

HUMAN LIFE HISTORY VARIATION AND SEX DIFFERENCES IN MORTALITY RATES

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Abstract

Sex differences in mortality rates stem from multiple causes that are best understood when integrated in an evolutionary life history framework. This study investigates the relationship of sex differences in mortality rates across nations to indicators of the life history characteristics of populations. Controlling for gross national income per capita, the overall sex difference in mortality rates was directly related to the adolescent fertility rate, the percentage of newborns with low birth weight, and was inversely related to the average mother's age at birth of first child. Sex differences for behavioral (external) causes of mortality were also directly related to the difference between the average age of males and females at first marriage. These findings indicate that the sex difference in mortality rates is an important life history indicator, and is related to reproductive patterns. Greater sex differences in mortality may reflect greater degrees of male competition for resources, social status, and mates.

Keywords: life history, mortality, sexual selection, sex differences

Introduction

Evolutionary Life History Theory (LHT) is a powerful framework for understanding behavioral strategies as functional adaptations to environmental conditions. LHT illuminates how physiological and behavioral strategies reflect tradeoffs of effort across the lifespan and how these strategies are adaptive given the environmental conditions in which organisms live (Roff, 1992; Stearns, 1992). These inherent trade-offs include somatic vs. reproductive effort, mating vs. parental effort, current vs. future reproduction, and quantity vs. quality of offspring (Roff, 1992; Stearns, 1992).

Species living in environments with resource instability and unpredictability of future events (due to high predation rates, for example) will tend to evolve clusters of traits associated with rapid and prolific breeding with relatively low investment in offspring (MacArthur & Wilson, 1967; Pianka, 1970). Species living in stable and predictable environments instead have a long-term strategy of investing more so in

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somatic and parental effort with lower reproductive rates and longer intergenerational times than those in less predictable and stable environments. Species living in resource instable and unpredictable environments are said to be "r-selected" (r is the growth rate of the population), species living in more stable and predictable environments are said to be "K-selected" (K is the carrying capacity of the population). The terms fast and slow life histories are also used respectively, especially when describing individual differences within species.

Hormonal and endocrine mechanisms (such as testosterone levels) moderate and may mediate many sex differences in life history traits as well as aspects of phenotypic plasticity (Sinervo & Svensson, 1998). These systems are likely related to both the development of physical and social competencies associated with male-male competition and the higher mortality rate and shorter maximum life span for males (Geary, 2002).

In most species females make a greater parental investment than males, and are more discerning in choice of mates, so male fitness depends on success in competing for reproductive access to females (Bateman, 1948; Darwin, 1871; Trivers, 1972). The fitness benefits of both being chosen as a mate by a female and of winning male-male competitions tend to select males for higher levels of risk-taking and decreased investment in repair capacity and disease prevention (Daly & Wilson, 1978; Møller, Christie, & Lux, 1999). In brief, males in many species are selected more strongly than females are for mating success at the expense of health and longevity. In species where males provide parental care, protection or resources, this shapes female choice for males with higher than average such capacities (Mealey, 2000). The current study reveals that the sex difference in human mortality rates may be an important indicator of the life history characteristics of a population.

Sex differences in mortality rates

The discrepancy in lifespan between men and women has been recognized since at least 1662 (Lopez & Ruzicka, 1983), but only in the past half-century have biologists focused on how these differences could result from differential sexual selection pressures on male competitiveness and risk taking (e.g., Bateman, 1948). Modern researchers attribute the higher incidence of male mortality to an interconnected set of biological and behavioral proximate causes (Carey, Leido, Orozco, Tatar, & Vaupel, 1994; Hazzard, 1990; Kraemer, 2000). Evolutionary researchers have described how sex differences in mortality are explained by traits shaped by sexual selection interacting with cultural and environmental factors (e.g., Daly & Wilson, 1985; Kruger & Nesse, 2004, 2006).

In humans, mortality rates are higher for men than for women across the lifespan, especially for behavioral (external) causes of death, and exhibit a peak sex difference in young adulthood (Kruger & Nesse, 2004, 2006). It is not surprising that the sex difference in human mortality rates peaks when males reach reproductive maturity and compete intensely for resources, social status, and mates. The discrepancy between male and female mortality rates is higher for those of comparatively lower socioeconomic status and the unmarried (Kruger & Nesse, 2006). These results suggest that males experiencing greater uncertainty or deprivation in social status and resources may develop riskier life strategies, leading to higher mortality rates. Economic uncertainty and variation and skew in social status and resources is related to the extent of mortality from risky male behavior and the impact of stress on physiological susceptibility to internal causes of death (Kruger & Nesse, 2007). When there is greater skew in male attributes

such as social status and economic power which are historically related to reproductive success, men are more likely to die from riskier behavioral patterns as well as the physiological embodiment of the stress of competition.

Life history and mortality

Mortality patterns are an integral part of life history, along with size at birth, growth pattern, age and size at maturity, allocation of reproductive effort, age schedules of birth, and number and sex ratio of offspring (Low, 1998). The relationship between life history and sex differences in mortality is evident when comparing fertility patterns and mortality patterns in hunter-gatherer and modern post-industrial populations. In hunter-gatherer populations, male mating effort is often high throughout adulthood (e.g., Hill & Hurtado, 1996), and male fertility is substantially higher in middle and late adulthood than for modern populations (Tuljapurkar, Puleston, & Gurven, 2007). Unlike in modern populations, which experience a decline in the sex difference in mortality rates after young adulthood, the mortality disparity remains high throughout the adult lifespan in hunter-gatherer cultures (Kruger & Nesse, 2006).

Optimal age at first birth is the result of tradeoffs in fertility and mortality; the greater the adult mortality rate, the earlier the age at first birth (Low, Simon, & Anderson, 2002). Women who grow up in contexts with high risks of violent death begin reproducing at an earlier age and have more children during their reproductive lifespan than do women who grow up in low-risk, high resource ecologies (Wilson & Daly, 1997). These strategies reflect an emphasis on current opportunities and a discounting of future possibilities. Under these conditions, men may focus more so on mating effort as they may have more to gain from increasing the quantity of offspring than investing paternal effort in the quality of offspring, given their uncertain futures. Higher levels of male mating effort correspond with higher levels of male competition, and the degree of male competition over limited resources is related to the risks of violent death (Wilson & Daly, 1997; Kruger & Nesse, 2006, 2007). Thus, the sex difference in mortality rates is expected to correspond with earlier average fertility incidence, as indicated by the adolescent fertility rate. The sex difference in mortality rates is also expected to be inversely to the average mother's age at birth of first child.

Litter biomass, or biomass per reproductive bout, varies substantially among mammalian species (Low, Simon, & Anderson, 2002). Single births are the norm for humans, but the occasional twins each weigh less than single birth individuals, indicating trade-offs in finite investment. Size at birth is a life history trait considered central to any analysis (Low, 1998). Per capita somatic investment declines when adult mortality rates are high, the ability to invest parentally is low or uncertain, and offspring that require high levels of parental investment are at risk (Low, Simon, & Anderson, 2002). Greater female investment in the quality of offspring (at the expense of investment in quantity) may suggest greater expectations for paternal investment. Paternal investment is inversely related to male mating effort, thus somatic investment in offspring should be inversely related to the sex difference in mortality rates. Thus, a greater difference in mortality rates will be directly related to the percentage of newborns with low birth weight.

In species with greater male-male competition, males grow more slowly and evidence both a longer period of rapid growth (i.e. the growth spurt), and a longer overall

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development period than females. For example, male development takes twice as long in the elephant seal, where males compete for harems and 80% of males die before reproducing (Harvey & Clutton-Brock, 1985). Peahens begin to reproduce at 2 years of age, although peacocks do not develop their full trains until 3 years of age and do not establish a lekking display site until 4 years of age (Manning, 1989). Some males successfully mate at 4, whereas other males do not mate until later years and some not at all- thus lengthening of the developmental period and increasing the size at maturity.

Sex differences in the age of first reproduction are related to the degree of male competition across human societies (Low, 1998). The intensity of competition for cultural resources and social status is predicted to result in corresponding delays in men's reproductive opportunities beyond the age of physical maturation, older men will fare better in both female choice and male-male competition (Geary, 2002). Thus, the degree of male competition for resources and social status, as indicated by the difference between the average age of males and females at first marriage should be directly related to the magnitude of sex differences in mortality rates.

In summary, the sex difference in mortality rates should be directly related to the adolescent fertility rate, the percentage of newborns with low birth weight, the difference between the average age of males and females at first marriage, and should be inversely related to the average mother's age at birth of first child. These relationships may be particularly strong for the sex difference in mortality rates from direct behavioral (external) causes.

Method

The M:F MR (male to female mortality ratio, the ratio of male to female mortality rates) was calculated with the most recent data available from the WHO Mortality Database (World Health Organization, 2007), 80% of data were from 2000-2003 with the remainder from 1991-1999. This included the overall M:F MR, the M:F MR for behavioral causes (external causes, including homicides, violence, accidents, and suicides), and the M:F MR for internal causes (those not directly caused by behavior). Mortality data was matched with corresponding data from the Central Intelligence Agency's (2007) *World Factbook*. These data included the total fertility rate, adolescent fertility rate, percentage of newborns with low birth weight, average mother's age at birth of first child, average age of males and females at first marriage, and gross national income per capita.

Results

The overall sex difference in mortality rates was directly related to the total fertility rate, $r(75) = .379, p < .001$, the adolescent fertility rate, $r(75) = .586, p < .001$, and the percentage of newborns with low birth weight, $r(75) = .432, p < .001$. Controlling for gross national income per capita, the relationship between the overall M:F MR (male to female mortality ratio) and adolescent fertility rate, $r(63) = .251, p = .044$, and the percentage of newborns with low birth weight, $r(63) = .396, p < .001$, remained significant. The relationship between the overall M:F MR and the total fertility rate approached significance, $r(63) = .242, p = .052$, when controlling for gross national income per capita.

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The relationship between the adolescent fertility rate and the M:F MR for behavioral (external) causes was particularly strong, $r(63) = .487$, $p < .001$ (controlling for gross national income per capita). The relationship between newborns with low birth weight and the M:F MR for non-direct behavioral (internal) causes was particularly strong, $r(63) = .548$, $p < .001$ (controlling for gross national income per capita).

Controlling for gross national income per capita, average mother's age at birth of first child was inversely related to the overall M:F MR, $r(27) = -.443$, $p = .016$, and the M:F MR for behavioral (external) causes, $r(27) = -.469$, $p = .010$. The difference between the average age of males and females at first marriage (indicating the degree of male competition for resources and social status) was directly related to the behavioral cause M:F MR, $r(34) = .364$, $p = .034$. The relationship with the internal cause M:F MR only approached significance, $r(34) = .326$, $p = .060$, however this may be due to the scarcity of countries where data are available.

Discussion

The results confirmed the expected relationships between mortality patterns and other life history parameters and are consistent with the notion that sex differences shaped by natural selection interact with aspects of the current environment to result in mortality rates considerably higher for men than for women. These findings indicate that the sex difference in mortality rates (the M:F MR) is an important human life history indicator and is related to reproductive patterns. Greater sex differences in mortality rates may reflect greater degrees of male competition for resources, social status, and mates. The patterns seen here suggest that excess male mortality is directly related to male mating effort and inversely related to paternal investment. This pattern has been documented across anthropoid primates, where the degree to which males invest in offspring is directly related to their longevity (Allman, Rosin, Kumar, & Hasenstaub, 1998).

The current results further support the notion that there are individual differences in life history strategies within species, which are contingent upon environmental conditions (Rushton, 1985). The constellation of cross-species differences associated with the intensity of male-male competition was found across populations of humans. These include relationships between female allocation of somatic effort and reproductive timing with male trade-offs in reproductive effort. It is remarkable that there were strong associations across male and female physiological characteristics and behavioral characteristics. Average female somatic investment in a developing fetus was strongly related to male somatic investment, as indicated by mortality rates from internal causes. The adolescent female fertility rate was strongly related to male mortality rates from behavioral causes, indicating convergence in risky behavioral strategies across sexes. Future research may clarify the causal pathway between ecological conditions, life history investment strategies, and mortality patterns.

As early as 1929, demographers noted a transition from high fertility and mortality rates in pre-industrial countries to low fertility and mortality rates in industrialized countries (Thompson, 1929). This "demographic transition" entailed a shift from a triangular population pyramid to one that was more rectangular, first in industrial Europe during the 19th Century and in other industrializing countries in the 20th Century. The most developed countries, especially those with restricted immigration, are witnessing fertility rates below the replacement rate (for more discussion, see Luttbeg,

Borgerhoff Mulder, & Mangel, 2000). Access to modern contraception, progressive social norms, and the increasing importance of and extent of tertiary education are resulting in the delay or avoidance of reproduction in post-industrial nations. The increase in altriciality is becoming so extreme in Japan that parents are surreptitiously using matchmaking services for “parasite children” who are still living at their parents’ home in their 30s (McNeill, 2008). Some of the less developed areas of the world have yet to make or complete this transition, and the national degree of demographic transition may partially underlie the cross-national variation in life history patterns examined in this study.

Limitations to the data should be noted. The WHO Mortality Database provides statistics for a range of nations; however most of these nations are developed or developing. Most of the nations with the least economic and technological development are not included. This calls into question whether the database is truly representative of the entire human population, although it is not a requirement for tests of life history hypotheses. The restricted range of populations may make predictions more difficult to confirm due to reduced life history variability. Not all indicators are available for every nation, particularly age at marriage and gross national income per capita. Controlling for gross national income per capita provides a more stringent test of hypotheses, however it would be desirable to have more detailed data that could better illustrate the relationship between economic factors and life history patterns.

Also, the data available are at the national level. Few nations are demographically and ethnically homogenous. Thus, there is likely life history variation within nations that is lost when the data are collapsed at the national level. It would be very helpful to have life tables for numerous specific populations, such as those Hill and Hurtado (1996) have developed for the Ache. The combination of restricted national range, elimination of within nation variance, and reduced sample size due to missing data create a more difficult test for the hypotheses. Thus, it is all the more remarkable that significant results were found.

Overall, the results suggest that the Male to Female Mortality Ratio (M:F MR) should be recognized as an important life history indicator of a population. This simple demographic statistic may serve as a heuristic for the intensity of male competition, the relative male allocation to mating and parenting effort, and future discounting in male behavioral and physiological strategies. The study also demonstrates, once again, the utility of an evolutionary framework for explaining the relationship amongst seemingly divergent health and demographic characteristics of a population. [22]

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