AN ADAPTIVE MODEL FOR PREDICTING !KUNG REPRODUCTIVE
PERFORMANCE: A STOCHASTIC DYNAMIC PROGRAMMING
APPROACH

By

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Abstract

A stochastic dynamic programming model is presented that supports and extends work on the reproductive performance of the !Kung Bushmen (Lee 1972), (Blurton Jones et al. 1978), (Blurton Jones 1986) proposing that !Kung women and their reproductive systems may be maximizing reproductive success. The stochastic dynamic programming approach allows the construction of a "whole-life" model where the physical/environmental constraints along with the uncertainty about future events !Kung women face when making reproductive choices can be explicitly built in. The model makes quantitative predictions for the optimal reproductive strategy assuming !Kung women are maximizing expected lifetime reproduction (ELR) given the physical parameters of !Kung life.

The model relies on data gathered from the works cited above and some considerations from simple probability theory. The model predictions for optimal birth spacing match the !Kung reproductive data very well and support earlier findings (Blurton Jones and Sibly 1978), (Blurton Jones 1986). The utility of the dynamic modeling approach is illustrated when the effects of varying certain model parameters are investigated.

By including the effect of the mother's mortality which was not included in the Blurton Jones and Sibly (1978) analysis, the model allows for further exploration of the application of an adaptive approach to human reproductive performance. By adding some considerations about the risks of childbirth for the mother the model not only predicts optimal birth spacing which is site specific but also predicts the optimal time for a woman to begin and cease having children. These predictions coincide with menarche and menopause and shed light on their possible adaptive value.

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Chapter 1

Introduction

The objective of this paper is to present a stochastic dynamic programming model which predicts optimal birth spacing for the !Kung women of Botswana who live by foraging alone. The model is based on data presented in earlier works and serves to support findings therein. The utility of the dynamic modeling approach is illustrated by investigating how changes in parameters affect the model outcome. Of specific interest are parameters concerning the maximum backload a woman can carry, the extent to which a woman's offspring depend directly on the mother's provisioning, and the woman's state dependent mortality. These considerations suggest how the model could be modified to investigate many other questions concerning related issues in the study of human fertility.

1.1 Background

N. Blurton Jones and R. M. Sibly (1978) investigated the birth spacing of the !Kung in an evolutionary framework, i.e. women are spacing births to maximize Expected Lifetime Reproduction (ELR). Blurton Jones and Sibly computed the expected backload a woman would have to support on a foraging trip for children from one to 14 years of age. They then computed total backload assuming that !Kung women provide 58.8% (Lee, 1972) of the family food in the form of mongongo nuts. There is a fixed load comprised of the food requirements of the mother, her husband and possibly a dependent relative totaling 4400 cal/day requiring 3.08 kg of mongongo nuts daily. The variable load made up of children and their food requirements is a function of inter-birth-intervals (IBI).

By computing total expected backload for different IBIs, assuming that the women forage every third day, Blurton Jones and Sibly (1978) reached two important conclusions: 1) There is a sharp increase in total weight carried when the IBI falls below four years and 2) An IBI of four years provides a very even level of backload over a woman's career. The four year IBI in these findings coincides with the mean IBI for !Kung women of around four years reported by Lee (1972) and Howell (1979) and suggests that the backload a woman carries when foraging could play a significant role in birth spacing.

In a subsequent paper Blurton Jones (1986) extended the analysis further and correlated reproductive success with backload. Reproductive success was computed using !Kung demographic data (Howell, 1979) by calculating the proportion of births at a particular IBI that yield a surviving teenager then multiplying this proportion by the number of births in a 20 year career that arise from this particular IBI. The resulting figure represented the expected reproductive success for each IBI. Blurton Jones found that backload was a good predictor of reproductive success and that the maximum reproductive success occurred near an IBI of four. This work provided further evidence that !Kung women may be behaving adaptively in their birth spacing decisions.

The more detailed whole-life model presented herein, based on fundamental ideas from behavioral ecology coupled with data specific to !Kung life, helps to support this conclusion. The stochastic nature of the model allows for the inclusion of unpredictable events that effect the reproductive life history of organisms. This allows for a more realistic representation of the life of an organism; e.g. instead of assuming direct functional relationships between a specific state variable and the foraging efficiency or mortality of an individual, the state variable is assumed to affect the probability that an individual will forage successfully or die given their state. The flexibility inherent in this approach aids in understanding how not only birth spacing, but other behavioral traits could be adaptive, i.e. the model predicts that early birth intervals will be shorter

as proposed by Blurton Jones (1987) and predicts the optimal time to begin and cease having children corresponding to the timing of menarche and menopause.

1.2 The Modeling Approach

The model proposed herein is the result of an effort to add to the theoretical work that has focused on human fecundity decisions in an evolutionary framework and to add to the repertoire of available tools with which to approach the problem. In addition to work already discussed, examples of work in this area include Rogers' (1990) and Beauchamp's (1994) efforts to model how different aspects of wealth and income affect reproductive decisions in modern human populations, both in an evolutionary framework. Rogers (1990) uses a formalism based on the Leslie Matrix to study the effect on heritable wealth on reproductive decisions while Beauchamp (1994) developed a stochastic dynamic program to investigate how income profiles, uncertainty in income profiles, wealth, and other factors affect the quantity and "quality" of offspring, and the timing and spacing of births. The model developed herein is based on the same concepts as that of Beauchamp, but is closer in flavor to models in behavioral ecology.

Stochastic dynamic programming is a discrete, multiperiod modeling approach that has been used extensively on animal behavior (Mangel and Clark, 1988). With this approach, two things happen in each period: the organism being studied makes a decision, and the state of the organism changes based on the outcome of the decision allowing for stochastic events. The object of the decision is assumed to be maximization of lifetime fitness represented as the total expected number of fitness units (depending on the nature of the model) at the end of the given organism's life, given the organism's state at the time the decision is made. The total number of periods used in the model will then be representative of the lifetime of the organism being studied. Key issues that must be

addressed while constructing the model are:

- Clearly defining the period length and number of periods to be modeled.
- Defining what decision is to be made and when it is to be made in each time period.
- Characterizing the key state variables influencing the decision to be made and defining how the state variables evolve from one time period to the next.
- Defining the form of the stochastic element faced in each period by the organism.

In our case, each of these issues can be resolved quite easily by considering the physical environment of the !Kung discussed below.

1.3 The Ethnographic Basis for the Model

The core assumptions of the model are based on the observations made and the testimony of !Kung women documented by Lee (1972). They are:

1. It seems unlikely !Kung Bushmen practice a conscious program of fertility control – they want as many children as possible.
2. The women say it is bad to space births too closely.
3. They believe that three years is the proper duration for nursing a normal healthy child.
4. The women carry children up to age five.

These four points provide the basis for our general modeling framework characterized by the following:

- Since the !Kung women express a high desire for children, the assumption that they are trying to maximize ELR is reasonable. Thus ELR measured as the number of offspring potentially able to reproduce at the terminal time is the appropriate “currency” for our model.
- The fact that women explicitly say that it is bad to space children too closely and believe three years is the proper time to wean a healthy baby suggests that women must face tradeoffs in their fertility decisions.
- The women must carry children on foraging trips, so that physical limits to backload play a critical role in child spacing.

These points suggest that the appropriate state variable characterizes the woman's present family situation, i.e. the number and ages of her children. The woman's decision in each period is then whether to attempt to have a child or not. The physical environment of the !Kung suggests the appropriate period length, the timing of decisions, total periods, and the nature of the stochastic element. The following brief description of the habitat of the !Kung is based on Lee's 1972 work.

The habitat of the !Kung exerts survival pressure on the !Kung women in the form of heavy backloads. The !Kung divide the year into five seasons one of which is the spring dry season. In all other seasons obtaining food is in general not a problem. It is this one hot, dry season that creates the burden for the !Kung women when food is available only at considerable distances from permanent camps near water.

In this dry season, the !Kung women, who provide more than half of their family's food by foraging, must travel several (12 or more) kilometers in potentially life threatening weather conditions to collect mongongo nuts. This suggests that much of a woman's decision about family size must be based on the knowledge that she will have to carry and provide for these children through the hot dry season.

From this we see that the most important periodic event is the dry season. This is an annual event, thus the period of the model should be one year. The one year period suggests that the model have approximately 30 - 40 periods to represent the reproductive life span of a typical !Kung woman i.e. from 18 to 50 years of age. The woman makes her decision between dry periods by assessing her present state and evaluating the upcoming dry period based on previous experience and expectations. Finally, the stochastic element of the model is the uncertainty about the severity of the next dry season and the risk of injury or death on foraging trips for a given state. The next section summarizes these ideas and translates them into mathematical terms.

Chapter 2

The Construction of the Dynamic Programming Model

2.1 Preliminaries and Definitions

Before expressing the model in mathematical terms, a short description of the decision process of a typical !Kung woman as cast in the framework of the model will make the mathematical presentation more comprehensible. Over a !Kung woman's reproductive years she is faced each year with the decision to attempt to have a child or not. She makes this decision just after the difficult dry season, in the time of plenty when she can assess her 'state'. Her state consists of seven elements: her age and the number of children she has in each of seven age categories; 0-1, 1-2, 2-3, 3-4, 4-5, 5-15, and over 15 years old. When making decisions, she is more concerned with children up to age five since she must carry them in possibly lethal conditions during the hot dry season on foraging trips. Children 5-15 also impose a burden as she must provide food for them. Children over 15 do not influence her decision as girls often marry by this time, and boys over 15 tend to rely (informally) on the group for their food (Blurton Jones, personal communication). The woman is faced with this decision each year from the time she begins having children around age 18 (Howell, 1979) to age 50. Over this period, the female's goal is to maximize the number of offspring she has over her lifetime who are potentially able to reproduce. In order to cast the model in mathematical terms, we need to give precise definitions for the objects just described - her state, the decision variable and the objective function.

The woman's "state" is described by a vector which contains the state variables. The "state vector" is written as $\vec{x}(t) = (x_0, x_1, x_2, x_3, x_4, x_5, x_6, x_7)$ and we will often use $\vec{x}$ as shorthand when referring to this vector. Each component of $\vec{x}$ contains a piece of information concerning the woman and her family defined as follows:

$$\begin{aligned}
 x_0(t) &= \text{mother's age} \\
 x_1(t) &= \text{children age 0 to 1} \\
 x_2(t) &= \text{ " " 1 to 2} \\
 x_3(t) &= \text{ " " 2 to 3} \\
 x_4(t) &= \text{ " " 3 to 4} \\
 x_5(t) &= \text{ " " 4 to 5} \\
 x_6(t) &= \text{children age 5-15} \\
 x_7(t) &= \text{children over age 15}
 \end{aligned}$$

State Variables: $\vec{x}(t) =$

We then define the decision variable as $D(\vec{x}, t)$. $D(\vec{x}, t)$ refers to the woman's decision to reproduce or not at time t given that her state (i.e. the size and age structure of her family and her age) is $\vec{x}(t)$. $D(\vec{x}, t)$ takes on only two possible values: $D(\vec{x}, t) = 1$ if the decision is to reproduce and $D(\vec{x}, t) = 0$ if the decision is not to reproduce. As an example, the woman's state would be expressed as $\vec{x}(t) = (32, 0, 0, 1, 0, 1, 0, 0)$ which means the woman is 32 years old has no children in the 0-1 age class, no children in the 1-2 age class, one child in the 2-3 age class, no children in the 3-4 age class, one child in the 4-5 age class, and no children over five years old.

The point of the dynamic modeling process is to map out a sequence of optimal decisions that depend on the woman's state as it evolves over time. It is thus necessary to specify the rules that govern the dynamics of changes of state. In our case, the woman's state evolves over time according to very simple dynamics—each age class is graduated then the 0-1 age class, $x_1(t)$, is assigned the value $D(\vec{x}, t)$. For example if $\vec{x}(t) = (32, 0, 0, 1, 0, 1, 2, 0)$ and $D(\vec{x}, t) = 1$, then $\vec{x}(t+1) = (33, 1, 0, 0, 1, 0, 3, 0)$. Now

we must translate the woman's objective to maximize her ELR as defined earlier into a mathematical form. We do so by defining the "objective function" as follows:

$$F(\vec{x}, t) = \text{maximum ELR from year } t \text{ on, given that } \vec{x}(t) = \vec{x} \quad (2.1)$$

$F(\vec{x}, t)$ represents the maximum total expected reproductive success to be obtained by the woman given that she is in state $\vec{x}(t)$ at time t and provided that she follows the optimal decision sequence from time t on. The woman's objective in period t is to select $D(\vec{x}, t)$, the first element of the optimal decision sequence from time t on. In so doing, she will put herself in the best possible position to maximize her ELR from $t + 1$ on. If the woman does this for each period over her entire productive lifespan then she will maximize her total reproductive success. In this way $F(\vec{x}, t)$ depends on $D(\vec{x}, t)$, i.e. the payoff for the best decision at t is $F(\vec{x}(t + 1), t + 1)$. In order to obtain this payoff, the woman must first get to $\vec{x}(t + 1)$. To do so the woman must:

1. Survive over the year given her state and decision.
2. Meet her family's nutritional needs over the entire year given her state and decision.

This is where the "expected" in ELR comes in to play, allowing stochastic events to be incorporated into the model. If in one period there are n possible events each occurring with probability p_i and having a fitness f_i , then the expected reproductive fitness associated with that period is the quantity $p_i \cdot f_i$ summed over the n possible events. In our case there are three possibilities:

1. The woman survives and forages successfully to meet her families nutritional needs.
2. The woman survives and does not forage successfully, i.e. forages at some level below that required to meet her family's minimum nutritional needs.
3. The woman dies.

To model these events we define two probabilities: ρ_s - the probability that the woman survives and ρ_f - the probability that the woman forages successfully. Both of these probabilities depend, of course, on the woman's state, i.e. $\rho_s = \rho_s(\vec{x})$ and $\rho_f = \rho_f(\vec{x})$. It seems natural to assign probabilities to the mother's survival - either she lives or does not. The same can not be said of ρ_f . What does it mean to not forage successfully? Based on our definition it would mean the woman did not meet her family's nutritional needs over the one-year period t to $t + 1$. This says nothing about what happens to the woman and her family, i.e. what if she almost meets her family's nutritional needs. The result would be the reduced probability of survival of the woman's dependent family members. To model this precisely would require assumptions about how the survival probabilities of children in each age class would be reduced, how the mother would choose to distribute the food she was able to collect, and so on. Since there is no body of data concerning these issues, any choice of relative survival probabilities for different age classes and so on is arbitrary.

In order to make the model tractable and for the sake of simplicity we divide the effects of unsuccessful foraging into two groups. If the woman does not forage successfully children under five all die due to malnutrition with probability ρ_{cd} while the survival probabilities of children over five are unaffected by one period of being malnourished. This assumption is an attempt to capture the fact that the younger children are more susceptible to malnutrition than older children. The incorporation of ρ_{cd} into the model splits event number two leaving us with four possible events:

1. The woman survives and forages successfully to meet her families nutritional needs, i.e. $\vec{x}(t) \rightarrow \vec{x}(t + 1)$ with probability $\rho_s \times \rho_f$ and the woman obtains the payoff $F(\vec{x}(t + 1), t + 1)$ (abbreviated F_{t+1}).
2. The woman survives and does not forage successfully but her family is unaffected,

i.e. $\vec{x}(t) \rightarrow \vec{x}(t+1)$ with probability $\rho_s \times (1 - \rho_f) \times (1 - \rho_{cd})$ and the woman obtains the payoff $F(\vec{x}(t+1), t+1)$.

3. The woman survives and does not forage successfully and her youngest children succumb to malnutrition i.e. $\vec{x}(t) \rightarrow \vec{x}^*(t+1)$ ($\vec{x}^*$ represents the case when all children under five die) with probability $\rho_s \times (1 - \rho_f) \times \rho_{cd}$ and the woman obtains the payoff $F(\vec{x}^*(t+1), t+1)$ (abbreviated F_{t+1}^*).
4. The woman dies and obtains the payoff $(1 - \rho_s)(\beta \sum_{i=1}^6 d_i x_i + \gamma x_7)$. The woman receives credit for her existing children but those 15 and under are discounted because they are 1) not mature – discount factor d_i and 2) the mother has died – discount factor β . The parameter γ represents the fraction of fitness units contained in offspring over 15 that the mother receives if she dies.

We can now state the dynamic programming equation. Since $F(\vec{x}(t), t)$ is the maximum expected value of the above outcomes over the decision set we have by definition:

$$F_t = \max_{D \in \{0,1\}} \left\{ \rho_s \left[\rho_f F_{t+1} + (1 - \rho_f)(\rho_{cd} F_{t+1}^* + (1 - \rho_{cd}) F_{t+1}) \right] + (1 - \rho_s) \left[\beta \sum_{i=1}^6 d_i x_i + \gamma x_7 \right] \right\} \quad (2.2)$$

Equation 2.2 embodies the essence of the model and allows us to predict the optimal decision at any time t . In our case, this involves computing just two numbers, $F(x, t)$ if $D(x, t) = 0$ and $F(x, t)$ if $D(x, t) = 1$. Whichever decision produces the largest value of $F(x, t)$ is the optimal one. Clearly the probabilities in Equation 2.2 drive the model and relate the model to reality - everything up to now has followed from the definitions. We now turn to incorporating the physical life parameters faced by !Kung women into the model.

2.2 Model Implementation

As mentioned before the probabilities ρ_s and ρ_f depend on the woman's state. The decision $D(\vec{x}, t)$ is linked to these probabilities because it affects the woman's state. This linkage then gives Equation 2.2 its physical meaning. The crux of the model then is to establish the functional dependence between ρ_s , ρ_f , and a woman's state. This relationship is developed using very basic field data available on the !Kung (Lee, 1979; Howell, 1979; Blurton Jones and Sibly, 1978) and some common sense considerations. We begin with considering $\rho_f(\vec{x})$.

A major factor governing a woman's foraging success is the backload she must bear on her foraging trips. Since it is difficult, if not impossible, to establish a convincing set limit to backload, we merely assume that the higher the backload, the more physically demanding a 12 kilometer walk becomes. This has the effect of decreasing $\rho_f(\vec{x})$. This is a common sense consideration which allows the mother to carry very heavy backloads but in doing so she makes a trade-off by risking reduced foraging success. This is a key difference between this model and the Blurton Jones and Sibly (1978) model which assumed a set limit to backload. The field data comes into play in computing the actual backload for a given state. If we define the woman's backload as $BL(\vec{x})$ then

$$BL(\vec{x}) = 9.24 + \sum_{i=1}^6 w_i x_i \quad (2.3)$$

The quantity 9.24 represents the weight in kilograms of three days worth of food for herself, her husband, and a dependent relative. The woman must carry this load regardless of the number of children she has. The summation term represents the variable load due to her children. Each of the constants w_i represents the total weight carried for one child in age class i . For $i < 5$, w_i would consist of the body weight of the child carried plus the food requirements of that child. For $i = 6$, w_i consists of food requirements only,

i.e. !Kung women do not carry children above age five on foraging trips. Values for w_i along with all other physical data used in the model were obtained from Blurton Jones and Sibly's 1978 paper. Table 2.2 summarizes the backload information required for the model. The body weights shown in Table 2.2 represent "net body load" carried on a foraging trip. This net body load is computed by taking the body weight of a child in a particular age class and scaling it by the proportion of time children in that age class are actually carried. This scaling procedure is an effort to capture the fact that as children grow up, they begin to intermittently walk with the mother on foraging trips so the mother only carries them for a portion of the journey. This is why the body load for a 4-5 year old is less than that for a 3-4 year old - the older child is able to walk for longer distances.

<i>Age Class</i>	<i>Backload Required to Rear Child (kg)</i>		
	<i>Body Weight</i>	<i>Food Weight</i>	<i>Total</i>
0-1	4.8	1.59	6.39
1-2	8.1	2.46	10.56
2-3	8.7	3.47	12.17
3-4	6.8	3.84	10.64
4-5	1.2	3.15	4.35
5-15	0.0	3.42	3.42

Table 2.1: Backload data by age class and load type. Source: Blurton Jones, 1978, p.142, Table 1.

The probability of foraging successfully may also depend on the woman's age. If a woman is older, she may not be able to carry as heavy a load as a younger woman. Figure 2.1 illustrates some possible functional responses of ρ_f to backload for given ages

which were used in the model. The assumptions underlying the shape of the curves are as follows:

- For low backloads, ρ_f is constant and close to one. This is to say that if a woman only has to carry a light load her probability of foraging success is high and increasing this load, for example, from five to ten kilograms affects ρ_f very little.
- Only when the backload gets quite heavy and approaches some physical limit does ρ_f begin to decrease rapidly. Since there is no data on what a limiting backload is for a typical !Kung woman, we do not assume that there is any limit but rather test the model output for several different functional forms.
- The effect of age is to reduce the maximum backload a woman is able to carry but the functional response remains unchanged for light loads, i.e. an older woman can still forage successfully at lower backloads.

Figure 2.2 shows the probability surface for any combination of age and backload, i.e. for any backload-age coordinate in the plane, the height of the surface at that point is the probability of foraging success.

We now turn to examining the nature of the relationship between $\rho_s(\vec{x})$ and $\vec{x}$. Clearly as a woman ages, the probability that she survives any one year period decreases. A more interesting scenario is to assume that $\rho_s(\vec{x})$ is not only state dependent but also decision dependent. Suppose that the probability of surviving a period depends on whether the woman gives birth or not - i.e. a woman's mortality risk is increased by childbirth. The top graph in Figure 3.3 illustrates two examples of functional forms of $\rho_s(\vec{x})$ used in the model. The top curve is based on actual !Kung mortality data which we will discuss in more detail later. Similarly, the top graph in Figure 3.4 illustrates examples of functional forms of $\rho_s(\vec{x})$ that are decision dependent. Assumptions underlying these curves will be

Figure 2.1: Probability of foraging success versus backload. The figure illustrates two families of possible functional responses for two different ages. One remains constant at low backloads and then decreases sharply as the weight nears a maximum while the other decreases more smoothly - both of course are equally plausible.

discussed in more detail later as well. With the model now fully specified we are now ready to explore its predictions for several different scenarios.

One last loose end merits comment. The right hand side of Equation 2.2 depends on $F(x, t)$ in the next time step. This is equivalent to the woman looking into the future to make her decision as to whether to have a baby or not. Unfortunately, we do not know F_{t+1} at time t , thus can not run the model forward in time.

To implement this 'forward looking' procedure we begin at the final time step T and work backwards in time. This is easy since we know $F(x, T)$ —it is simply the number of offspring potentially able to reproduce at $t = T$. Of course a 15 year old child is more valuable than a one year old child. The older child is like money in the bank while the younger child is an investment that has not yet matured. The children are

Figure 2.2: Probability surface for all possible combinations of backload and age.

thus ‘discounted’ based on their probability of survival from their present age to age 15. These probabilities are computed based survivorship information from B. Jones and Sibly’s (1978) paper and are shown in Table 2.2. Since in our model children from ages five to 15 are combined, an average probability of survival is applied to the 5-15 age class. Once $F(x, T)$ is computed, $F(x, T - 1)$, $F(x, T - 2)$,, $F(x, 0)$ can be computed. In this way a ‘decision’ matrix is generated containing the optimal decision for each state at any time t .

<i>Age Class</i>	<i>Probability of Survival to Age 15</i>
0-1	0.75
1-2	0.80
2-3	0.86
3-4	0.88
4-5	0.90
5-15	0.95

Table 2.2: Survival probabilities by age class. Source: Blurton Jones and Sibly, 1978, p.142, Table 1. Note: The Figure shown for the 5-15 age class is an average over individual survival probabilities in that age class.

Chapter 3

Model Results

The final step in the implementation of the model is to generate a !Kung woman's reproductive career using the decision matrix constructed as outlined above. Every woman begins at the state 000000 at some time after she reaches reproductive age. As she progresses through her career, for each state she reaches, she can consult the decision matrix to determine the action she should take. It is important to realize that the decision matrix is the analytic solution of the problem of maximizing ELR in a stochastic environment. The life histories generated in the following test runs of the model should therefore be interpreted as the optimal trajectory - not necessarily what is actually attained by a typical !Kung woman. This is so because a woman can not control stochastic events. As mentioned earlier, the power of this modeling method lies in the ability to investigate how changes in parameters affect the model and how different stochastic events in the life of a typical !Kung woman would affect her overall life history. Here we exploit this power to explore the model's response to changes in four areas:

1. Investigate the impact of changes in the functional form of $\rho_f(\vec{x})$.
2. Investigate the affects of changes in ρ_{cd} .
3. How does including the effects of the mother's mortality, especially when it is decision dependent, affect the model outcome.
4. How do certain stochastic events such as the death of children affect optimal life histories generated by the model.

We address each of these in turn below.

3.1 The form of $\rho_f(\vec{x})$

As mentioned earlier, the functional response of ρ_f to a woman's state plays an important role in the model outcome. In order to illustrate that the specific shape of ρ_f and any assumptions about limits to backload do not significantly alter the qualitative predictions made by the model we run four cases. The results of these runs suggest that all that is required to generate IBIs observed in the field is the general assumption that it is harder to carry a heavy load for 12 kilometers than to carry a lighter load for the same distance. Referring to the top graph in Figure 3.1 the curves have the following physical interpretation: Case 1) A woman who can carry up to 30 kilograms without risking a large decrease in the probability of foraging success. Above this load her probability of foraging success begins to decrease very rapidly. Case 2) A weaker woman whose probability of foraging success decreases more at lower backloads e.g. her ρ_f is approximately 0.9 at a backload of 20 kilograms. Case 3) A very weak woman for whom $\rho_f < 1$ even with no backload and ρ_f decreases almost linearly with backload. Case 4) A relatively strong woman able to carry 40 kilograms without significantly reducing ρ_f .

The bottom plot in Figure 3.1 shows the optimal life history trajectories predicted by the model for each of the four cases assuming that $\rho_s = 1$, $\rho_{cd} = 0.5$ and represents the specific situation where the woman starts her reproductive career at age 18 (Howell, 1979), lives to 50 and none of her children die. Each discontinuous jump in the life history trajectories corresponds to an increase in family size so the number of points between each of these discontinuous jumps is exactly the number of years between births. From these trajectories we can see that the mean IBIs for Cases 1 and 2 are both four. The weakest woman (Case 3) spaces children at around five years while the strongest (Case 4) spaces

Figure 3.1: Life Reproductive history for !Kung woman adopting the optimal reproductive strategy (bottom) for each of the different functional forms for $\rho_s(\vec{x})$ (top).

them at around three years. Since it is probable that each !Kung woman has her own personal ρ_f function similar to the four cases investigated, it is reasonable to postulate that these different forms could be one source of the variation in IBIs seen in the field. Figure 3.1 demonstrates that the specifics of the shape ρ_f and limits to backload are not at all critical to the model outcome as they produce similar model results over a wide range of shapes and values. This is so because the decision to have a child increases backload by 6.4 kilograms which has a major effect on foraging success over a large family of possible functional forms for ρ_f .

3.2 Changing ρ_{cd}

In the above case ρ_{cd} was set at 0.5 which means that if a woman did not meet the nutritional needs of her family over the period t to $t + 1$, there is a 50% chance her children under five would die due to malnutrition. To examine the role this parameter plays in the model we keep ρ_s constant at one, use a functional form for ρ_f similar to Case 2 in Figure 3.1, and run four cases with $\rho_{cd} = 0.3, 0.4, 0.6$, and 0.8 . The results from these runs are shown in Figure 3.2. For $\rho_{cd} = 0.4, 0.6$, (middle two trajectories in Figure 3.2) the model output suggests that the optimal birth spacing is approximately four years while for $\rho_{cd} = 0.8$ the spacing is closer to five years. The wider spacing for $\rho_{cd} = 0.8$ is due to the fact that the cost of unsuccessful foraging has increased, making a more conservative strategy optimal. For $\rho_{cd} = 0.3$, however, the model predicts much closer optimal spacing. This result is sensible and consistent with the definition of ρ_{cd} . The point here is that the model produces IBIs consistent with those observed in the field for any value of ρ_{cd} above a certain critical level, ρ_{crit} (around 0.35 in this case). The existence of this critical value has some interesting physical interpretations as discussed in more detail below.

Figure 3.2: Life Reproductive history for !Kung woman adopting the optimal reproductive strategy for four different values of ρ_{cd} .

The interpretation of the dramatic difference in the model predictions for values of ρ_{cd} above or below ρ_{crit} is that there are basically two strategies. If $\rho_{cd} > \rho_{crit}$ there is a significant risk to a woman's children if she is unable to provide food for them, so the optimal strategy is to space births four years apart. If, on the other hand, $\rho_{cd} < \rho_{crit}$, it is best to space births much more closely as depicted in the bottom-most trajectory in Figure 3.2. To give this result meaning we must consider what external factors would determine the value of ρ_{cd} . Physically, a low value for ρ_{cd} would represent the situation in which the woman is not penalized for her lack of foraging success and has access to a mechanism other than foraging to make up her shortfall. If this is the case, spacing births closely makes sense. Viewed this way, ρ_{cd} is a measure of the severity of the effect the mother's lack of foraging success will have on her children under five years of age.

Alternatively, if the mechanism by which the woman makes up her shortfall is by

depending on someone else in her society to provide these resources, ρ_{cd} could be interpreted as a measure of the level of responsibility placed on women by society to feed their own children. For example, if ρ_{cd} is set to zero, the woman's lack of foraging success has no effect on the survivorship of her children (put $\rho_{cd} = 0$ in Equation 2.2 to see this). A woman not providing enough nourishment for her children without affecting their survivorship means that someone else in her society makes up the difference. This is equivalent to lowering or removing the mother's responsibility to be the sole provider for her children. Once this has occurred, birth spacing becomes shorter as is the case for agrarian societies. For a hunter-gatherer society such as the !Kung, where each adult is expected to carry his or her own load, it is reasonable to expect ρ_{cd} to be above the critical level. In this case the birth spacing observed in the field would be approximately optimal.

3.3 Examining the effects of mother's mortality

For the simulations that produced the life history trajectories in Figure 3.2, the time to begin having children was set at 18 years of age based on demographic data suggesting that the average age for the first birth for a !Kung woman is 18.8 years (Howell, 1979). The age of last birth was not set - the model was simply run to age 55. An obvious question arises: If the object is to maximize ELR, why don't the !Kung women begin their families at a slightly earlier age and continue having children beyond 50? The mean age of last birth for !Kung women is 34.5 (Howell, 1979). The model suggests that continuing to have children until the terminal time is optimal, i.e. extending the reproductive span outside of the age 18 to age 35 interval could significantly increase ELR.

It has been suggested that menopause may be an adaptation resulting from the large

parental investment and long time to maturity for humans. There have been efforts to explain menopause based on the “grandmother hypothesis” which suggests that by grandmothering a woman may increase her ELR through her grandchildren more than by having more of her own children. Examples of work in this area are Mayer (1982) and Hill and Hurtado (1991). Mayer analyzed the genealogies of four New England families over a period of 199 years and suggested that “as measured by inclusive fitness, adult women who died after age 50 were evolutionarily more successful than those who died at an earlier age.” (p. 486). Hill and Hurtado based their study on demographic data that they gathered on the Ache foragers of eastern Paraguay. The authors state that the Ache data enables a test of the grandmother hypothesis “under very specific conditions, not necessarily related to the origin of menopause but relevant to its maintenance in the Ache population...” They concluded that “The data do not support the proposition that reproductive senescence in the Ache population has been maintained via natural selection favoring women who ceased to reproduce in order to invest in their grandchildren.” They were, on the other hand, not able to firmly reject the grandmother hypothesis either because for certain estimates of the effect mothering has on helping adult children reproduce, the model indicates “that reproductive senescence might be favored near an age at which menopause occurs in the population” (p. 337).

With my dynamic model we can explore exactly what assumptions concerning ρ_s and how it is affected by birth decisions are required to generate menopause in the !Kung population. Before exploring this interesting question we first must determine if including the effects of the mother’s mortality has any effect at all on birth spacing! In order to accomplish this, we again run several cases. Until now, we have not considered the parameters β and γ because they have not yet played any role; ρ_s has been set to one up until now causing the term including these two parameters to vanish. For the initial runs we set $\beta = 0.5$, i.e. survival probabilities of children fifteen and under are cut in

half by the death of their mother, and $\gamma = 1$ which is equivalent to children over fifteen being unaffected by the death of the mother. All the cases were run with $\rho_{cd} = 0.6$ and a backload function like Case 2 in Figure 3.1. The Base Case was run with $\rho_s = 1$. Case 1 is run with the ρ_s functional response given by the topmost curve shown in the upper graph in Figure 3.3. This functional response is based on actual mortality data on the !Kung from Howell (1979). Howell used data from the field to compute the probability of dying over five year periods as a function of age (Howell, 1979, p. 96, Table 4.6). These data points are plotted along with the functional response of ρ_s in Figure 3.3. The smooth line through these points is the fit used to compute ρ_s for each period. We compute ρ_s by first subtracting the probability of dying over a five year period for a given age (given by the smooth curve fit to the actual data) from one to get the probability of surviving over a five year period. We then take the fifth root of this result (assuming that the probability of surviving each year within a five year period is constant and independent, $\rho_{s(t,t+5)} = [\rho_{s(t,t+1)}]^5$) thereby generating the uppermost curve alluded to earlier.

The life history trajectory for Case 1 is shown in the lower graph in Figure 3.3. Notice that this trajectory agrees exactly with the Base Case suggesting that the mother's mortality schedule does not affect her birth spacing decisions. Why is this so? A very probable reason is that a long term event like mortality over an entire lifespan will not play a significant role in a decision over a one-year period. This is easy to see mathematically, the per period survival probabilities must be at least 0.99 for an individual to have at least a 60% chance of living to age 50. Since ρ_s is so close to one, the model outcome is identical to the case when $\rho_s = 1$. In order to see how sensitive the model is to assumptions about ρ_s we run one more case. Case 2 was run with the hypothetical curve shown in the upper graph in Figure 3.3. This curve is drastically different from Case 1; an individual with per period survivals in the hypothetical example would only have a 15% chance of living to age 35. The life history trajectory (top trajectory in lower graph

in Figure 3.3) for this case shows that even if mortality is much higher only the first interval and last few intervals are affected. The first interval is reduced from two years to one and the last two intervals drop to one year as mortality risks increase with age; both occurrences would be expected. Over the bulk of the fertility span, however, the birth spacing is four years - identical to Case 1 and the Base Case. This suggests that backload plays a much more critical role in birth spacing than does maternal mortality.

The last and more interesting case is to consider a decision-dependent-survival probability. It is reasonable to assume that there is a slight increase in risk of death in one period associated with childbirth in that period. As with limits to backload, it is difficult to establish how survival probabilities change given childbirth. Howell (1979) does mention that within the !Kung population it seems that complications during pregnancy have been selected against observing that very few women die during childbirth. We assume then that over some period of a !Kung woman's life her survival probability is reduced very little by giving birth. This is not to say that the same is true over her entire life.

For a very young mother, the large size of the human infant and the small size of her body are certainly at odds so it is reasonable to postulate the her per period survival is significantly compromised by giving birth. Hill and Hurtado (1991), when discussing possible alternatives to the grandmother hypothesis note that human fertility does appear to be exceptionally high during the early the part of the lifespan,... and conjecture that "Perhaps this 'racing' of the female reproductive machinery and required parental investment leads to parity-related depletion of physical condition and reproductive physiology that ultimately will not support further reproduction." (p. 340). Hill and Hurtado give the example that rapid reproduction may be related to increased susceptibility to skeletal fractures around the age of menopause (five to ten fold increase in fracture rate by age 60). This provides some basis for the assumption that as with very young mothers, older mothers also suffer decreased per period survival probabilities given childbirth.

Figure 3.3: Life Reproductive history for !Kung woman adopting the optimal reproductive strategy (bottom) when maternal mortality is included in the model (top).

Certainly, all traits coevolve and there is no way to single out any trait as independent of others and specify how it is adaptive. For example, we can show that given the above assumptions about survival during childbirth the model predicts menopause as a mechanism to protect investment in existing offspring. One could argue that if it paid to have more children, safer childbirth would have been selected for. This is of course reasonable, but what would be the expense of such an adaptation? Selection can only work on available variation and is certainly constrained. The modeling approach herein can only be used to explore how certain behaviors can be adaptive given a certain set of constraints. Thus, assuming that a woman's ability to safely give childbirth is constrained, we can explore how either the grandmother hypothesis, reduced survival probabilities due to childbirth, or a combination of the two could select for menopause.

Based on the discussion above, the functional forms for the conditional probabilities for per period survival, i.e. $\rho_s(\vec{x}(t)|D(\vec{x}, t))$, are shown in the top graph in Figure 3.4. In Case 1, $\rho_s(\vec{x}(t)|D(\vec{x}, t))$ begins to decrease significantly around 40 while in Case 2 this decrease begins much later, around 60. A more challenging task is to make reasonable assumptions about the values of β and γ . Recall that β is the probability that children under 15 will survive if the mother dies. It is difficult to estimate what this value is, but Howell (1979) suggests that it is well below one. In discussing child custody, she states that "If the mother dies, the maternal orphans may be cared for by the father with the help of his female relatives or by adoption by relatives of the dead wife. If the child is young enough to require breast feeding, the chances of the child's survival are slight. There were no cases in the population of a woman being called upon to 'altruistically' raise a child of her husband and his previous wife. Older children are left with relatives for care for months or years without being abandoned by the !Kung." This passage makes it fairly clear that for children under five β is quite low, perhaps less than 0.5. For older children between five and 15 β could be quite high, between 0.5 and 1. Over the entire

age class, a reasonable range for β would seem to be 0.2 to 0.8. In the model, we make no assumption about β and, as with previous runs, explore the model over a range of values.

Unlike β , there is really no way to get an idea for a “reasonable range” of values for γ . Recall that the definition of ELR is the number of offspring a woman has over her life that are potentially able to reproduce. Because of this definition, all children under 15 are discounted in the model because their reproductive potential is really not realizable until age 15. If γ is set to one, this is to say that the mother is awarded the full reproductive potential of children over 15. If γ is less than one, this discounts even older children’s reproductive potential. In this way we can model the “grandmother” effect. If the mother dies too early, she can not claim the full reproductive potential of even children over 15. Equivalently, she must live long enough to help children over 15 reproduce successfully to claim this portion of her ELR, no matter what form this “help” takes. Again, we make no effort to estimate γ but use the flexibility of the dynamic modeling approach to investigate how much reproductive potential must be lost if a woman does not “grandmother” to make the trade off between existing and future reproduction great enough to forgo the latter. The bottom graph in Figure 3.4 shows the region in β - γ parameter space for which the onset of menopause around 45 or 50 is optimal when the Case 1 mortality curve is used. The Case 2 mortality curve produces the same results except that the age of last birth is five years later than for Case 1. This is reassuring, the timing for the increase in mortality due to childbirth is not critical to producing menopause. Even a difference of more than 30 years in the time of onset of increased mortality only extends the age of last childbirth by five years.

If we examine the parameter space plot we can get an idea of the importance children in the 5-15 and over 15 age classes play in determining the mother’s life history strategy. If $\beta \leq 0.05$ no “grandmother” effect is needed to select for menopause. In this case the

Figure 3.4: Decision dependent mortality curves (top) and $\beta - \gamma$ parameter space (bottom) showing parameter combinations for which cessation of reproduction around 45 to 50 is optimal.

immediate danger of losing immature children is enough to shut down reproduction in the mother. As discussed earlier this value of β is probably not reasonable. For $\beta = 0.2$, at the low end of the reasonable range, menopause would be selected for γ values up to approximately 0.97. At the high end of reasonable values for β (around 0.7) menopause is selected for when γ is between 0.3 and 0.4.

The interpretation of these combinations of parameter values is as follows: if children have a fair chance of surviving to 15 and children over 15 have a fair chance of reproducing successfully without the mother, then it pays to take the risk of having more children rather than to devote energy to existing children. If γ is one, then it pays to have more children for most reasonable values of β . Once even a small "grandmothering" effect is added by reducing γ to 0.97 and there is a significant risk to children under five, the combination of these effects is enough for menopause to be selected for. Then, as the probability of children under 15 surviving to 15 increases, an increasing "grandmother effect" must be present before it is worth while to devote time to existing offspring at the expense of having more. For example if $\beta = 0.4$, suggesting that youngsters have a pretty good chance of surviving without the mother, a strong "grandmother effect", $\gamma = 0.6$ (adult children's reproductive potential is only 60 % of what it would be if their mother helped them reproduce) is required to make early reproductive senescence optimal. In conclusion, the model suggests that a combination of mothering and grandmothering effects is required to select for menopause. Unless children under 15 have little chance of survival if their mother dies, a woman must increase her offspring's reproductive potential significantly before it pays for her reproductive system to prematurely shut down.

Figure 3.5 shows the optimal life history for a woman under the assumption that childbirth increases her mortality risk with $\beta = 0.4$, $\gamma = 0.6$, and using the Case 2 mortality curves. The optimal first birth is at age 13, and the optimal last birth is at age 52. The estimate for first birth is five years earlier and the last is 17 years

later than observed values. The reasons for this discrepancy are twofold. First, this trajectory is optimal, not what would be observed for a !Kung woman *attempting* to achieve the optimal case. Second, there are surely other factors that play important roles in determining the optimal life history trajectory that have not been included in the model. It is interesting to note however that birth spacing remains unaffected by these considerations. This illustrates the interplay of the physiological processes that are not in the direct control of the individual and those that are. The !Kung frequently engage in sexual activity long before they actually have children (Howell, 1979) so there is no behavioral mechanism to prevent early pregnancy. The evolutionary response is therefore physiological in nature. Similarly, infant suckling can not suppress ovulation for the extended period at the end of a woman's reproductive career; again, a direct physiological means is necessary. Birth spacing on the other hand is controlled by a behavioral mechanism and is independent of these other two mechanisms.

Figure 3.5: Life history trajectory under the decision dependent mortality assumption.

3.4 A life history trajectory with stochastic events

Up to now, I have been stressing that all the life history trajectories generated by the model have been examples of optimal trajectories, i.e. the woman and her children survive each period. The observed life history trajectories of !Kung women almost surely would not resemble those discussed herein. This does not mean, however, that !Kung women are not following an approximately optimal trajectory given certain stochastic events. Such events might include the death of children, divorce, death of spouse, climatic variation, and so on. The state dependent nature of the dynamic approach allows for trajectories to “adjust” to these events. For example if a woman’s child dies, her state changes. The dynamic model predicts the optimal trajectory beginning at her new state until the terminal time. So although not optimal, her new trajectory is as close to optimal as possible given this stochastic event.

Using the model one could investigate the effects of all the different possibilities listed above but here we investigate only one, the death of a child. We investigate how the trajectory changes given the death of a child in two age classes. The results of these two simulations are shown in Figure 3.6. The top trajectory is the Base Case run with $\rho_{cd} = 0.6$, a backload function similar to Case 2 in Figure 3.1, the mortality curve based on actual !Kung data, the Case 2 decision dependent mortality shown in Figure 3.4, $\beta = 0.4$, and $\gamma = 0.6$. The choice of age classes to test was motivated by the idea that if a woman loses an older child, she probably would not add a new child immediately because the demands placed on her by existing younger children would preclude such an action, i.e. the backload demands from older children are less than for younger children. If one of her younger children dies, however, immediately adding a new child would not change her backload demands and thus would be expected.

The model predictions agree with these hypotheses. Case 1 in Figure 3.6 depicts the

Figure 3.6: Life history trajectory including the stochastic event of the death of a child in two age classes: Case 1 – five or younger, Case 2 – six to fifteen.

situation in which a child three years of age dies when the mother is 33. She immediately adds a new child and shifts her fertility schedule beginning in year 34 in the sense that the times of births no longer agree with the Base Case. Case 2 on the other hand depicts the situation where a ten year old child dies. The mother does not immediately add a new child but maintains the four year interval. Although she has one less child over all, from year 34 on her trajectory matches the Base Case in terms of timings of births. Although not shown, if a child over 15 dies, the result is the same as for Case 2. To conclude, a mother will only add a child if the child that it replaces is five or younger, she will not replace older children.

3.5 Discussion

3.5.1 Dynamic State variable modeling

The original intent of constructing a dynamic programming model of !Kung women's reproductive behavior was to attempt to build an adaptive model to explore !Kung birth spacing behavior related to the findings of earlier work by Lee (1972), Blurton Jones and Sibly(1978), and Blurton Jones(1986, 1987). The model does indeed support this earlier work by showing that if the goal is to maximize ELR, the !Kung women are behaving approximately optimally in their reproductive decisions. A second objective in the construction of this model was to attempt to more clearly define the components of the !Kung's birth spacing adaptation. The quantitative nature of the dynamic state variable modeling approach allows the components of the adaptation to be examined more closely.

In exploring the model under several different conditions, I was able to show that the optimal birth spacing predicted by the model is robust to varying input parameters. Specifically, I found that no assumptions about either set limits to backload or specific characteristics about the response of foraging success to backload are critical to produce results consistent with field observations. All that is required is the rather mild assumption that foraging success decreases in some way as backload increases. Instead, varying these parameters merely produced mild variation consistent with observed variation in the field. This result suggests that differences in individual backload curves could be a source of observed variation in IBIs. This is a major difference between my approach and the earlier efforts of Blurton Jones and Sibly (1978) which assumed a (very difficult to quantify) set limit to backload. I believe their assumption was reasonable, but it is comforting to establish by a different approach that it is not critical to the model.

By incorporating actual !Kung mortality data from Howell's demographic work (1979)

into the model, it was shown that mortality does not play a major role in birth spacing but that backload and foraging considerations are much more important factors. Even when the model was run using the hypothetical very high mortality population, only the first and last intervals were shortened, again illustrating the robustness of the birth spacing predictions made by the model. Only when decision dependent mortality was included did the overall life history strategy change. This change was not manifest in different IBIs but rather in the timing of first and last births. By exploring model predictions for different parameter combinations of β and γ which can be interpreted as a measure of the importance of mothering and grandmothering effects respectively on existing fitness units, it was possible to show that the onset of menopause could be adaptive in certain situations. If the society in which the woman lives is such that the chances of survival of young children are low if their mother dies, menopause can be adaptive even without a "grandmother effect". There seems to be some evidence that the !Kung may be such a society. Unfortunately, there is no quantitative data to support the particular choice for β necessary to give menopause adaptive value without some effect from grandmothering. If grandmothering effects are included by allowing γ to take on values less than one, the model predicts menopause over a wide range of reasonable values for both parameters. Unfortunately, although reasonable, there is no way to support any particular parameter choice in this case so the model results are speculative. If work could be conducted to establish values for these parameters for hunter gather groups, then the model results could be improved greatly.

3.5.2 'Whole-Life' model implications

As mentioned earlier, dynamic programming is a whole-life approach. This allows for the construction of and comparison of entire life history trajectories which aids in making more subtle points salient, for example the time dependence of IBIs. Notice that for

all of the life history trajectories generated by the model, IBIs change over the course of a woman's life. In every case the earlier intervals are shorter which agrees with the previous results of Blurton Jones (1987). Further, the interplay of culture and society was illustrated by the critical dependence of four-year IBIs on the level of responsibility mother has in providing food for her young. The model suggests that such an adaptation could only be expected in a society where each mother is primarily responsible to provide for her children. If society were to change, the adaptive value of four-year IBIs would be lost. This was illustrated by the shortening of birth spacing intervals when ρ_{cd} was reduced below a certain critical level (see Figure 3.2). This result is consistent with the observed shortening of IBIs associated with the transition of societies from hunting and gathering to agriculture.

One possible 'whole life' suggestion is made by the output in Figure 3.2 concerning the effects of birth spacing strategies on child rearing and subsequent effects on society as a whole. Note that a !Kung woman would never have several children under eight at any one time. She would have at most two. Western cultural practices often result in closer birth spacing than that of the !Kung. This puts parents in the position of having many more than two children under eight years of age at any one time. The ability of parents to provide emotional nurturing may be compromised when they are overwhelmed by too many young children. By spacing children more widely, parents possibly would be able to devote more time and effort to any one child. This additional time and effort might improve the emotional stability of the child and in turn of society as a whole. This possible adaptive value of !Kung birth spacing strategies may be being tested presently in western society. This 'whole-life' aspect of dynamic programming makes it a possibly valuable tool in the continued development of a sociobiological perspective on demography, adding to work already begun (Blurton Jones, 1989).

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