Introduction

Determinants of fertility have long been investigated by demographers, largely through empirical studies that seek correlates of fertility, but without any strong theoretical paradigm. Evolutionary anthropologists have also become very interested in reproductive decision making and thus reproductive rates. Evolutionary life history theory is concerned with the timing of vital processes from birth, through to growth, reproduction and senescence (Stearns 1992). As such, it has great relevance to human demography. If a useful theoretical framework for the analysis of reproductive decision making can be found, then it will give us the ability to predict the consequences of environmental and social changes on birth rates, and other demographic phenomena. In this paper I shall describe a model of reproductive decision making in Gabbra pastoralists, and use it to predict the influence of demographic risks (such as adult and child mortality risk) on the reproductive decisions of parents.

Evolutionary theory predicts that parental behaviour is adapted to maximise long-term reproductive success. Life history theory predicts that there are trade-offs between reproduction and mortality (Williams 1957, Stearns 1976), which has been used to explain why people might not always reproduce at the maximum rate. High fertility might increase the mortality of both mothers and their children. For example, Blurton-Jones (1986) found that closely spaced births in !Kung hunter-gatherers increased the risk of infant mortality, making an intermediate interbirth interval optimal in terms of maternal reproductive success. In agricultural and pastoral societies, heritable wealth is an important part of parental investment in children. There is very good evidence that, in traditional societies, reproductive success correlates positively with resources owned. I have shown that this is true in the case of the Gabbra (Mace 1996a). In many cases, heritable resources provide the seeds, or even the major part, of each child’s future opportunities to generate income. As such, heritable resources provide an additional reason why parents may not maximise fitness by reproducing at the maximum possible rate. Children that cannot be given sufficient resources to form their own households may have low or no reproductive success. Hence children that are born without hope of inheriting resources may simply use up family resources with little likelihood of contributing to the long-term fitness of their parents.

This is the situation that prevails for Gabbra pastoralists – a group of camel-keeping, nomadic pastoralists that inhabit the area east of Lake Turkana in northern Kenya (Map 1). This area is extremely arid and remote from government
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Map 1. Northern Kenya, showing the Gabra area, and surrounding groups

services. Nomadic households live almost exclusively off herds of livestock, of which female camels are the key resource. Families will generally use milk from camels and the meat from male or ageing female small stock to feed the family. If the needs of the family grow faster than the herds, then the amount of milk taken will increase, competing with the young livestock and slowing herd growth rates; and slaughter may extend to more immature males and to females, further reducing the productivity of the herd. The singulate mean age at marriage (a period measure describing a hypothetical synthetic cohort, which is calculated from the proportion of never-married people in each age-group and therefore does not rely on their reporting of past events: Newell 1994) of Gabra women is 21, and 33 for men. This relatively late marriage is likely to be due to the slow reproductive rate of camels. Sons are almost entirely dependent on camels inherited from their family, in order to marry and set up their own household herd. Mace (1996a) shows that brothers are in competition for their father’s herd, and the number of elder brothers is a significant negative correlate of both age at marriage and the size of the herd at marriage. A similar explanation for late marriage in the neighbouring, camel-herding Rendille has been proposed by Roth (1993).
In this paper, we shall use a model of reproductive decision making in a pastoralist system, based on the Gabbra herding system, that has been described in Mace (1996b). The model is informed by data from a demographic survey of about 5,000 Gabbra camel pastoralists, undertaken in 1993/1994 (see Macé 1996a for details). We will use the model to predict the scheduling of births that we would expect to see given the demographic risks (such as child and adult mortality risk) and will compare these predictions with data on Gabbra completed family size.

The model is a dynamic model in which decisions are evaluated in terms of their impact on the expected fitness of the parents at the end of their reproductive lives. The decision to have another baby is assumed to depend on both the wealth of the family and the number of children they already have. The demographic risks that a parent is assumed to be avoiding are thus the risk of having too many children whose food demands will diminish the family herd, versus the mortality risks of children and adults. Evolutionary theory predicts that adults will attempt to maximise the number of children they can successfully raise and marry off, which involves trading off the risk of destitution (from having too many children) against the risk of a family size below the optimum due to losing children due to mortality risks, or dying oneself (as an adult) before the family has reached its optimal size.

Figure 1. The completed family size of women over 45 years of age (bars, n = 421), and the predicted distribution generated by the model.

Note: Figure 1 is based on estimated mortality rates (Table 2, solid line) and double the best estimate of mortality rates (dotted line) – see below for how these mortality estimates were derived, and how the model generated the predicted distributions.
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Figure 1 shows the number of surviving children born to Gabra women who have completed their fertility, based on all the post-menopausal women in the survey. Fertility is high (Total Fertility Rate = 5.63), but there is variation between families. We shall estimate appropriate parameter values for the Gabra, in order to test whether this distribution of completed family size is the one we would expect to arise given the mortality risks inherent in the system.

**Estimating mortality risk**

Demographic data was collected on the Gabra in a single round survey, and thus levels of mortality had to be estimated by indirect methods.

**Adult mortality**

Adult mortality was estimated from data on orphanhood and widowhood. The proportion of children reported as orphaned, and men and women whose first spouse had died are shown in Table 1. This data suggest that over about thirty years, a child has about a 15 per cent chance of having lost its mother, which is similar to the probability that a man will have lost his first wife over the same period, or roughly 0.005 chance of losing a mother each year. These data can be used, with the help of models based on standard life tables, to estimate life expectancy. There is no model life table for sub-Saharan Africa, so we used the UN south Asian model which appeared to be the closest fit. The estimated life expectancy at age 20 for males and females, using the widowhood methods (which uses standard UN programs which use the data from the proportions with first wife alive and with husband alive columns in Table 1), was around 66 years for women and approximately 63 years for men. These are very high life expectancies, which could be due to problems with the techniques used, for example choosing an inappropriate model (the accuracy of indirect methods for the estimation of mortality has been questioned by some authors: Blacker and Mukiza Gapere 1988), or to adult mortality being under-reported in our sample. The orphanhood method (which uses standard UN programs which use the data from the proportions with mother alive and with father alive columns in Table 1) gave estimated life expectancies of around 70 years, which seems very unreliable. We have no reason to believe that mortality in the Gabra area is high (malaria is not frequent and population density is very low), however we do suspect these mortality estimates may be too low. We shall use the estimate of 0.005 annual risk of mortality amongst adult women as the best estimate we have for the baseline case, and then use the model to explore what difference we would expect it to make on reproductive decision if mortality were actually higher.

In the particular case of maternal mortality risk (death of mother in or around childbirth) we have estimated that elsewhere to be in the region of 600 deaths per 100,000 births (Mace & Sear 1996). For reasons outlined below, the Total Fertil-
Table 1. Proportion of individuals reporting widowhood (first spouse dead) and orphanhood (mother dead).

<table>
<thead>
<tr>
<th>Age group of respondents</th>
<th>Mother alive</th>
<th>First wife alive</th>
<th>Husband alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-4</td>
<td>0.980</td>
<td>0.925</td>
<td></td>
</tr>
<tr>
<td>5-9</td>
<td>0.950</td>
<td>0.852</td>
<td></td>
</tr>
<tr>
<td>10-14</td>
<td>0.926</td>
<td>0.799</td>
<td></td>
</tr>
<tr>
<td>15-19</td>
<td>0.925</td>
<td>0.722</td>
<td>0.980</td>
</tr>
<tr>
<td>20-24</td>
<td>0.885</td>
<td>0.608</td>
<td>0.966</td>
</tr>
<tr>
<td>25-29</td>
<td>0.862</td>
<td>0.484</td>
<td>1.000</td>
</tr>
<tr>
<td>30-34</td>
<td>0.860</td>
<td>0.348</td>
<td>0.974</td>
</tr>
<tr>
<td>35-39</td>
<td>0.735</td>
<td>0.239</td>
<td>0.943</td>
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<tr>
<td>40-44</td>
<td>0.714</td>
<td>0.233</td>
<td>0.977</td>
</tr>
<tr>
<td>45-49</td>
<td>0.523</td>
<td>0.009</td>
<td>0.918</td>
</tr>
<tr>
<td>50-54</td>
<td>0.369</td>
<td>0.053</td>
<td>0.936</td>
</tr>
<tr>
<td>55-59</td>
<td>0.267</td>
<td>0.052</td>
<td>0.867</td>
</tr>
</tbody>
</table>

Child mortality

Ever-married women were asked to report full birth histories, including those children that were born alive and had since died. However, in common with many other such populations, we know that they were reluctant to report dead children. For example, in one case, a woman whose teenage son had died quite recently, and who knew that everyone knew of the death, gave a birth history that omitted that son. Therefore we could not take reported child mortality rates at face value. In order to estimate a true risk of child mortality, we took a new approach, suggested by Leslie et al. (1988), and applied more rigorously here. We assumed that those women who had reported dead children were giving accurate birth histories. We assumed that deaths occurred with a fixed probability, and used the binomial distribution to see how many deaths we would expect to see in families of six births. We do not have a value for no deaths because we assume that we cannot distinguish those who genuinely did not experience any deaths among their children, and those that were simply failing to report any deaths. Thus we do not have the value for 0 deaths per family in the distribution (because we are only using data from mothers that did report deaths). But we can use the distribution of 1, 2, 3 and 4 deaths to estimate what the probability of a child dying actually is, assum-
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Figure 2. Number of dead children reported by Gabra women

Note: Figure 2 is excluding those mothers that did not report any death, (bold line), and predicted numbers of deaths assuming 25 per cent (dashed line), 20 per cent (dotted line), 15 per cent (dashed and dotted line) and 10 per cent (solid line) mortality.

The observed distribution of deaths per mother appear to fit that distribution predicted if each child had a 15 per cent chance of child dying before age 15 (Figure 2).

On the basis of this model, if we use the 15 per cent mortality curve in Figure 2 to read off how many families with no deaths we would have expected, we estimate that 431 women who reported no deaths were accurate, and 529 women who reported no deaths were failing to report births where the child had subsequently died. Parameters used in the model are 0.02 annual risk of death in under 4s, and 0.008 annual risk of death in 4-15 year olds, which totals 0.15 risk of death by age 15 (0q15).

The model

The model we use here has been described in detail in Mace (1996b). The model is designed to investigate under which circumstances parents aiming to maximise their reproductive success should decide to have another baby, which thus determines the expected size of their completed family. In Mace (1996b), the model
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was used to investigate how the cost of marriage influenced optimal family size; here we use it to see how mortality risks would influence optimal family size.

In the model, the marriage system is assumed to be monogamous i.e. only one wife is reproducing. This reflects the majority of Gabbra households: 88 per cent of women in a survey of 848 households were monogamously married, and a large number of the cases of polygyny occur when the first wife is approaching menopause i.e., akin to serial monogamy. Under true monogamy, there is no reason to expect any conflict of interest between husbands and wives regarding family size and thus the model could be considered to represent the decision making of either partner in a monogamous marriage.

The modelling technique used is stochastic dynamic programming (see Houston et al. 1988, Mangel and Clark 1988 for reviews, Mace 1993 for an application to pastoralist subsistence systems). As with other optimality models, they have explicitly defined a decision, a currency (i.e., costs and benefits) by which that decision is evaluated, and constraints (which determine the range of possible options). Dynamic optimality models have, in addition, a state variable (or variables), which enables decision to be state-dependent; this adds much greater realism. Dynamic models also have an advantage over 'static' optimality models in that they can identify strategies that maximise long-term fitness. In this case, fitness is maximised at the end of the parents' reproductive life. Thus they have the potential here to make more realistic and specific predictions regarding reproductive decisions, and hence fertility, than could be done either with simple optimality models or simple life history models.

In the case described here, the decision pastoralist parents make is whether or not to have another baby. Every two years throughout their reproductive life the parents make this decision. Decisions are evaluated in terms of the expected lifetime reproductive success of the parents, which is calculated as the total number of children, still alive at the end of the parents' reproductive lives, that the parents can afford to marry off. Decisions are state-dependent, and state is described by two variables: herd size and family size. In other words, the decision will depend upon their wealth (w) and the number of living children they already have (ch). The minimum interbirth interval is assumed to be two years; very few birth intervals were observed shorter than this (Mace & Sear 1997). Reproductive life is taken as thirty years from marriage, so the maximum family size is 15 children. There is a minimum cost of marrying off a child that has to be paid (p), so fitness is a function of both number of children (ch) and wealth (w). Fitness at the end of thirty years reproductive life is thus w/p, or just ch, whichever is the lower number. Decisions are evaluated in terms of the extent to which they maximise this fitness function.

Each year, enough food to feed the family will have to take from the herd. The food requirements of the family are a function of the number of children and their average age. The produce from the herd (milk and male offspring) is a function of the herd size. If this is not enough to feed the family, then adult females have to be
sold or slaughtered, reducing herd size. It is assumed that families are aware of the expected rates of reproduction and mortality in a herd animal, which will depend in part on whether or not it is a drought year. Droughts occur with frequency 0.2. But these are probabilities, so the actual rates of herd growth and production, experienced by a family will vary stochastically. If the herd size, measured in adult female camels, falls to zero at any time then the family is considered destitute and fitness is zero.

Children experience a stochastic risk of mortality each year, which is assumed to be a function of the average age of the children. If an adult dies, children are assumed to continue to experience these risks of mortality, and the final fitness value of the family is taken as that number of children that expected to survive to the time at which the parent would have ended their reproductive life had they survived.

Assumptions regarding child and adult mortality are similar in the model to those concerning livestock mortality. That is, it is assumed that decisions are made on the basis of knowledge of the mortality that exists in the system, but no foreknowledge of the precise level of mortality that a particular family will experience. That will be stochastic. Thus we are investigating decisions in the face of a known risk (rather than uncertainty). The perception of risk in the environment is more likely to be based on cultural knowledge rather than individual experience (as parents will probably have to make decisions about reproduction before they experience much, if any, child mortality amongst their own children). However, the mechanisms of transmission of this knowledge are not addressed here. Whether the predictions made by the model in fact explain observed reproductive behaviour is a matter for empirical investigation.

The predicted schedule of reproductive decisions

Table 2 outlines the parameter values of a baseline model that is realistic for Gabra pastoralists. This model was used to predict a decision rule which will say whether it is optimal for a family to have another baby at any time, based on how many living children and how many livestock a family has at that time. (Optimal, in this case, means that decision that is likely to leave the family with as many children that they can afford to marry off as possible at the end of their reproductive lives, as described above). The decision rule under the baseline case is the dark line in Figure 3 (parameter values are listed in Table 2). Fitness is never increased by having a baby if household wealth is less than 6 camels. For each additional living child in the family, the minimum wealth at which fitness is increased by having another baby increases. Such a decision rule would be predicted to give rise to a positive correlation between wealth and reproductive success, which has been shown in this population (Mace 1996a). In the case of the Gabra it is actually the males that are by far the more costly sex to marry off, as the parents of the groom are responsible for providing newly weds with their own
Table 2. Parameter values used in Figures 2 & 3

<table>
<thead>
<tr>
<th>Variables per one female stock unit*</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>p(birth) − p(death) (with frequency 0.8)</td>
<td>0.11</td>
</tr>
<tr>
<td>p(birth) − p(death) (with frequency 0.2)</td>
<td>−0.14</td>
</tr>
<tr>
<td>Food yield when living</td>
<td>10 units/year</td>
</tr>
<tr>
<td>Food yield if sold/slaughtered</td>
<td>20 units</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variables for people</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Food requirements of an adult (&gt;=15 years)</td>
<td>15 units/year</td>
</tr>
<tr>
<td>Food requirements of a child (&lt;15 years)</td>
<td>*age units/year</td>
</tr>
<tr>
<td>Probability of adult death</td>
<td>0.005 per year</td>
</tr>
<tr>
<td>Probability of maternal death</td>
<td>0.005 per birth</td>
</tr>
<tr>
<td>Probability of child death (&lt;3yrs)</td>
<td>0.008 per year</td>
</tr>
<tr>
<td>Probability of child death (15&gt;yrs&gt;=3)</td>
<td>0.02 per year</td>
</tr>
<tr>
<td>Reproductive life span of an adult</td>
<td>30 years</td>
</tr>
<tr>
<td>Minimum interbirth interval</td>
<td>2 years</td>
</tr>
</tbody>
</table>

Note: 1 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).

herd of livestock, in addition to the payment of a brideprice. We have shown elsewhere that the reproductive rate of both men (as measured by likelihood of taking another wife when the first wife reaches menopause, Mace 1996b) and women (as measured by the length of each birth interval, Mace & Sear 1997) is clearly altered according to the number of sons that a family has rather than number of daughters. These studies suggest active decision-making by the Gabbra with respect to some aspects of reproductive rate.

The dotted line in Figure 3 shows the decision rule that would be optimal in an environment where the extrinsic risks of child and adult mortality were double those assumed in the baseline case. The minimum wealth at which it is optimal to have another baby decreases slightly. This is because the probability that any child is still alive at the end of the parents’ reproductive life span is lower than in the low mortality scenario.

These decision rules can be used to make an estimate of the demographic profile of a population where individuals were following such a decision rule. We ran a simulation designed to generate a distribution of completed family sizes, based on parameters realistic for that cohort of this Gabbra population that have now completed their fertility (i.e., those over 45 years of age by 1994). This cohort of women, whose completed family size distribution is shown in Figure 1 (bars), reported an average of 10 camels as the starting herd size at household formation. We ran a simulation of households, starting with 10 camels each, and reproducing according to the decision rules shown in Figure 3. Wealth, child and adult mortal-
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ity, as well as food needs, were assumed to fluctuate according to the rules already described (i.e., those conditions for which this optimal decision rule was derived). These simulations generated the curves shown in Figure 1. The curves give the predicted distribution of completed family sizes (living children only) of women still alive at 45 years. The dark line gives the distribution predicted in the baseline case, and the dotted line gives the distribution predicted if mortality were double this.

It is interesting to note that the two curves are almost indistinguishable. This is because, under high mortality conditions, it is optimal for the women to have slightly more children, compensating for the more children that will die. Thus the predicted distribution of completed family sizes observed is predicted to be not very sensitive to levels of mortality, within a realistic range. It is living children that matter. If parents are following a decision rule based on number of existing children, dead children are effectively 'replaced' by additional births, especially as most of the mortality is concentrated amongst very young children. Thus, whilst high mortality risks can greatly influence the birth rate, we do not expect them to have a great influence on the completed family size of living children.

The decision rule (optimal policy) of when to have another baby, on the basis of current wealth (in camels) and the number of living children the family already has. The lines show the points above which families would not be likely to increase their fitness by having another baby but if below will increase their

![Figure 3: Relation between wealth (number of camels) and reproductive success (number of children)](image)

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expected fitness, on average, by having another baby. Dark line is for an environment as described by Table 1 (the baseline case). The dotted line is for an environment where the extrinsic mortality risks are all doubled: infant mortality risk 0.04 per year, child mortality risk 0.016 per year, adult mortality 0.01 per year, maternal mortality 0.01 per birth.

The bars shown in Figure 1 are the actual data on completed family sizes of this cohort of women. The model predictions and the real data are quite closely matched. The model simulations generate virtually no women with 0 or 1 child, whereas such women are found in the population. This is likely to be due to infertility problems in some women, rather than ‘decisions’ to have so few births that they are likely to be left with such small families. There are also predicted to be slightly more larger families than observed. However, the modelling framework does appear to be generating broadly accurate predictions on the basis of this broad fit between predicted and observed distributions of family size, and thus may well be capturing the nature of the processes that lead to the patterns of birth scheduling observed in the Gabbra.

Conclusion

Evolutionary theory has provided a framework with which to make very detailed demographic predictions, including predictions about the distribution of family sizes observed, and how family size might change should the environment change in the future. The case modelled here predicts that changes in mortality alone are unlikely to be the cause of any major shifts in observed family size in the Gabbra.

Acknowledgements

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Résumé

Les auteurs emploient dans cette étude un des principaux postulats de la sociobiologie – à savoir que pour obtenir le meilleur succès sur le plan de la reproduction il faut mettre au monde le plus d’enfants possible, qui, à leur tour, puissent se reproduire avec succès. Chez les populations pasteurs élever un enfant jusqu’à son mariage implique des dépenses économiques qui peuvent mener à la réduction du troupeau. Ceci veut dire que, à leur tour, les autres enfants ont une chance amoin-drie de faire une bonne alliance. S’appuyant sur l’hypothèse déjà mentionnée, les auteurs analysent les données démographiques recueillies chez 5000 pasteurs gab-bras du Kenya du Nord.

Resumen

Maximizar el éxito reproductivo implica tener solo tantos chicos como los que puedan reproducirse con éxito. Por lo tanto, cuando matrimonios de pastores deci-
den tener un bebé, tienen que evaluar la probabilidad de poder criar a este hijo y casarlo con éxito frente al riesgo de que su alimentación cause la disminución del rebaño familiar, dañe las perspectivas matrimoniales de los otros hijos o hasta pueda desarticular a la unidad doméstica. La decisión de padres de tener otro bebé depende, por lo tanto, de la riqueza de la unidad doméstica y de la cantidad de hijos que ya tienen. En el trabajo se aplica un modelo dinámico, de optimización estado-dependiente, que se basa en datos demográficos sobre 5000 pastores Gabbra. Se analiza con el modelo la influencia del riesgo extrínseco de mortalidad sobre decisiones reproductivas. El riesgo de mortalidad es estimado a partir de datos sobre viudez y muertes de niños y hermanos. Se describe una simple técnica para estipular muertes no reportadas. Usamos estos parámetros en el modelo para predecir la distribución de la fertilidad en la población estudiada. Los resultados indican que modelos evolutivos pueden predecir con éxito planificaciones de fertilidad humana. Además predicen que cambios bastante grandes en la mortalidad no causan muchos cambios en la distribución del tamaño de familias con hijos vivos.

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