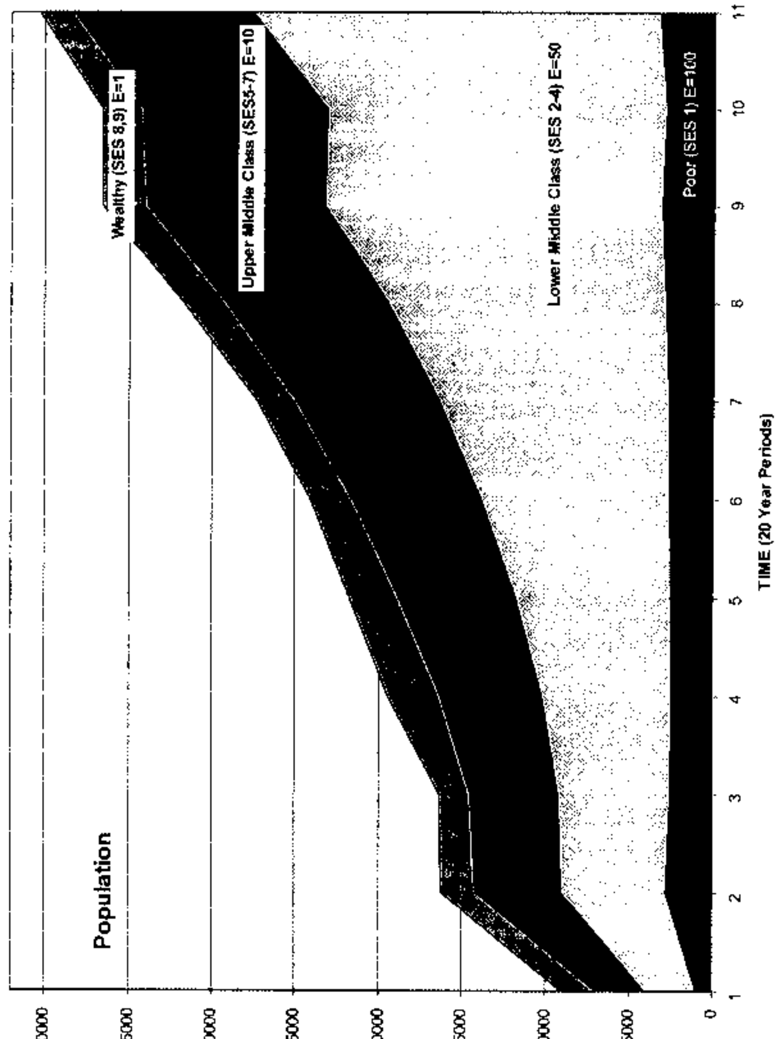

Figure 4c: When the poor are hardest hit by impending resource crunches (exponent=1) while the lower middle class (E=10), upper middle class (E=50) and the wealthy (E=100) are correspondingly less affected, then population numbers [a] and wealth [b] distribution are as shown. When the wealthy respond earliest to impending resource crunches (exponent=1), while the upper middle class (E=10), lower middle class (E=50) and the poor (E=100) respond correspondingly more slowly, population numbers [c] and wealth distribution [d] are as shown.

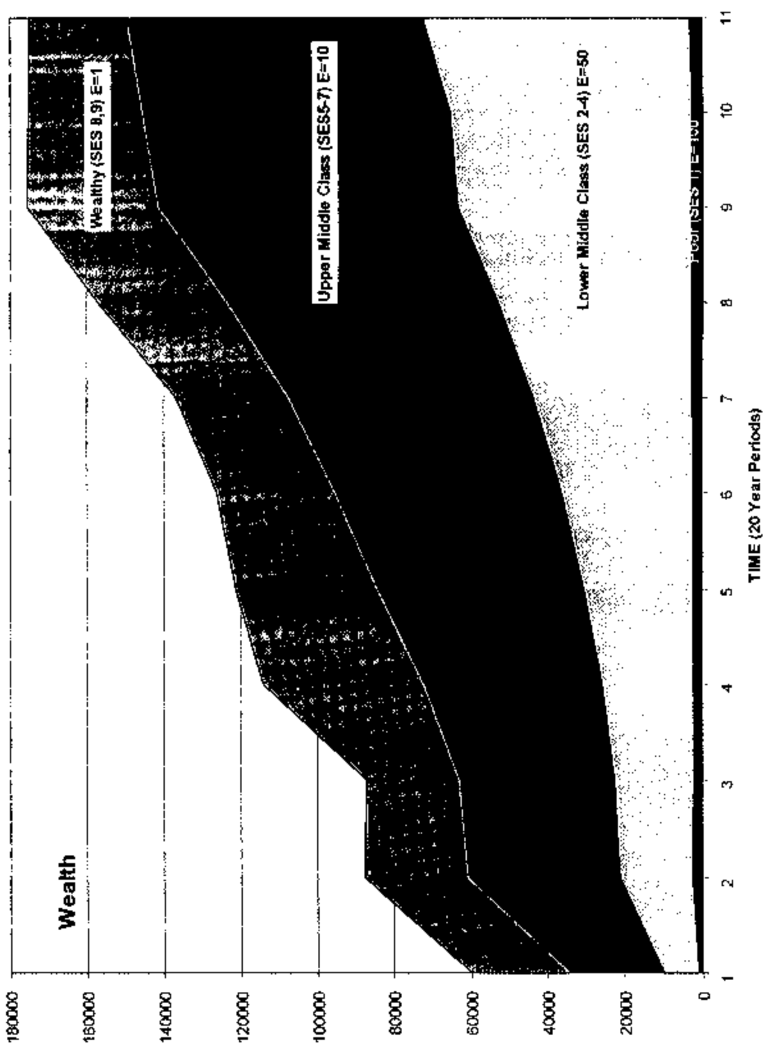

Figure 4d: When the poor are hardest hit by impending resource crunches (exponent=1) while the lower middle class (E=10), upper middle class (E=50) and the wealthy (E=100) are correspondingly less affected, then population numbers [a] and wealth [b] distribution are as shown. When the wealthy respond earliest to impending resource crunches (exponent=1), while the upper middle class (E=10), lower middle class (E=50) and the poor (E=100) respond correspondingly more slowly, population numbers [c] and wealth distribution [d] are as shown.

When the responsiveness was reversed, and the wealthy decreased fertility sooner than the poor in the face of constraints (cf. Figures 4a, 4c), population numbers stabilized much later. In fact, by the end of the runs, it was not clear that population numbers under Condition 2 had yet stabilized. We suspect this is true because the fertility of the wealthier women is later; thus "delayed response" produces far less dramatic shifts than those seen when the responses for the poor are delayed. As Figures 4b and 4d show, the wealth distribution is not shifted so much as most of us would predict. But the limitations of wealth per individual among the wealthiest, combined with their late fertility, means that numbers stabilize.

Figure 5 shows the cross-section of population numbers and wealth at the beginning and end of the two Conditions. It suggests that differential responses to impending resource constraints by sub-groups can affect the composition of the population. In all conditions, the wealthiest, late-reproducing women declined as a proportion of the population, from 11.1% in the starting population, to 7.37% per cent when their exponent was 100 (very late response; protection from shortages), and to 5.04% when they carried the standard exponent of 1 (Figure 5; see Figure 3 for the impact of exponents). Even protection from resource effects on fertility did not compensate for the comparatively late fertility of these women. The numbers of the poorest women also declined, regardless of the interactions of resources and fertility (Figure 5).

Most interesting were the effects of interactions between the fertility and mortality, and resource responses (exponent) on upper- and lower-middle class women. The values we used in attempting to mimic empirical data caused the lower middle class group (SES 2-4) to increase proportionately, both with an exponent of 10 (33.33% to 53.96%) and with an exponent of 50 (33.33% to 60.22%). Their relatively early reproduction and good childhood and adult survivorship combine to produce this result. Upper-middle class women (SES 5-7) declined very slightly (33.33% to 31.0%) with an exponent of 50, and declined more (33.33% to 26.7%) with the lower exponent of 10.

In all cases modeled here, *wealth was insufficient to compensate for the late fertility required to gain education and earn wealth.* Nonetheless, early response led to more dramatic declines of any group. When the poor respond more rapidly and directly to resource constraints, their proportion in the population at carrying capacity is reduced more dramatically than when their response is delayed. Similarly, when the wealthy, late-reproducing women had an exponent of 1 while the poor had an exponent of 100, the proportion of women of significant wealth was relatively small.

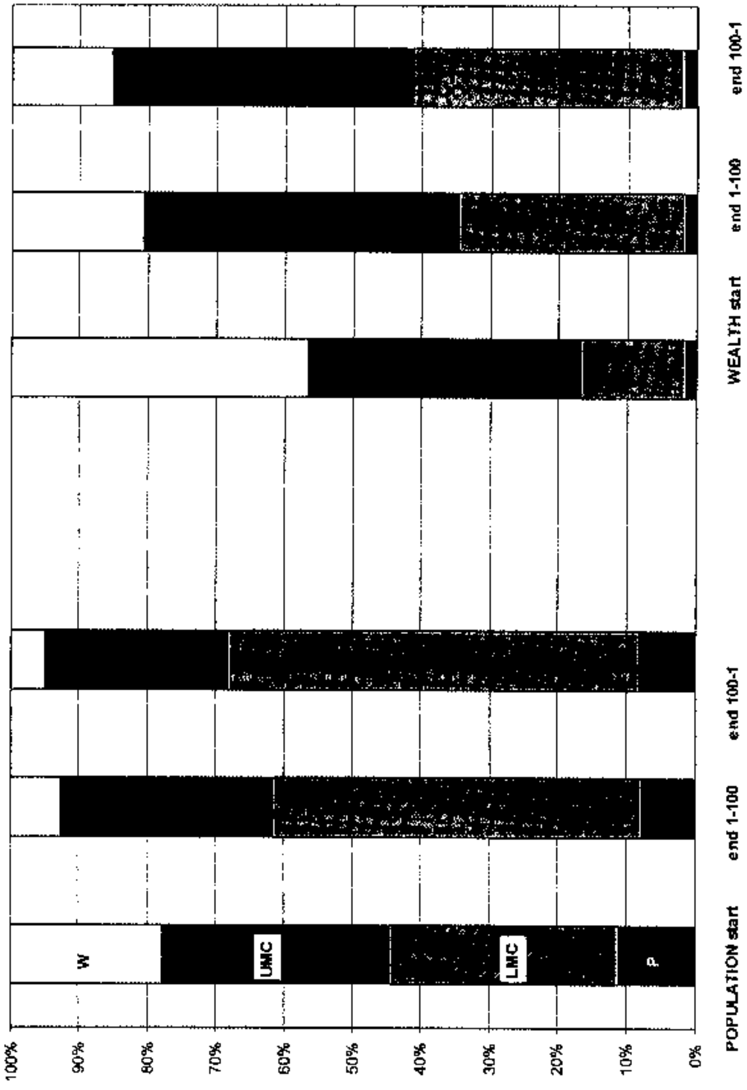

Figure 5: The population and wealth distributions under the specified conditions after the equivalent of approximately 220 years in the model. "End 1-100" represents the conditions in which the poor are affected earlier and more seriously than the wealthy; "end 100-1" means that the wealthy respond earlier and more dramatically to impending shortages than do the poor.

What Constitutes Lineage Protection?

Biologists typically begin demographic explorations with an assumption not often shared by demographers: that higher fertility *within* a population is profitable in terms of lineage persistence. *Ceteris paribus*, when resources become constricting, lineages with more members are less likely to go extinct. It is fairly easy to show that if "genes identical by descent" is the measure, lineages whose individuals trade off fertility for education and wealth will decline (e.g., Kasarda et al., 1986; Lancaster, 1997; Kaplan et al., 1995a, 1995b; Kaplan and Lancaster, 2000; Low et al., 2002).

We suggest that we need to re-think our assumptions. We need to think carefully about precisely what measures best predict future persistence of competing human genetic lineages. The model explored here suggests that even when high resource levels provide real advantage during resource constrictions, it is difficult to create conditions in which lineages with very late fertility may persist relatively better than earlier-fertility lineages (Figures 4,5). The very wealthy declined under all circumstances.

However, women in the upper- and lower-middle classes (with somewhat earlier fertility than the very wealthy) did not suffer when poor SES lineages responded relatively early (that is, when the poor suffered relatively low fertility and high mortality earlier than others in the face of a resource constraints). In the real world today, such resource constrictions are common. We further suspect that persistence of these tradeoffs for lineages will be enhanced when the threshold levels of education and wealth required to establish themselves -- to marry, raise children (not directly tested here) -- are substantial.

We could not test directly another possible advantage to the accumulation of resources: whether accumulation could completely protect fertility and mortality patterns from the constraints of carrying capacity. In Figure 3, that is the "no limit; e=infinity" line. In that case, whatever r, the intrinsic rate of increase, exists for a sub-group, it will remain unaffected by any approach of consumption to resource limits (until, of course, no resources remain). In societies with very unequal wealth distributions, this pattern may be possible at least for the wealthiest women.

Women's shift from reproductive to resource value – working to accumulate resources at the expense of delayed fertility – could accomplish this protection if the delay of fertility were not extreme. Women's work has always appeared to present women with a fertility tradeoff not existing for men. Empirical studies (Tasiran, 1995) are informative in showing how the tradeoffs may work: when women's time in the workforce is controlled for, women's wages have several positive effects on fertility (first births for Swedish and non-white US. women, second births for white US. women). The longer women work, the fewer chances they have to have children, and the higher wages they earn. Education and work have time and opportunity costs for women, while in Taşiran's study income had a positive impact on fertility. It can be very difficult to separate the effects of these three influences. Thus, in many analyses, prescriptions of women's work and women's education to lower fertility may be ineffective, depending on their relationship with women's incomes.

We hope to develop the model further. Two very important limitations exist currently. One is marriage: many women gain resources through marriage rather than their own human capital. Our simulated world of women who gain most of their resources on their own is rather limited in that way. Second, we may simplify the model to treat fertility as a yes/no concept. Fertility in developed countries is so low that this may be appropriate; how does the proportion of childless women affect our model?

Sustainability

The problems of wealth, health, and fertility for women are not just of academic interest to a few evolutionary anthropologists and behavioral ecologists. They are important in a highly applied context -- the global issues often called "population and environment"--as well as for their own intellectual merit. Both the number of people alive and the consumption per person today are higher than at any time in the past. Population patterns -- birth, reproduction, and death patterns -- are the sum of what individual men and women do: they mate and marry, have children, and die, consuming resources along the way. At the 1992 Rio Conference, and again in its 1996 follow-up, the "Northern" (developed) and "Southern" (developing) nations squared off; these were the central issues of conflict, with little progress and no resolution. We approach the 10-year anniversary of the Rio Conference, with as yet little progress on the politics of trading off fertility and consumption.

At the heart of the debate are conflicts over resources and fertility multiplied up from individual to population levels. These are precisely the tradeoffs we explore here: when resources become limiting, how do resource allocation rules affect the composition of strategies within the population? The central paradigm of evolutionary and behavioral ecology, that genes matter, and that in any environment strategies that best promote the relative success of a genetic lineage (e.g., Krebs and Davies, 1997; Low, 2000a), seem abstract. Yet these are precisely the (unperceived and unconscious) driving forces underlying conflicts like those of the Rio Conference.

The ecology of reproduction is vastly different for men and women in developing, versus developed, nations, and their appropriate reproductive strategies are likely to differ--yet we are only beginning to ask the evolutionarily appropriate questions. Demographers quantify the components of population change. Life history theorists primarily ask evolutionary ecological questions about other species. Ecological economists focus on environments, ecosystems, and evaluation procedures of economics; the concept of "population" is a vague entity (if high, bad). In texts (e.g., Miller, 2001; Chiras, 1992) we find some early, superficial discussion of "the two kinds of overpopulation." Evolutionary ecological work on human demography is beginning (Anderson, 2000; Mace, 2000; Low, 1993; Low et al., 1992; Hill and Hurtado, 1996; Kaplan et al., 1995a, 1995b; Hill and Kaplan, 1988a, 1988b; see especially Cronk et al., 2000), but it is not yet connected to these issues. If we can quantify and understand demographic components better, in the context of human ecology and genetic self-interest, perhaps we can come to a useful understanding.

Note that "K" is calculated here, as in all standard population models, as if the system were closed. Here we make that true; however, in the real world one could only claim the system is closed if the entire world comprises the system (but that, of course, raises other serious reality problems). With regard to any level less than the entire planet, the system is clearly not closed. An issue raised by the (incomplete) connectedness of ecological subsystems is that one subsystem can usurp productivity from other systems in order to externalize costs (see Low et al. in Costanza et al., 2001). For example, the cod fisheries of the eastern US exhausted one after another of the cod sub-populations in a structured metapopulation; no one understood the overall population structure (see Costanza et al., 2001). By the time this was realized, the estimated time to recovery had increased greatly. As another example, most Western developed nations are far from resource independence – they are import economies – with regard to many basics. We have not modeled these complexities; they mean that our models will consistently underestimate how close we might be to K. In the real world, such underestimates mean delayed consideration of strategies, and increased likelihood of "overshoot." Real difficulties become more likely under these circumstances.

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