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Phil. Trans. R. Soc. Lond. B 1998 **353**, 389-397
doi: 10.1098/rstb.1998.0217

The Royal Society

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Life history theory concerns the scheduling of births and the level of parental investment in each offspring. In most human societies the inheritance of wealth is an important part of parental investment. Patterns of wealth inheritance and other reproductive decisions, such as family size, would be expected to influence each other. Here I present an adaptive model of human reproductive decision-making, using a state-dependent dynamic model. Two decisions made by parents are considered: when to have another baby, and thus the pattern of reproduction through life; and how to allocate resources between children at the end of the parents' life. Optimal decision rules are those that maximize the number of grandchildren. Decisions are assumed to depend on the state of the parent, which is described at any time by two variables: number of living sons, and wealth. The dynamics of the model are based on a traditional African pastoralist system, but it is general enough to approximate to any means of subsistence where an increase in the amount of wealth owned increases the capacity for future production of resources. The model is used to show that, in the unpredictable environment of a traditional pastoralist society, high fertility and a biasing of wealth inheritance to a small number of children are frequently optimal. Most such societies are now undergoing a transition to lower fertility, known as the demographic transition. The effects on fertility and wealth inheritance strategies of reducing mortality risks, reducing the unpredictability of the environment and increasing the costs of raising children are explored. Reducing mortality has little effect on completed family sizes of living children or on the wealth they inherit. Increasing the costs of raising children decreases optimal fertility and increases the inheritance left to each child at each level of wealth, and has the potential to reduce fertility to very low levels. The results offer an explanation for why wealthy families are frequently also those with the smallest number of children in heterogenous, post-transition societies.

Keywords: human life history; fertility; mortality; wealth inheritance; primogeniture; demographic transaction

1. INTRODUCTION

Humans, like most large mammals, invest a great deal in each offspring. Competition for parental investment can be fierce through the long period of childhood. In societies with high fertility, there is evidence that the length of both the preceding and subsequent birth interval influence the risks of mortality and morbidity of babies and young children (e.g. Madise & Diamond 1995; Alam 1995; Bohler & Bergstron 1995). There is also evidence that older children compete for food (e.g. Ronsmans 1995; LeGrand & Phillips 1996). At maturity, siblings may compete for their parents' heritable resources. There is considerable evidence that wealth is positively correlated with reproductive success in traditional societies. When key resources, such as land or livestock, are individually owned, resources inherited by children from their parents can be an important determinant of their future reproductive success (e.g. Low 1991; Mace 1996*a*). Thus evolutionary models of parental investment should help us to understand patterns of wealth inheritance. Parents would be expected to allocate resources among their children in such a way as to maximize their own long-term, reproductive success.

In societies where inherited resources are crucial, children with no prospect of any inheritance may contribute little or nothing to their parents' long-term fitness. The cost of feeding those children may even reduce the potential reproductive success of their siblings by reducing the wealth of the household. Thus decisions about how many children to have and about how many resources to give each of them at the end of the parents' reproductive lives will be related, and both are likely to depend on the wealth of the parents.

In this paper I use a stochastic dynamic model to analyse which combinations of fertility and wealth inheritance strategies maximize the expected number of grandchildren. I use the term fertility in the sense that demographers do, to indicate the number of children born (not to be confused with fecundity, which is used in demography to mean the ability to conceive). Dynamic optimality models can be used to find behavioural decisions that maximize fitness over a given time period (Houston *et al.* 1988; Mangel & Clark 1988). Beauchamp (1994), Anderies (1996) and Mace (1996*b*) have all used dynamic optimality models to analyse family size in humans over a single generation. Beauchamp (1994) and Anderies (1996) use lifetime reproductive success as the

Phil. Trans. R. Soc. Lond. B (1998) **353**, 389–397
Received 14 February 1997 *Accepted* 10 March 1997

currency to be maximized, not taking into account any effect the level of parental investment in each child might have on their future reproductive success once they have survived childhood. Mace (1996*b*) presents a version of part of the model presented here, which is based on a traditional African society, in which only fertility decisions are considered. In Mace (1996*b*), I used married children as the currency to be maximized, and explored how varying the minimum investment necessary to marry off a child will influence optimal fertility. I demonstrated that the costs of marriage are predicted to have a strong influence on reproductive decisions. In this paper, I use a dynamic optimality model to find decisions that maximize number of grandchildren, given an optimal allocation of family wealth between children. Thus the key variable of optimal investment in each child through inheritance (or marriage gifts, which are effectively similar) is derived from the model rather than assumed.

McNamara & Houston (1992) have shown how dynamic optimality models can be used to calculate very long-term reproductive success, and thus to solve life history problems such as the one addressed here. Marrow *et al*. (1996) have applied this to life history evolution in a population of wild sheep. However, these models assume one time-step to be one generation; the complexity of such models would be greatly increased if that were not the case. The fertility decisions I investigate here are made many times within one generation. I measure the reproductive value of children as the number of grandchildren they are expected to produce, given the wealth allocated to them at the beginning of their reproductive lives. The strategy that maximizes grandchildren is not necessarily identical to the strategy that maximizes very long-term fitness in every case, although it will roughly approximate to that for most purposes (e.g. Fisher 1930). I use stochastic dynamic programming to find the combination of the optimal allocation of wealth to children, and the reproductive decisions that maximize the reproductive value of the whole family, given the optimal allocation of wealth between siblings. I shall test these predictions against data from the Gabbra, a traditional African pastoralist group.

2. THE DEMOGRAPHIC TRANSITION

A large proportion of the research in human demography over the last few decades has focused on the demographic transition. This is the term used for a phenomenon observed throughout the world, when, in societies formerly with high fertility and high mortality, an increase in living standards and a decrease in mortality risks are generally associated with a decline in fertility. Most societies in the developed world underwent a demographic transition in the last century or earlier; those in the developing world entered this phase much later, with Africa only now entering it. Most human populations are actually still growing rapidly, but the rate of growth is now declining virtually everywhere. A single, socioeconomic correlate of the onset of demographic transition has remained the elusive goal of demographers. Evolutionary anthropologists have, however, taken a broader, cost/benefit approach to understanding determinants of family size. On the face of it, the observation of smaller families in the presence of enhanced resources represents a serious challenge to evolutionary theory; although a number of mechanisms by which some quantity/quality trade-off might be occurring have long been familiar to evolutionary ecologists, going back to Lack (1968).

I use the model described here to investigate the influence of a number of parameters on optimal fertility and inheritance strategies, to see which are likely to produce outcomes similar to those observed in societies undergoing fertility decline. I investigate mortality risk, risk in the environment (which I model by reducing the risk of drought), and the economic costs of raising children (such as their food requirements). These are three variables generally assumed to be associated with the demographic transition. Development agencies (such as governments and non-governmental organizations) normally concentrate on the first two of these, in an effort to increase people's standard of living. The last is often a consequence of an increased standard of living. That such economic changes lead to demographic change, albeit not in consistent ways, is certainly well documented, although a theoretical framework for predicting that change has been largely lacking.

3. THE MODEL

(a) *A traditional African subsistence system*

The model I present here is based on a traditional African pastoralist system. In pastoralist systems, livestock are the key units of wealth. They provide food directly, through milk and meat, and indirectly, through cash raised from their sale. They can also provide transport, leather and other necessities. They are used for social transactions, such as for brideprice and dowry. The food and other yields from a herd relate directly to the size of that herd. Pastoralists' herds have often been likened to investment accounts: when pastoralists are given other opportunities to earn money, they frequently put that money straight into increasing herd size. Wealth will rise and fall when the herd grows or shrinks, as a result of births and deaths from consumption, sales or wasted mortality (such as in drought). These features of the system characterize many other systems based on the individual ownership of resources; in particular, they encapsulate the processes whereby those with a great deal of wealth will find it easier to maintain and increase their wealth, whereas those with very low levels of wealth are at greater risk of destitution.

This particular model is based on the system of the Gabbra, a group of camel-keeping pastoralists in northern Kenya. Camels provide milk, even in harsh conditions, and transport. They are rarely bought or sold, but are inherited or given as brideprice. Goats are also kept for meat, milk, sale and dowry. The Gabbra inhabit an arid area, which is remote from government services even today. They are subject to frequent but unpredictable droughts; the most recent were in 1984, 1992 and 1997, all of which caused livestock mortality and, but for the provision of food aid from the government of Kenya and the international community, could have led to some human starvation. These pastoralists are among the most nomadic in Africa, moving according to the availability of grazing.

The social system is patrilineal and patrilocal. When a man marries, his family must pay a fixed brideprice to the family of the bride; but the greater expense is that he must provide a herd of livestock (almost always given by or inherited from his father) with which to support his new family. Frequently, a son does not separate his herd from that of his father for many years after marriage; he is often expected to simply wait until his father's death, when he then stands to inherit the herd anyway. Polygyny is limited (88% of women were the only living wife of their husbands). Virtually all women marry between the ages of 15 and 25. Most men marry between the ages of 25 and 45. The singulate mean age of marriage (a period measure describing a hypothetical synthetic cohort, which is calculated from the proportion of unmarried people in each age-group and therefore does not rely on their reporting of past events and is not sensitive to fluctuations in the age-structure of the population; Newell 1994) is 21 in women and 33 in men. The mean age of reproduction is 28 in women and 40 in men. Women do not reproduce before marriage; nor do they remarry if widowed, but may continue to bear children, which society considers to be the legitimate children of the dead husband. Men allocate wealth among their sons as they please, or, if they fail to do so, on his father's death, the eldest son inherits the herd. Daughters virtually never inherit camels, but may receive a small dowry from their parents on marriage, normally in goats.

In most societies, the gifts given to sons on marriage or as inheritance are much greater than those given to daughters; the World Ethnographic Atlas (Murdock 1967) describes over 50% of societies as showing male-biased inheritance and none as showing female-biased inheritance. Reproductive success is much more strongly related to wealth in males than in females in the Gabbra (Mace 1996*a*), as in many other cultures, and thus male-biased parental investment would be expected on evolutionary grounds (Trivers 1972; Trivers & Willard 1973; Hartung 1982). The brideprice Gabbra receive for daughters is generally not much more than the dowry they take with them at marriage; thus, daughters may be roughly 'cost-neutral' to their parents (Mace 1996*a*). In societies such as the Gabbra, reproductive decisions appear to be based more on number of sons rather than number of children. I have shown that the number of sons in a family has a much greater influence than the number of daughters on the birth interval to the next child (Mace & Sear 1997*a*), the probability that a son will be fostered out to another family (R. Mace and R. Sear, unpublished data) and on the probability that a man will take a second wife when his first wife reaches menopause (Mace 1996*b*). All these results indicate that it is sons that comprise the major cost consideration in Gabbra reproductive decision-making. Thus the optimal family may be defined by number of sons, as number of daughters is not particularly important to the decisions considered here.

(b) *Assumptions in the model*

This model is of reproductive decision-making in a subsistence system based on a herd of livestock with dynamics described in table 1, and a human population with the demographic parameters described in table 2. Mortality risks were estimated in Mace & Sear (1996) and Mace & Sear (1998). But, in respects other than precise parameter values, the model is general enough to apply to a range of subsistence systems based on individually owned resources. It will be used to predict patterns of fertility and wealth inheritance in a traditional, pastoralist society; and then parameter values will be altered to predict the influence on fertility and inheritance patterns of changing environmental conditions.

Table 1. *Parameter values used to describe herd dynamics*

annual probability of drought	0.2
variables per one female stock unit[a]:	
p(birth) $-$ p(death) in non-drought year	0.11
p(birth) $-$ p(death) in drought year	-0.14
food yield when living (i.e. milk)	10 units yr^{-1}
food yield if sold/slaughtered	20 units yr^{-1}
variables for human food requirements:	
food requirements (fr) of an adult ($\geqslant 15$ years)	15 units yr^{-1}
food requirements (fr) of a child (<15 years)	$1 \times$ age units yr^{-1}
household food requirement (children + two parents)	$fr(ch, t)+30$
maximum herd size	45

[a] One stock unit approximates to one female camel, although reproductive potential has been enhanced to account for the fact that, for each camel owned, Gabbra will also own a number of faster-reproducing sheep and goats (which are not included explicitly in the model to simplify calculations).

This model is used to investigate the decisions of parents in a monogamous marriage. Male and female reproductive decisions would not be expected to differ under monogamy, so the decision-making unit is referred to as the household. Given that daughters do not inherit wealth, the model considers only sons. This simplification means that marriage decisions (which determine the reproductive success of daughters) do not have to be considered in the model. When parents decide to have another baby, that baby is assumed to have a 50% chance of being male. The parameter values used to determine the cost of raising a son are double those assumed to be the cost of raising one child (as used in Mace 1996*b*), on the assumption that for each son, a family will also have, on average, one daughter. Thus reproductive and inheritance decisions are based on number of living sons in the family, which empirical evidence suggests is the case for the Gabbra (Mace 1996*b*; Mace & Sear 1997*a*).

Decisions will depend on the state of the household, which is described by three variables, wealth (w), number of living sons (ch) and the number of time-steps of reproductive life that have passed (t, measured in two-year steps). Households have a finite reproductive life of 30 years, or whenever the mother dies if sooner, and a finite life (or economic life) of 40 years. Reproductive decisions about whether or not to have a baby are made every two years throughout the reproductive life of the mother. Decisions about how to allocate wealth are made at the end of the parents' life, which is taken as ten years after the end of their reproductive life, i.e. 40 years after marriage. Thus the generation time in the model is 40 years (which is the

Table 2. *Parameter values used to describe human demographic parameters*

probability of adult death	0.005 per year
probability of child death (< 4 years)	0.05 per year
probability of child death (< 15 years ≥ 4)	0.008 per year
reproductive lifespan of an adult	30 years
economic lifespan of a household	40 years
minimum inter-birth interval	2 years
risk of maternal mortality (death in childbirth)	0.005 per birth

mean generation time of males in Gabbra society) and generations do not overlap. The separation in the timing of the decisions to have babies and the decisions about how much wealth to give each son does reflect the human condition. Children take many years to raise, over which time some children may die, parents risk death and household wealth may rise or fall. Thus parents have to make decisions about when to have another baby based on their current circumstances combined with their knowledge of the environment in which they live, and of the value of heritable wealth to their sons' future reproductive success. The time at which each decision is made may be separated by up to 40 years, but the rules of wealth inheritance that the parents plan to follow will influence their reproductive decisions throughout their life.

This model contains a number of simplifications, in the interest of reducing the number of state variables. This reduces the number of required calculations, and makes the results more accessible and easier to present.

As discussed above, daughters are not considered. Daughters' reproductive success is maximized by parents ensuring that they marry as wealthy a man as possible, which is a decision outside this model.

The age of each individual child is not tracked in the model, but food requirements and child mortality risk after their first year are assumed to be related to t, the average age of the household divided by two. This approximates the average age of the children if the births of children were distributed at random over the time-steps that the household has been in existence.

Wealth inheritance strategy is described by a single parameter, i, which is the number of sons to be given an equal inheritance. This enables a range of strategies to be considered: from giving all wealth to one son (unigeniture, of which primogeniture—inheritance by the first-born son—is the most common among those cultures listed in Murdock (1967)); the equal division of wealth between all sons; and the equal division of wealth between any number of sons between those two values. w and i are integer values, so if w is not exactly divisible by i, one son gets the extra units of wealth.

It is assumed that inherited resources are essential to reproductive success. This assumption is not necessarily true in many societies (external sources of earned income, raiding livestock from neighbouring tribes or extra-pair matings are examples of means by which men could achieve reproductive success without inherited wealth in the Gabbra); but a model where wealth inheritance and reproductive success are strongly related are more likely to give us insights into decisions about wealth allocation and its relationship with fertility.

(c) *Dynamic model, state variables and transition probabilities*

To model these reproductive decisions, several quantities need to be defined. Consider a household in state w,ch. Then:

(i) $p(w,w')$ is the probability that a herd of size w will be a herd of size w' after two years, based on a binomial probability of each female animal giving birth to another surviving female, and a binomial probability that each animal will die. Details of parameters that influence this probability are given in table 1.

(ii) $p(ch,ch')$ is the probability that a household with ch sons, will have ch' sons after two years, after having experience the risk of child mortality ($ch' < ch$). The parameters determining the risk of mortality are shown in table 2.

(iii) b is the decision whether to have another baby ($b=1$) or not ($b=0$). $b=0$ if $t>15$ (which is after 30 or more years of marriage).

(iv) $ps(b)$ is the probability that the mother survives two years, given decision b.

(v) $R(w,ch,T)$ is the reproductive value of a family of ch sons with w units of wealth allocated optimally between them, at the end of the parents' household's life ($T=20$, which is 40 years after marriage). $R(w,ch,t)$ is the expected reproductive value of a family in state (w,ch) when t is the number of time-steps of reproductive life that have passed. $R(w,0,0)$ is therefore the expected reproductive value of a newly-wed couple with wealth w, at the beginning of their reproductive lives. $R(w,ch,T)$ is estimated for the first iteration of the model (to values between 0 and 1), but thereafter can be calculated by:

$$R(w,ch,T) = \max_i R(w/i,0,0)i \qquad (1)$$

where i is the number of sons between which the household wealth will be divided in order to maximize grandchildren, where i is less than or equal to ch.

(vi) $R(w,ch,t)$ is the reproductive value of a household at time t in state w,ch and given that they always make the optimal decision b, and it can be calculated from $R(w,ch,t+1)$ by

$$\begin{aligned} R(w,ch,t) = &\max_b \Sigma_{w'ch'}(p(w,w') \times p(ch,ch') \\ &\times (ps(b)R(w' - fr(ch,t),ch' + b,t+1) \\ &+ (1 - ps(b))R(w' - fr(ch,t),ch',T)) \end{aligned} \qquad (2)$$

where the summation is over all possible values of w' and ch, and $fr(ch,t)$ is the food requirements of a family of ch sons aged t (see table 2 for parameters that influence $fr(ch,t)$). If w falls to zero at any time, the household is considered destitute and fitness, R, is 0.

Initially, $R(w,ch,T)$ is simply estimated (to values where $R(\max(w),\max(ch),T)=1$ and $R(0,ch,T)=0$ and $R(w,0,T)=0$). $R(w,ch,T-1)$ can then be calculated from equation (2), as can $R(w,ch,T-2)$ and thus, by backward iteration, after 20 time-steps $R(w,0,0)$ is calculated and the optimal scheduling of births over the whole reproductive lifespan is also known.

When $t=0$, $R(w,ch,T)$ for the next iteration is recalculated by equation (1), which gives the optimal value of i over all combinations of w and ch. $R(w,ch,T)$ is then normalized (by dividing all values by $R(\max(w),\max(ch),T)$ and the process is repeated. After a small number of iterations, $R(w,ch,t)$ and the optimal values of i and b for each value of w and ch converge. This is the optimal strategy set of fertility and inheritance rules for maximizing grandparental fitness.

The model can thus be used to predict both the decision rules that parents should follow to maximize their reproductive success (b and i for each state), and these rules can be used to find the population outcomes of a group of people following those decision rules. The population outcomes are determined by running a simulation of a population following the optimal decision rules, subject to the same environment for which that decision rule is optimal. That environment includes, of course, the stochasticity inherent in the system, which has been taken into account in determining the optimal decision rules. The starting conditions for the simulation were estimated for the first iteration. Thereafter, the distribution of herd sizes at household formation gained by inheritance from parents, that is generated by the model, is used as the starting state of the population. After a small number of iterations, a stable distribution of initial herd sizes is reached.

4. RESULTS

(a) *The Gabbra case*

Figures 1 and 2 show the predicted stable state population outcomes of a population of Gabbra following the optimal strategies of fertility and wealth inheritance, for the case of a pastoralist system in an environment described by the parameters in tables 1 and 2. These are the variables that characterize the lives of those women who were still alive but had completed their fertility in 1993. In 1993, I conducted a demographic survey of the pastoralist Gabbra in northern Kenya, collecting data on birth histories, marriage histories and household wealth for 850 households (Mace 1996*a*). The predicted distributions are compared with those observed for this cohort of Gabbra.

The bars in figure 1 show the number of living sons reported by all women in the sample aged between 49 and 69 ($n=267$). The curve in figure 1 shows the predicted distribution of the number of living sons for those women, had they been following the optimal reproductive decisions predicted by the model, and started with the range of initial herd sizes at marriage that are also predicted by the model in the stable state. The fit is fairly good. The largest proportion of women who had completed their fertility had three sons, as the model predicts. Women with no children or one child are over-represented; however, it is likely that these women have suffered either primary or secondary infertility rather than decided to have so few children that they ended up with no sons. Infertility is not included in the model. Commensurately, the proportion of women observed with large numbers of sons is below that predicted.

Figure 2 shows, in bars, the distribution of initial herd sizes at household formation reported by those households that started between 30 and 50 years ago (i.e. the initial household herd sizes of those women that have now completed their families ($n=67$; many families did not report any figure)). A peak of reported initial herd sizes at 10 camels corresponds with that predicted by the model. However, the distribution is overdispersed. Although median and mode correspond at 10 camels, the mean in the data was 17, partly due to two families (not shown) reporting herd sizes of 100 camels at household formation. A number of families also reported very small herds, whereas the model predicts that so many small herds would not be seen (nor, indeed, be able to survive). One major simplification in the model, that may be largely responsible for this mismatch, is that of discrete generations and thus a single date of inheritance; in fact, livestock can be inherited gradually. Some herders may have reported herd sizes at marriage before they were living independently of their father or elder brother's herd. Looking at the results from figures 1 and 2 together suggests that the Gabbra may have been surviving on slightly smaller herd sizes than the model predicts, yet not

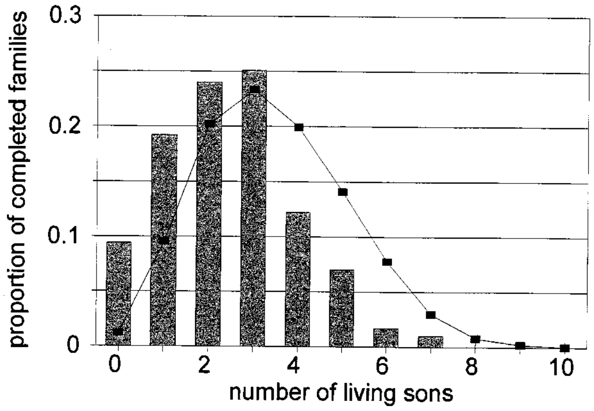

Figure 1. Observed and predicted completed family sizes. Bars are observed number of living sons of Gabbra women aged 49–69 in 1993. The curve is the predicted stable state distribution of number of living sons for living women after 40 years of marriage.

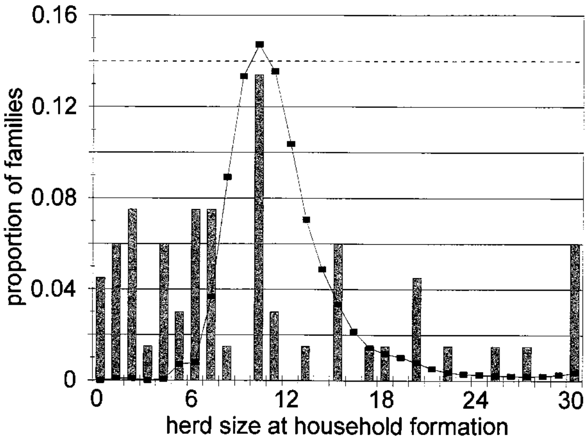

Figure 2. Reported and predicted herd sizes at household formation. Bars are the reported number of camels owned at household formation of living men whose household's were formed between 30 and 50 years before 1993. The curve is the predicted herd sizes of sons who inherit camel herds from their parents when they form their own household.

dropping out of the system destitute, as the model assumes many of them would. This may be because I have overestimated the household subsistence requirement. A similar effect would be observed if the contribution of non-herding income was significant for many families, which, although these data refer to the nomadic section of the society, could be true. It is likely that some families were surviving with the support either of such other sources of income or with the help of animals leant by relatives, which is a common system in the Gabbra; this possibility is not included in the model.

It may be possible to improve the fit by adding such phenomena as infertility or other income-earning opportunities to the model, but it is not my central purpose here to provide a precise model of Gabbra ecology, although I am encouraged that the predictions appear broadly in line with the behaviour observed, given the number of simplifying assumptions that were made. My primary aim is to produce a framework general enough to be of much wider relevance.

(b) *Reproductive decision-making in a range of environments*

Once we are able to model these decisions entirely from within the framework of evolutionary ecology, in a way that has predictive power, then we can use the model to examine how changes in the environment might be expected to change human reproductive rate.

The model is used to explore how reproductive decisions, and hence population outcomes, would be expected to change if environmental circumstances changed. I explore these changes by comparing outcomes with a baseline case. The baseline case is that of the Gabbra cohort just described, the parameter values of which are given in tables 1 and 2.

Figures 3–6 all show optimal decision rules or stable state population distributions for four different environments: (i) the baseline case; (ii) a high costs case, where it assumed that the cost of raising a child is double that of the baseline; (iii) a low drought probability case, where it is assumed drought only occur half as often, raising the mean and reducing the variance in the productivity and growth rate of the herd; and (iv) a low mortality case, where all extrinsic mortality risks are an order of magnitude lower than the baseline case.

Figure 3 shows the optimal fertility strategy in each of these four cases. The fertility strategy shown is the optimal strategy for a couple that has been married for 20 years, who could thus have between zero and ten children, and have another ten years of reproductive life remaining. The line indicates the optimal number of sons for that level of wealth. Parents in households in the area below the line, who have more sons than the optimum for their level of wealth, would reduce their expected grandparental fitness if they had another baby. If a child died or herd size increased, they might move into a region where they were above the line again, and thus they should have another baby. Thus decision-making is dynamic, changing with current circumstances. Parents are predicted to 'replace' dead children quickly.

In all cases shown in figure 3, wealth would be expected to be positively correlated with reproductive success. This correlation has been shown in numerous traditional societies, including the Gabbra (Mace 1996*a*). The wealth at which it is optimal to have the first child is not especially sensitive to environmental conditions, but thereafter the environmental parameters altered here do have effects, in some case marked, on the minimum wealth at which to have subsequent children.

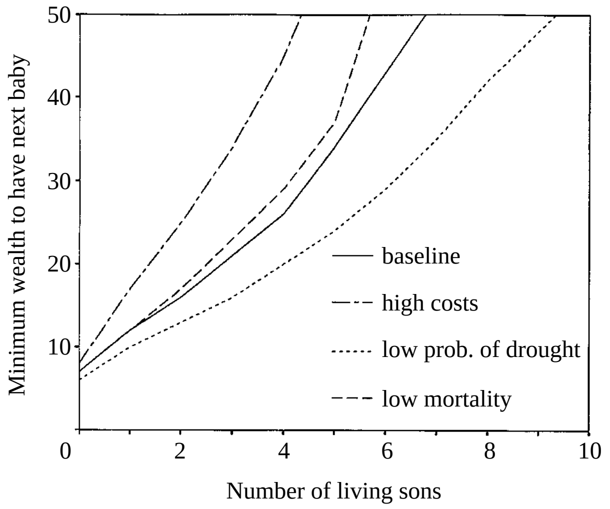

Figure 3. The optimal decision rule of the minimum wealth to have another baby, based on the number of living sons you already have, shown for four different environments: the baseline case (solid line), high costs of children (dashed and dotted line), low probability of drought (dotted line) and low mortality risk (dashed line).

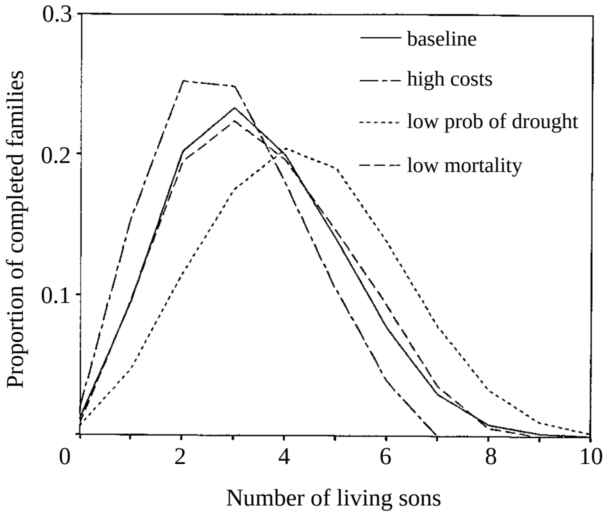

Figure 4. Predicted stable state distribution of completed family sizes of households after 40 years of marriage, for different environments: the baseline case (solid line), high costs of children (dashed and dotted line), low probability of drought (dotted line) and low mortality risk (dashed line).

Figure 4 shows the stable distribution of completed family sizes (living sons) that would result for women that lived throughout their reproductive lives, in each of the four cases. Most families are predicted to have many fewer than the maximum possible number of sons, in any of the environments modelled.

Figure 5 shows the decision rule for the optimal inheritance of wealth between sons at the end of the parents' economic lives. In all cases, the maximum

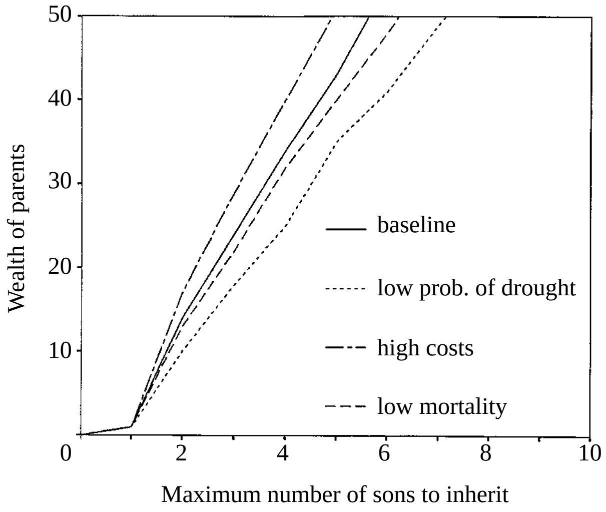

Figure 5. The predicted maximum number of sons between whom the household herd should be divided in inheritance, given the level of parental wealth, for four different environments: the baseline case (solid line), high costs of children (dashed and dotted line), low probability of drought (dotted line) and low mortality risk (dashed line).

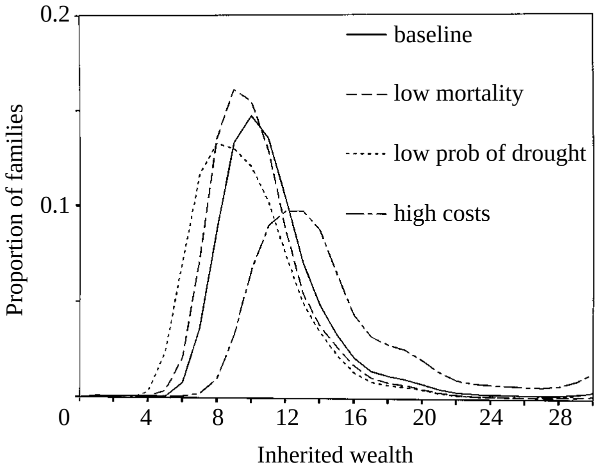

Figure 6. The predicted stable state distribution of the wealth of new families at household formation, which is the amount received in inheritance from parents, shown for four environments: the baseline case (solid line), high costs of children (dashed and dotted line), low probability of drought (dotted line) and low mortality risk (dashed line).

number of sons to be given an inheritance depends strongly on parental wealth. The wealthier the parents, the more sons they will give herds to. The lines are not curved, indicating that the size of the inherited herds would not increase with parental wealth, unless the number of sons living at that time was below the maximum to be given an inheritance. If the number of sons they have is above that maximum, then no parental fitness advantage is gained by giving the 'extra sons' any inheritance. I have shown elsewhere that in the Gabbra, on average, the more elder brothers a man has, the more he is disadvantaged with respect to inherited wealth, his age at marriage and his reproductive success (Mace 1996*a*).

Figure 6 shows the stable distribution of initial herd sizes (i.e. those herds inherited by sons starting their own households) predicted in each of the four environments. As is evident from figure 5, very few individuals are predicted to be given very large herds, as the division of resources between several sons (if they have them) is a better reproductive strategy for wealthy families.

(c) *Which effects are most likely to cause a demographic transition?*

(i) *Reducing the risk of drought*

It is clear that simply improving the productivity and reliability of the subsistence base is not predicted to lead to any of the effects generally considered to be a demographic transition; in fact the opposite occurs. The minimum wealth at which it is optimal to have another baby is significantly reduced, for all family sizes, and thus fertility above the level seen in the baseline case is predicted. Completed family sizes are significantly larger, and the inheritance given to each of those children is slightly smaller, such that the distribution of household wealth with which each new generation starts married life is slightly towards to poorer end of the spectrum than in the baseline case. When living conditions are easier, parents can afford more children and do not need to be so generous to each child, in order to maximize their grandparental reproductive success.

(ii) *Reducing the risk of mortality*

A reduction in mortality is probably considered one of the most important correlates of fertility decline, although the precise relationship with fertility observed across societies is highly variable; mortality decline can even follow after fertility decline (Cleland 1995). The case I model here investigates the lowering of mortality by an order of magnitude, which is the difference, in many cases, between the developed and developing world; it is also a level of difference that can nearly be achieved in developing countries when effective medical services are provided in an area that previously had none (e.g. Weaver & Beckerleg 1993; Pison *et al.* 1993). The model predicts that reducing mortality will definitely decrease number of births, as decisions are dependent on number of living children. Dead children are replaced by more births whenever possible. This has been shown to occur in numerous demographic studies.

However, what is of interest here, is that the effect of a very great decline in mortality on other aspects of reproductive and inheritance strategies is relatively small. Having children that die does use up time and resources, leading to slightly lower wealth and fewer new families each generation. The minimum wealth at which it is optimal to have another baby is higher in the low mortality environment, especially for parents with large families. This compensates, almost perfectly, for those children that would be expected to be lost in the baseline case, such that the stable distributions of completed family sizes are very similar in the baseline and low mortality environments. The maximum number of sons to be given an inheritance, for a given level of wealth, is slightly higher in the low mortality scenario; each son needs slightly less if he will not be wasting resources on raising children that do not survive. But the difference is not great. This model does assume that most mortality is concentrated among very young children, and the impact of higher mortality might be greater if it occurred throughout childhood; however, in most societies it is the infants that are at by far the greatest risk of early death.

Demographers have focused on changes in fertility, i.e. rates of giving birth, not least because these are relatively easy to measure. But it is living children that really matter. Lowering mortality does lower fertility, but, according to this model, it is not expected to greatly lower family size or increase the level of parental investment in each child, which are probably the most characteristic features of post-transition families.

(iii) *High cost of children*

Doubling the cost of children causes a marked change in both fertility and inheritance strategies. The minimum wealth at which to have another baby is much higher than in the baseline case. This leads to much smaller completed families, most with only two sons. The number of sons to be given an inheritance, for each level of wealth, is lower than in the baseline case, and each son is given a larger inheritance. This leads to more families starting out their married life with larger inherited herd sizes. The average family in the stable population is wealthier.

These are all features of post-transition societies. Such an increase in costs could be associated with sending children to school, either because it costs money to send children to school or because their labour is lost to the household economy when they are at school. Education is frequently cited as a correlate of low fertility, although most demographers concentrate on the educational status of the mother, rather than the costs to her of educating her children, which this model suggests would be more explanatory of her fertility. Why parents feel the need to educate children is beyond the scope of this model, although it does seem unlikely that uneducated children would be successful (either economically or in competition for mates) in societies where all the other children were educated.

5. CONCLUSION AND DISCUSSION

Increasing parental investment in children is the key to fertility decline. An important contribution to fitness from inherited resources and high costs of raising children successfully to adulthood will favour small families. The model described here is not based on a society in a developed country, but these are factors that might change as a less-developed society becomes more developed. All parents like to raise children at least to a standard of living approaching their own, and the cost of education and other costs are frequently referred to by parents as deterrents of large family size in modern societies. Girls are now generally as costly as boys and biased inheritance with respect to sex or birth order is not popular. In some cases it is not even legal; for example, primogeniture was outlawed in nineteenth-century France, causing a marked decline in fertility at that time (Johansson 1987). In the case where all children, rather than just sons, are costly and benefit from inheritance, then a model such as the one described here could clearly predict very low family sizes as optimal.

All the cases modelled here do, however, predict a positive correlation between wealth and fertility (as do other evolutionary models; see Rogers (1995)); yet such a correlation has not been widely demonstrated in post-transition societies. Usually, area-level or country-level statistics are used to explore comparative relationships, which frequently lead to the conclusion that wealth is negatively related to reproductive success. Some have used this to argue that evolutionary models are not appropriate models of contemporary human reproductive behaviour (e.g. Vining 1986). Yet, where this relationship has been investigated in clearly defined, homogeneous populations, such as is frequently the case in anthropological studies, then the opposite is found.

An important conclusion of this paper is that reproductive decisions concerning parental investment have to be investigated with respect to a very clearly defined group, if they are to be understood in ecological terms. Although none of the models presented here predict anything but a positive relationship between wealth and reproductive success within a homogeneous group, they do show that if a society actually comprised several different groups, each of which are following different decision rules, then this may not be true. If different people have different fertility policies, perhaps because they have different risks of mortality or different costs of raising children, or different perceptions of these risks and costs (which is not true of an unstratified society such as the Gabbra, but is true of most modern, heterogeneous societies containing peoples of many different origins), then it is possible that those in a higher income bracket might be following a decision rule leading to a smaller family than another family with a lower level of wealth because they are following a different policy. This scenario is likely, given that the model shows that in populations where the costs of children are highest, family sizes are smallest and the stable distribution of household wealth is also highest. When looking at correlation between wealth and fertility across society as a whole, fertility and wealth may appear to be decoupled or even negatively correlated.

Part of the difficulty in addressing this problem is that there are few studies of modern populations in developed countries that concentrate on strictly homogeneous groups. One rare example is that of Hubback (1957), who charts the reproductive success of English women graduates from Britain's best universities in the mid-twentieth century. She finds that, among this mostly highly educated and socially and financially privileged group, wealth correlated positively with reproductive success. So, incidentally, did the class of degree that these women obtained.

Kaplan *et al.* (1995) found that ethnicity and birth cohort were much stronger determinants of fertility than was wealth in a large sample of New Mexican men. Children of parents with large families had lower levels of educational achievement and lower incomes as adults, so some features of their reduced level of parental investment had the potential to influence future generations of offspring. Hispanics, originally from Mexico, had higher fertility than Anglos, and Kaplan *et al.* argue that they are reducing their fertility over time in order to take advantage of better educational opportunities, which are followed by opportunities to earn higher incomes.

However, those with the most children also had the highest number of grandchildren; thus, in this case, it is not clear whether a decision to limit fertility is evolutionarily adaptive in the long-term.

The presence of government-funded support systems may have ameliorated or even removed the costs of large families in some countries. One would not necessarily expect our decision rules to keep pace with recent social and political changes of this nature and reach an optimum, although there is plenty of evidence that economic change can have a near-instant effect on birth rates: fertility in East Germany dropped dramatically after unification with West Germany in 1989, when job security declined and many state benefits relating to children were removed (Conrad *et al*. 1996); and Hoem (1992) shows that increasing birth rates among Swedish women, particularly those in their thirties, coincided with the government increasing the generosity of maternity leave provision in the 1980s. Our reproductive decisions are constantly influenced by our environment, even in industrial societies, and that plasticity is in the directions predicted by an adaptive framework.

Although it is tempting to exclude modern societies from evolutionary analyses on account of their low fertility, I believe that evolutionary models have great potential to explain our decision-making in this area. Most social scientists have been slow to appreciate that evolutionary theory has anything to offer their fields of enquiry. Yet there are, increasingly, examples of evolutionary models making testable predictions about human behaviour, which have been found to be useful and successful. Evolutionary demography is one such field.

This research was funded by the Royal Society. A grant from the EC (DGXII) to IIED funded the fieldwork in Kenya. Bonaya Abiyo, Kame Kutu, Halima Adan, Sororo Orto and Galgallo Bonaya assisted with the data collection in Kenya, and Rebecca Sear helped with data analysis. A version of this paper was presented at the 1996 American Anthropological Association meeting in San Francisco, California.

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