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Low fertility in humans as the evolutionary outcome of snowballing resource games

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For decades, evolutionary biologists and anthropologists have puzzled over the negative relationship that exists between wealth and fertility in humans. Particularly mystifying have been that (1) humans do not appear to translate their reproductive resources into additional offspring, and (2) attempts to model natural selection resulting in a negative relationship between amount of economic resources and fertility have all predicted the opposite relationship. In this article, we use game theory to derive the evolutionarily stable ratio of offspring investment versus resource generation when the continuing survival of offspring lineages is strongly affected by long-term resource accumulation. The model generates the prediction that fertility should be lower when there are more resources available and when more intensive investment in resource generation has the potential to acutely increase the survival probability of descendant offspring lineages. This prediction provides a simple and general evolutionary explanation for why fertility negatively correlates with wealth both within and between human populations. Indeed, this may provide a new understanding of low fertility in contemporary human groups in addition to furthering our understanding the demographic transition in general. *Key words:* demographic transition, evolution, fertility declines, game theory. *[Behav Ecol 16:398–402 (2005)]*

Despite the abundance of economic resources available to individuals living in industrialized areas of the world to invest in reproduction, such individuals have the lowest fertility ever known or suspected for humans (Kaplan, 1996). Certainly, there are trade-offs between investing in resource generation and raising additional offspring and between investing generated economic resources into producing offspring and using those resources to increase offspring survival (Becker and Lewis, 1973; Lack, 1968; Williams, 1966). However, despite there being some evidence that within homogenous populations a positive relationship between wealth and fertility may sometimes exist (see Mace, 1998), no one has yet been able to demonstrate or model situations in which high-resource groups maximize their fitness by producing fewer offspring than do low-resource groups. Lack of a convincing evolutionary explanation for the fact that modern fertility is so low and wealthy individuals do not convert their wealth into higher levels of fertility (typically referred to as the demographic transition) has caused some to doubt the validity of evolutionary approaches to human behavior (Vining, 1986).

Traditionally, the demographic transition has been explored by demographers and economists seeking to investigate population growth trajectories in light of changing economic and social conditions. Demographic transition models developed for these means typically emphasize the synchronization of fertility and mortality patterns, placing mortality decline and industrialization as preconditions for fertility decline (for a full review, see Robinson, 1997). However, reductions in the birth rate are not always predicated upon the reduction of death rates, and urbanization has not been demonstrated to be a sufficient condition for the decline of birth rates (Coale and Hoover, 1958; Dyson and Murphy, 1985). Despite differences in patterns of demographic transition observed across societies, demographic transitions generally involve two key features (Borgerhoff Mulder, 1998). The first is a dramatic decline in offspring number corresponding to an increase in the availability of resources (Coale and Treadway, 1986). The second is that wealthy families reduce their fertility more markedly than does the rest of the population such that negative correlations between wealth and fertility often appear (Livi-Bacci, 1986).

Evolutionary biologists seeking to understand fertility restriction and demographic transitions have used one of three hypotheses to explain the phenomenon (for a full review, see Borgerhoff Mulder, 1998). The first hypothesis, championed by Boyd and Richerson (1995), suggests that the demographic transition is a consequence of Darwinian but nongenetic mechanisms of inheritance (i.e., *memes*). They hypothesize that fertility restriction can spread through the population as a result of imitation, with those having fewer offspring serving as models for others in the population who then copy their behavior. Population-wide fertility declines are thus explained to be the result of fertility-limiting behaviors spreading via cultural means. Although provocative, this hypothesis contains important conceptual problems that limit its explanatory power. Foremost, these investigators do not address the ultimate evolutionary question of why the trendsetting individuals would have lower fertility in the first place. In addition, this hypothesis lacks an explanation for why such a fertility-limiting phenotype should prevail in the face of selection for higher fertility.

The second evolutionary hypothesis regarding the demographic transition postulates that low fertility in contemporary human societies is a by-product of the novel environment in which modern humans now live. Such theorists cite the availability of cheap and efficient birth control methods as being responsible for current fertility restrictions. They reason that because the environment in which the human mind is said to have evolved contained no contraception, human brains are simply not equipped to reason appropriately about such a

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novel external condition (see Perusse, 1993). However, establishing that the presence of cheap and efficient birth control is responsible for fertility declines would require demonstrating that access to birth control automatically leads to fertility declines, which is contrary to observed behavior. Researchers have demonstrated that access to contraception does not automatically lead to its use, and programs offering free contraception are often rejected by many people to whom it is offered (Levine and Scrimshaw, 1983; Polgar and Marshall, 1976). Furthermore, similar to the hypothesis presented before it, this hypothesis fails to address why cheap and efficient contraception should ever arise in the first place and how fertility-limiting behavior could succeed in the face of selection for higher fertility (Kaplan, 1993).

The third type of evolutionary hypothesis that has been developed to explain the demographic transition uses evolutionary theory to reason that limiting fertility is an adaptation in response to changes in the social environment. Such hypotheses explain contemporary fertility declines in terms of their positive fitness effects, reasoning that low fertility is optimal in competitive environments when the cost of raising offspring is high (Beauchamp, 1994; Borgerhoff Mulder, 1998; Irons, 1983; Kaplan, 1996; Kaplan et al., 1995; Turke, 1989), when the positive effects of parental investment in offspring quality diminish slowly (Pennington and Harpending, 1988), and when resources inherited by children from their parents play a role in their future reproductive success (Low, 1991; Mace, 1996, 1998; Rogers, 1995). Although this class of hypothesis is appealing from an evolutionary perspective, its standard prediction that the number of grandchildren will peak at an intermediate level of fertility have not been supported empirically (Kaplan et al., 1995). Incorporating the passage of resources between generations into quantitative models designed to predict optimal fertility has fared no better, as such models also predict a positive correlation between wealth and fertility, opposite of what is observed (Mace, 1998; Rogers, 1995).

The problem with existing adaptationist hypotheses of human reproductive behavior is twofold. First, with few notable exceptions (Mace, 1998), resources typically are viewed as being used directly to raise or pass on to offspring rather than being at least partially invested in generating additional resources themselves. Such investment is characteristic of many human societies in which resources are abundant enough to invest in pursuits beyond mere survival and reproduction. That resources can be invested in this latter manner means that even small investments in resource generation made early on can "snowball" into considerably larger resource gains, which can themselves ultimately result in long-term fitness returns for descendant lineages.

Second, prior adaptationist hypotheses have generally not assumed that the optimal offspring/resource generating ratio will depend in part on the ratio chosen by the local competition within one's social group. However, it has been well documented that the demographic transition is a social phenomenon, emerging from individuals adjusting their strategy according to the behavior of others in their social group (Coale and Watkins, 1986; Donaldson, 1991). Indeed, the evolutionarily stable strategy (ESS) for investment in resource generation will necessarily depend on the amount invested by others. The optimal investment in resource accrual thus should be modeled as an evolutionary game among competitors in a social group. Below, in a logical extension of the adaptationist hypotheses that came before, we use game theory to derive the evolutionarily stable ratio (ESS) of investment in resource generation versus offspring production that incorporates both of the above-mentioned features.

General features of the model

Suppose that each individual in a social group must decide how much effort, E, to expend in generating resources at the expense of raising additional offspring. It is typically true in nature that the evolutionarily stable ratio of resource-generating effort to offspring production depends solely on the amount of resources required to rear a successful offspring to independence. However, in the case of humans, resources are easily monopolized and often abundant enough to invest in pursuits such as education, property, and other assets that themselves generate additional resources. The initial amount of resource that an individual cultivates can thus snowball, potentially translating into large increments of accumulated resource available to invest in offspring and descendants in the given offspring's lineage. Just as businesses that out-invest rival firms can decisively out-compete the latter in the long run (Keynes, 1964; Van Lear, 1999), lineages with larger amounts of resource have a greater chance of out-competing and even exterminating rival lineages (especially when there is large-scale, resource-based warfare). Thus, differences in the amounts of resource controlled by different offspring lineages may critically determine which lineages predominate in the long run (Betzig, 1986; Low, 1991; Mace, 1996).

How do we determine the survival function for the focal individual's offspring lineage? We first considered the simple case of two competing offspring lineages (this will be generalized to the case of an arbitrary number of lineages below). We required three properties of the survival function: First, S should increase as the absolute difference x (>0) in the amount of resource controlled by the focal lineage and the rival lineage increases, that is, $S = f(x)$, where $\partial S/\partial x > 0$. This is assumed because the absolute difference in resource should determine the likelihood that the focal lineage prevails in direct competition with the rival lineage. Second, S should equal to $1/2$ when x is zero, that is, when both lineages control equal amounts of resource. Third, for a given difference in initial investments x_0 by the lineages, S should increase the greater the rate r at which resources generate new resources between generations. (If resources grow over time t as in standard models of population increase, then $S = f[x] = f[e^{rt}\ x_0]$, with the result that $\partial S/\partial r = [dS/dx][t\ e^{rt}] > 0$, incorporating the effect of snowballing resources).

An appealingly simple functional form of S that has all three of the required properties is $S =$ (amount of resource controlled by focal lineage)^y/[(amount of resource controlled by focal lineage)^y + (amount of resource controlled by rival lineage)^y], where y is an increasing function of the resource growth rate r (i.e., $dy/dr > 0$). As required, if the focal lineage controls more resources, $\partial S/\partial r = (\partial S/\partial y)(dy/dr) > 0$.

Deriving the optimal resource generation effort for humans thus necessarily entails taking into account the degree to which additional investment in resource generation can ultimately translate into differential offspring lineage survival in a given society. The parameter y is a resource snowballing parameter that scales the degree to which additional resource accrual effort by the focal individual can ultimately translate into enhanced long-term offspring lineage survival. For instance, in societies where resources are not abundant enough to invest in generating additional resources, the resource snowballing parameter is equal to zero ($y = 0$) and the ultimate survival of the focal individual's offspring lineage becomes a constant, independent of resource generating effort. In such cases it would be maladaptive to invest heavily in resource generating effort, as it would have no effect on the ultimate survival probability of the focal individual's offspring lineage. However, when resources are abundant enough to successfully invest in generating additional resources, $y > 0$ and the degree to which resource generation can affect fitness becomes magnified. As y becomes larger, even diminutive increases in further resource generation and investment by the focal individual can translate into immense gains in the long-term survival probability of an offspring lineage. Thus, the snowball parameter y measures the degree to which competing individuals can ultimately enhance their offspring lineage survival probabilities by generating additional resources.

The model

Given the survival function described above, we will now construct a game-theoretic model that predicts the evolutionary stable resource-generating effort E^*. E^* will depend on (1) the number of directly competing individuals; (2) the degree to which additional investment in resource generation ultimately translates into differential offspring lineage success, that is, the strength of the resource snowballing parameter y in a given society; (3) the minimum effort required to raise a competitive offspring in a given society; and (4) the resource-generating effort of an individual's competitors.

Let T be the total amount of effort possessed by an individual. Successfully rearing a viable offspring in a given environment requires a minimum amount of effort equal to P. A high P is thus expected to be characteristic of industrialized societies in which children require a great deal of investment to remain competitive with their peers. The number of offspring reared by an individual investing amount E of total effort T in resource generation is thus equal to $(T - E)/P$. Thus, the resource generation effort per offspring is equal to $E/(T-E)/P = EP/(T-E)$.

Let n be the number of directly competing individuals. The parameter n includes only directly competing individuals (i.e., only individuals within one's social group) because it is likely that individuals only take their own social group (rather than society as a whole) into account when making reproductive and economic decisions (Frank, 1999; Neumark and Postlewaite, 1998). The ultimate survival probability (S) of the focal individual's offspring lineage is therefore equal to

$$S = \left(\frac{(\frac{EP}{T-E})^y}{(\frac{EP}{T-E})^y + (n-1)(\frac{E^*P}{T-E^*})^y}\right) = \left(\frac{(\frac{E}{T-E})^y}{(\frac{E}{T-E})^y + (n-1)(\frac{E^*}{T-E^*})^y}\right) \quad (1)$$

where E is the individual's effort and E^* is the effort of each of the remaining competitors.

We next seek an individual's evolutionarily stable amount of resource accruing effort given the effort required to successfully rear a competitive offspring in a particular environment. To do this, we must first derive the focal individual's long-term fitness, W. We represent an individual's fitness as the product of its number of offspring and the probability that each resulting offspring lineage will ultimately survive in the long run. This is also modeled as an evolutionary game to account for the fact that the probability of survival of an offspring lineage necessarily depends on the resource accrual strategies of competing individuals in the population. The focal individual's long-term fitness, W, is equal to

$$W = \left(\frac{(\frac{E}{T-E})^y}{(\frac{E}{T-E})^y + (n-1)(\frac{E^*}{T-E^*})^y}\right)\left(\frac{T-E}{P}\right) \quad (2)$$

Given the above, the evolutionarily stable effort E^* by an individual is that satisfying

$$\frac{\partial W}{\partial E}\bigg|_{E=E^*} = 0, \quad \frac{\partial^2 W}{\partial E^2}\bigg|_{E=E^*} < 0 \quad (3)$$

and is equal to

$$E^* = \frac{Ty(n-1)}{n} \quad (4)$$

for $y < n/(n-1)$. If $y \geq n/(n-1)$, the ESS is to produce the minimum number of offspring and invest all of the remaining effort in resource generation.

The number of offspring produced by an individual exhibiting the evolutionarily stable effort is $(T - E^*)/P$, which equals

$$\frac{T[n - y(n-1)]}{Pn} \quad (5)$$

Thus, the number of offspring produced decreases (1) as the number of directly competing individuals n increases, (2) as the resource snowballing parameter y (describing the degree to which offspring lineage success can be augmented by additional resource accrual) increases, (3) as the total available effort T decreases, and (4) as the effort required to raise an offspring P increases.

The fraction f of the maximum possible number of offspring that the individual actually produces is $(T - E^*)/T$, which equals

$$f = 1 - y\left(1 - \frac{1}{n}\right) \quad (6)$$

The latter fraction decreases as the number of directly competing individuals n increases and as the resource snowballing parameter, y, increases. Indeed, at evolutionary equilibrium, a small fraction of the maximum possible number of offspring is favored when the degree to which offspring lineage success can be amplified by additional resource accrual increases, that is, y is high. When the number of direct competitors n is large, as is typical of most industrialized societies, the latter fraction converges to just $1 - y$, approaching zero as y approaches 1.0. The resource snowballing parameter, y, is thus a critical determinant of the outcome of snowballing resource games. This is especially true of long-term offspring lineage success. Because success tends to feed on success (Hirshleifer, 2000), differences in the amounts of resource controlled by competing offspring lineages will decisively determine which lineages predominate in the long run unless the resource snowballing parameter is low.

Thus, low fertility should be characteristic of humans and other species involved in snowballing resource competition games. It follows that the low fertility characteristic of many contemporary human groups, and the demographic transition in general, cannot be taken as evidence that humans are currently evolutionarily maladapted as has sometimes been argued. It is well established from the optimal clutch size theory, motivated originally by the observations of Lack (1968), that selection does not necessarily maximize offspring number. The snowballing game extends this theory by showing that when offspring lineage success can be augmented significantly by additional resource accrual, selection for lower fertility becomes even stronger, possibly accounting for the trend of lowering fertility with increasing degrees of economic development and the unusually low fertility characteristic of many human groups today.

DISCUSSION

The snowballing resource model generates the prediction that fertility should be lower when snowballing resource competition becomes more potent, that is, the degree to which additional investments in resource generation can translate into long-term offspring lineage success increases. This type of competition is characteristic of contemporary industrialized societies, providing a simple and general explanation for why fertility negatively correlates with wealth both within and between human populations (Coale and Watkins, 1986; Donaldson, 1991; Huber, 1999; Pennington and Harpending, 1988; Weerasinghe and Parr, 2002; World Bank, 1984; World Factbook, 2001). Furthermore, this prediction is also consistent with a key feature of the demographic transition, that is, fertility declining with increased economic development. Although the onset and pace of such fertility decline has varied considerably over time and space, the general pattern of the demographic transition is for fertility decline to be prompted by and inversely related to economic development (Coale and Treadway, 1986; Livi-Bacci, 1986). Accordingly, the pace of fertility decline during demographic transitions is typically greatest in the middle stages of development when economic growth begins to accelerate (Donaldson, 1991). Moreover, countries with higher per capita growth rates during this phase tend to have higher rates of fertility decline. Both of these findings are consistent with this prediction of our model.

The prediction that offspring number should decrease as the number of directly competing individuals increases is also supported empirically. The trend of individuals in rural areas having higher birth rates than those in cities has been well documented (Donaldson, 1991; World Bank, 1984). Although this may be owing to the higher income levels in cities that tend to correspond to a high resource snowballing parameter (i.e., higher y), both of these effects are consistent with the predictions of our models. This aspect of the model is also supported by birthrate comparisons between many Western European nations and the United States. Although comparably industrialized, birthrates in population-dense European countries such as Germany, Italy, and the United Kingdom are significantly lower than they are in the comparably population-sparse United States (World Factbook, 2001).

Our model predicts that offspring number should decline as the effort, P, required to raise competitive offspring increases, a prediction made by other theorists on more intuitive grounds. However, it is not as obvious that P in wealthier societies is higher than P in poorer societies because P refers to the *minimum* investment to raise a competitive offspring. We suggest that the minimum cost of offspring increases in wealthier societies as a direct result of the snowballing resource games modeled here. That is, in wealthier societies the heightened costs associated with rearing offspring (e.g., education expenses) are really investments in an offspring's future resource generation. By investing heavily in offspring, wealthy parents can more readily ensure that their offspring can generate more future resources with the resources that they are given in the present. In fact, expenses associated with purchasing children certain expensive luxury items may even be considerably less frivolous than they first seem. To the extent that providing offspring with the right watch, the right car, or the right clothing or living in the right neighborhood may help his or her offspring land the right job or the right contract, these expenditures act as investments in future resource acquisition (Frank, 1999). Consistent with the prediction of our model, low birth rates characterize societies in which costly investments in offspring are critical to the child's success, such as is the case in industrialized places in the world (Beauchamp, 1994; Borgerhoff Mulder, 1998; Donaldson, 1991; Irons, 1983; Pennington and Harpending, 1988; Turke, 1989).

It is important to note that the current model applies to human resource investment decisions even if ancestral human populations rarely exhibited the intensity of snowballing resource competition that is characteristic of modern societies. All that is required for contemporary humans to exhibit the predicted behaviors is that ancestral environments differed from one another in the degree to which additional investment in resources could augment long-term offspring lineage success. Indeed, if environments varied even slightly from one another in this important regard, selection would have favored an ability to assess the intensity of snowballing resource competition and adjust behavior accordingly.

In sum, the apparent evolutionary paradox of declining fertility with increasing wealth can be resolved by properly taking into account the resource snowballing parameter and that individuals adjust their investment strategies according to those of others. Properly accounting for these factors accounts the negative correlation that is observed between fertility and wealth both within and between human populations. Furthermore, it also accounts for the decline in fertility with increased economic development, the most marked trend in the demographic transition. The resulting game-theoretic model of snowballing resource competition may eventually elucidate other seemingly maladaptive behavioral traits of modern humans, that is, traits that do not simply maximize offspring production.

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