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The marginal valuation of fertility

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ABSTRACT

Substantial theoretical and empirical evidence demonstrates that fertility entails economic, physiological, and demographic trade-offs. The existence of trade-offs suggests that fitness should be maximized by an intermediate level of fertility, but this hypothesis has not had much support in the human life-history literature. We suggest that the difficulty of finding intermediate optima may be a function of the way fitness is calculated. Evolutionary analyses of human behavior typically use lifetime reproductive success as their fitness criterion. This fitness measure implicitly assumes that women are indifferent to the timing of reproduction and that they are risk-neutral in their reproductive decision-making. In this paper, we offer an alternative, easily-calculated fitness measure that accounts for differences in reproductive timing and yields clear preferences in the face of risky reproductive decision-making. Using historical demographic data from a genealogically-detailed dataset from 19th century Utah, we show that this measure is highly concave with respect to reproductive effort. This result has three major implications: (1) if births are properly timed, a lower-fertility reproductive strategy can have the same fitness as a high-fertility strategy, (2) intermediate optima are far more likely using fitness measures that are strongly concave with respect to effort, (3) we expect mothers to have strong investment preferences with respect to the risk inherent in reproduction.

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1. Introduction

The highest average completed fertilities for human populations are still well below the physiological maximum (Wood, 1994). Most behavioral ecologists explain this disparity between biological potential and behavioral attainment by invoking trade-offs between quality and quantity of offspring under conditions of limited resources that create stabilizing selection for a fitness-maximizing intermediate value of offspring born (Lack, 1947; Smith & Fretwell, 1974). Models of intermediate optimal fertility, like the Lack Clutch, are appealing to behavioral ecologists because of the clear evidence for measurable demographic, energetic, and economic trade-offs associated with human reproduction in a wide range of societies.

One of the most important trade-offs is between fertility and resource production (Van Noordwijk & Dejong, 1986): some kinds of work provide more resources to support future reproduction or investment in existing offspring, but entail costs for current reproduction. Such trade-offs solved in favor of investments in work tend to increase interbirth intervals (IBIs) and thus lower fertility. For example, among Indian and Philippine women, autonomy and employment result in longer IBIs (Nath, Land, & Goswami, 1999; Upadhyay & Hindin, 2005). In Ghana, women who engage in “modern” types of work have significantly longer IBIs than those engaged in agriculture or “traditional” work and both types of

employment produce longer IBIs than no employment (DeRose, 2002). In 19th century Belgium, stable work that generated higher earnings for women resulted in a slower pace of reproduction, while work that could be done at home for lower pay (lace-making) had little effect on IBIs (Van Bavel & Kok, 2004). !Kung forager women faced backload and travel constraints during the dry season when they traveled more than 12 kilometers to collect mongongo nuts and these trade-offs may have played a large role in their lengthy average IBIs of 48 months (Blurton Jones & Sibly, 1978; Blurton Jones, 1986; Anderies, 1996). Such trade-offs in work efficiency diminished when !Kung become more sedentary, and IBIs subsequently decreased to an average of 24 months (Howell, 1979). Recent work on fertility and economic constraints shows substantial economic cost of higher fertility in the contemporary United Kingdom (Lawson & Mace, 2010) as well as reduced ability of parents to directly invest in the enrichment of the children in large families (Lawson & Mace, 2009). Similarly, a study from Sweden shows that high fertility is associated with diminished socioeconomic status outcomes (Goodman, Koupil, & Lawson, 2012).

Another significant trade-off is that between fertility and offspring survival. While very short IBIs might provide for the highest levels of fertility, they also carry costs for both maternal and child health. IBIs of less than 18 months are associated with small size at birth, stunting and underweight, and are one of the major causes of infant mortality (Hobcraft, MacDonald, & Rutstein, 1983; Conde-Agudelo, Rosas-Bermudez, & Kafury-Goeta, 2006, 2007), increasing the risks of death significantly regardless of a mother's age or socioeconomic status (George, Everson, Stevenson, & Tedrow, 2000; Whitworth &

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Stephenson, 2002; Rutstein, 2005). Short birth intervals also jeopardize the sunk investment of already-born children because of early cessation of nursing and the demands of pregnancy and lactation on mothers' energy and time budgets (Hobcraft et al., 1983; Hagen, Barrett, & Price, 2006). Short IBIs increase mortality by increasing nutritional stress to the infant, primarily through reductions in nursing (Manda, 1999; Whitworth & Stephenson, 2002; Gibson & Mace, 2006), but nutritional deficiencies and maternal depletion may also play a role (Bhalotra & van Soest, 2008; van Eijnsden, Smits, van der Wal, & Bonsel, 2008). Fertility has recently been shown to have a negative effect on child survival in a comprehensive analysis of studies from Sub-Saharan Africa (Lawson, Alvergne, & Gibson, 2012). Here, the mechanism producing the trade-off appears to be sibling competition.

Substantial evidence suggests that resource limitation can intensify these somatic investment trade-offs. Conditions of social and economic stress, both chronic and acute, lengthen IBIs (Anderton & Bean, 1983; Boserup, 1985; Gurmu & Mace, 2008) and those who lack risk-buffering mechanisms often suffer more (Van Bavel & Kok, 2004; Bengtsson & Dribe, 2006). For example, savannah Pumé women in Venezuela who experience seasonal nutritional stress have longer IBIs than river Pumé women who are buffered from such variability. River Pumé have lower infant mortality and shorter IBIs leading to a greater number of surviving offspring (Kramer & Greaves, 2007). Nineteenth century Belgian families reliant on a husband's unstable, badly paid job of day laborer also experienced longer IBIs relative to those supported by more stable, highly paid employment (Van Bavel, 2003). Such patterning may either be a simple function of physiological constraints on fertility such as lactational amenorrhea or nutritionally-mediated subfecundity (Ellison, Panter-Brick, Lipson, & O'Rourke, 1993), or the product of intentional spacing attempts by mothers facing fertility trade-offs (Anderton & Bean, 1985; Van Bavel, 2004). Using the Utah Population Database, Bean, Mineau, and Anderton (1990) showed that IBIs for mid-parity women increased during the economic crises of the Panic of 1893 and the banking crisis that inaugurated the Great Depression. These increases were particularly strong for the Great Depression, with intervals increasing from 3 to 34%.

There is thus extensive evidence for the existence of trade-offs between maternal production and maternal reproduction, maternal fertility, and offspring mortality. Both the extent and magnitude of these trade-offs suggest that there should exist some optimal level of fertility (i.e., below the physiological maximum) relative to these trade-offs that maximizes long-term fitness. However, such intermediate optima have been difficult to find in human populations (Borgerhoff Mulder, 1998).

Understanding lower-than-maximum fertility is a life-history problem of reproductive effort. Intermediate fertility corresponds to a reduced reproductive-effort tactic. In their pioneering paper, Gadgil and Bossert (1970) note that intermediate levels of reproductive effort can only be optimal when there are diminishing marginal returns to effort. The typical measure of fitness in human populations, lifetime reproductive success (LRS), does not show diminishing marginal returns to increasing fertility as it is a linear measure of fitness with respect to fertility. Fitness increases identically by unity with each additional birth so that the second derivative with respect to effort (i.e., the curvature of the fitness function) is zero. Other similar measures such as mortality-discounted LRS or the number of grandchildren may show a degree of concavity with fertility, but this is typically modest and fitness is typically quite linear across a wide range of observed fertilities (Kaplan, Lancaster, Bock, & Johnson, 1995; Strassmann & Gillespie, 2002; Lawson et al., 2012). Other fitness measures frequently used in population biology can show a substantial degree of concavity with respect to fertility and are thus of great interest for life-history studies of trade-offs.

2. On fitness measures

Historically, the most common measure of fitness in the behavioral ecology of human life histories is individual LRS (Barkow, 1977; Turke & Betzig, 1985; Boone, 1986; Chagnon, 1988; Volland, 1988; Cronk, 1989; Borgerhoff Mulder, 2000). The use of LRS as a fitness measure implies that there are no inter-temporal preferences for births. In other words, births are perfectly substitutable for one another, conditional on maternal survival. Every child counts as much as every other child, regardless of when it was born or the mother's age when she gave birth. Furthermore, using LRS as a fitness measure entails the assumption of population stationarity – births are exactly offset by deaths and population size remains constant. When a population is not assumed, *a priori*, to be stationary, LRS is not an appropriate fitness measure (Caswell, 2001). The population-level expected fitness that corresponds to LRS is the net reproduction ratio, R_0 , a generational measure of mean fitness. R_0 is also the ratio of the population size from one generation to the next as shown by the identity from stable population theory

$$R_0 = \lambda^T, \quad (1)$$

where λ is the intrinsic rate of increase (i.e., the exponentiated instantaneous rate of increase, r) and T is the generation time (i.e., the mean age of childbearing).

Sophisticated studies will discount the count that determines LRS by the probability of child survival under different fertility regimes (e.g., Lawson et al., 2012), but this does not change its dynamic properties. The use of LRS as a fitness measure implies that the timing of reproduction does not matter for fitness. In a population that is growing by some period rate λ , the size of the population will increase by a factor of λ per period meaning that a delay of reproduction by t periods needs to be discounted by a factor of λ^t . Thus, all things being equal, it pays to reproduce early. This population discounting induces time preferences in reproduction on the part of parents. A parent prefers a living child to one not yet born because the living child has higher reproductive value. Note that the Fisherian notion of reproductive value is really a way of accounting for time preference in reproductive decision-making (Fisher, 1958).

For an age-structured population, mean fitness is given by the unique real root, λ , of the Euler-Lotka equation, written here in discrete-time form,

$$1 = \sum_{x=\alpha}^{\beta} \lambda^{-x} l_x m_x, \quad (2)$$

where α is age at first reproduction, β is age at last reproduction, l_x is age-specific survivorship and m_x is the fertility rate in age-class x .

The simplest way to calculate λ is via the Leslie matrix, a compact means for representing the age-specific mortality and fertility schedules that are applied in each time step to a vector of the population age structure. A Leslie matrix contains the age-specific fertility rates along the first row, and the probabilities of surviving from one age class to the next along the subdiagonal. Everywhere else, there are zeros. In addition to being a convenient and compact means of representing the demography of an age-structured population, the Leslie matrix provides a wealth of dynamical and evolutionary information (Jones, 2009). The mean fitness of a population characterized by a Leslie matrix \mathbf{A} is given by the dominant eigenvalue λ_0 of the matrix. This is the same as the real root of Eq. 2. λ_0 is the asymptotic growth rate of the population (i.e., once it has converged on its stable age distribution). Fitness is thus a growth rate. To maintain relative representation in a population, one must pace reproduction so one's lineage grows at a rate at least equal to the population at large.

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