
Sex Ratio and the Timing of Pubertal Maturation in Girls: A Life History Approach

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Sex ratio, defined as the ratio of males to females in a given population, is an important factor influencing a variety of mating and parental behaviors in both animals and humans. In this review, I draw on the framework of Life History Theory, which predicts that mating and parenting decisions are influenced by environmental cues about resource scarcity, to propose that sex ratio may serve as an indicator of resource scarcity – particularly the likelihood of finding and keeping a long-term mate. I therefore suggest that skewed sex ratios should influence mating behaviors in the same way that other scarce resources do. Specifically, in female-skewed environments where the availability of long-term mates for females is limited, women may experience earlier pubertal timing, because (1) it lengthens their reproductive lifespan and (2) energy put into embodied capital would be better spent on intra-sexual competition for mates and reproductive effort.

The sex ratio is demographically defined as the number of men per 100 women in a given population (Guttentag & Secord, 1983). A male-skewed sex ratio occurs when there are more males than females, whereas a female-skewed ratio occurs when there are more females than males. Various Asian countries have recently become intensely male-skewed (Gu & Roy, 1995; Guilimoto, 2009; Jha et al., 2006; Sahni et al., 2008). In the most extreme instance, China will soon have an excess of over 40 million men, resulting in a sex ratio of more than 120 men for every 100 women (Hesketh, 2009). Furthermore, variation in the sex ratio is not unique to individual countries; skewed sex ratios often occur within regions of a single country. For example, inequalities within the United States penal system often lead to female-skewed sex ratios in communities of color and lower socioeconomic status (Sampson, 1995). This happens because men of color, and men of lower socioeconomic status, are far more likely to be imprisoned than Caucasian men or men of higher socioeconomic status. These high rates of imprisonment, in turn, lead to an unequal distribution of men and women in communities of color or lower socioeconomic status. These variations in sex ratio may have significant societal consequences: Various research studies have shown a strong correlation between sex ratio, mating/parental investment pat-

terns (e.g., rates of marriage, divorce, and out-of-wedlock births), and spending and career related decisions.

One unexplored and potentially negative consequence of skewed sex ratios is a shift in the timing of pubertal maturation. Pubertal maturation is a complex biological process that marks the shift from the pre-reproductive to the reproductive portion of one's life. Most studies exploring pubertal maturation in girls have measured a single signal of pubertal timing: menarche, or the onset of first menstruation. In the United States mean age at menarche is 12.9 years ($SD = 1.2$) in Caucasian girls and 12.2 years ($SD = 1.2$) in African-American girls (Herman-Giddens et al., 1997). Because most pubertal development occurs before menarche, the onset of menarche serves as an indicator that a girl has reached an advanced level of pubertal maturity.

There is considerable variation in the timing of pubertal development. Some individuals mature early, completing pubertal development in grade school, whereas others do not complete their development until the end of high school or even the beginning of college. Evidence suggests that there are a variety of factors that impact the timing of pubertal maturation, including body mass, psychosocial stress, genetic influences (such as mother's pubertal timing), and nutritional history (reviewed in Ellis, 2004).

There is a less known, but well researched framework for understanding individual differences in pubertal timing: Life History Theory (Charnov, 1993; Roff, 1992; Stearns, 1992). I contend that, when examining sex ratio through a life-history framework, sex ratio in the local population emerges as an additional factor that may impact the timing of pubertal maturation. Because there are negative consequences of early menarche, understanding this previously unexplored connection between sex ratio and pubertal timing is important, and could potentially inform future research in biology and psychology.

Sex Ratio

The study of sex ratio and its relationship to behavior began with the study of animal behavior and evolutionary biology (James, 1987) and has mainly focused on the disparity between the number of males and females of reproductive age in a given population. This is referred to as the operational sex ratio (Emlen & Oring, 1977). Mating behaviors are dependent on the availability of prospective mates, as well as on the level of competition for those mates. The operational sex ratio affects mating behaviors by changing the way one competes for a mate. In most mammals, including humans, females have inherently higher levels of required parental investment than males, due to factors such as length of gestation and lactation (Trivers, 1972). Consistent with these different levels of parental investment, a skewed sex ratio affects each sex differently. Male-skewed sex ratios give females the chance to be more selective about their mates and to require more from potential mates (e.g., greater parental investment, nuptial gifts, higher levels of fidelity). In contrast, female-skewed sex ratios result in less selective females because males don't have to compete as intensely for access to mates.

A large body of correlational research has shown that sex ratio is related to mating/parental behaviors (Barber, 2001; James, 1987; Kruger, 2009; Licher et al., 1992; Pollet & Nettle, 2007). Most sex ratio research has focused on the relationship between sex ratio and its effects on marriage and family. Guttentag and Secord (1983) postulate that, in female-skewed populations, men and women are more likely to stay single, if married are more likely to divorce, and are more likely to have children out-of-wedlock. In support of Guttentag and Secord's hypotheses, Barber (2001) found that

rates of teen out-of-wedlock births rose as sex ratio shifted from male- to female-skewed. Barber explains that the sex ratio serves as an indicator of one's marriage prospects, and interprets the relationship between sex ratio and out-of-wedlock births to mean that the decision to reproduce early (whether conscious or unconscious) is shaped by the existing sex ratio as well as by one's marriage prospects. In addition, male-skewed sex ratios are associated with lower rates of non-marital births, higher rates of paternal investment, higher marriage rates, and fewer out-of-wedlock births to 15-19 year olds (Fossett & Kiecolt, 1999). These particular patterns make sense, given the idea that an unfavorably skewed sex ratio changes the behaviors of the majority sex to match the desires of the minority sex (Kenrick, Li, & Butner, 2003).

Although the vast majority of sex ratio research has been correlational, there have been at least two notable experimental studies of sex ratio. Griskevicius et al. (in press) manipulated sex ratio by showing participants either male-skewed or female-skewed photo arrays, as well as news articles that described the local population as either female-skewed or male-skewed. These primes were followed by questions about financial choices, saving and borrowing habits, and decisions about how financial resources are spent. The authors found that male-skewed sex ratios led men to discount the future, making them more likely to incur debt in an effort to attract a mate and less likely to save money for the future. Male-skewed sex ratios also led men and women to expect men to spend more on dating/mating related expenses such as dinner, gifts, or an engagement ring (Griskevicius et al., in press). This happens because male-skewed environments afford women the luxury of being choosier, while men need to exert more mating effort to attract and keep a mate. Durante et al. (in press) manipulated sex ratio in a similar way, using both picture arrays and news articles that gave the impression of either a male-skewed or female-skewed local population. These sex ratio primes were followed by questions gauging the importance of career versus family. The authors found a significant relationship between female-skewed sex ratios and women's increased desire for a career. Durante et al. suggest that sex ratio cues serve as indicators of the availability of potential romantic partners, as well as how much effort one needs to put into attracting a potential mate. Therefore, when the sex ratio is female-skewed and women have a lower likelihood of finding and maintaining a long-term

mate, they will place more importance on their career.

As discussed, variations in sex ratio influence a number of mating behaviors. However, I propose that researchers may gain an even deeper understanding of sex ratio and mating behaviors by accounting for Life History Theory and its predictions for an individual's reproductive choices. Life History Theory makes very specific predictions about the effects of scarce resources on the timing of various life events, such as puberty or age at first reproduction. In particular, Life History Theory suggests ways in which skewed sex ratios may impact not only general mating behaviors but also pubertal timing.

Life History Theory

Life History Theory (Charnov, 1993; Daan & Tinberg, 1997; Horn, 1978; Roff, 1992; Stearns, 1992) is a major theoretical framework that spans the life sciences. It has been frequently utilized in research regarding animal behavior, anthropology, ecology, evolutionary psychology, and developmental psychology. Life History Theory was developed by evolutionary biologists as a way of explaining how and why organisms allocated their energy expenditures across their lifespan. Life History Theory explains that the timing and duration of specific events in an organism's lifetime have been shaped by natural selection to maximize each organism's fitness. The goal of Life History Theory is to understand variations in life-history strategies – why do some individuals reproduce early and quickly while others delay reproduction in favor of growth and development? Life History Theory analyzes life-history events, or distinct events that define one's life course. The most important of these events are: (1) Age at first reproduction; (2) reproductive lifespan; (3) number and survival of offspring; (4) inter-birth interval; and (5) age at sexual maturity (Charnov, 1993; Roff, 1992; Stearns, 1992).

Central to Life History Theory is a biological fact: Energy used for one task cannot be used for another. Because energy and resources are limited, organisms must make important resource trade-offs (Kaplan & Gangestad, 2005). One can either invest in growth and development – “embodied capital,” such as somatic tissue, strength, speed, skills, and knowledge, which can often be converted into future reproduction – or invest in current reproduction – intra-sexual competition, gestation,

birth, and nurturing of offspring. These approaches, which are labeled “slow” (growth, embodied capital, future reproduction) vs. “fast” (current reproduction), also result in trade-offs between the quantity and quality of offspring (Kaplan & Gangestad, 2005). Individuals taking a fast approach will reproduce early and quickly, which results in a focus on the quantity of offspring. Individuals taking a slow approach often use their embodied capital to focus on the quality and survival of offspring.

How do organisms “decide” between fast and slow life-history strategies? Life History Theory suggests that two main environmental factors determine life-history strategies: the local mortality rate and the availability of resources in the local environment (Stearns, 1992; Kaplan & Gangestad, 2005). When mortality is high and/or resources are scarce, investing energy in somatic effort and embodied capital is not an effective strategy. As the risk of death is much higher when resources are low and/or mortality is high, energy invested in embodied capital will most likely be wasted, since the individual is unlikely to survive in a low resource/high mortality environment. Individuals in these situations are far more likely to take a fast life history approach, reproducing more frequently and earlier in life. In comparison, when mortality is low and resources are plentiful, individuals have the luxury of delaying reproduction; these individuals invest in growth and embodied capital, which allows for higher quality offspring when reproduction does take place.

Life History and Pubertal Maturation

As previously mentioned, two of the most important life history events are (1) age at first reproduction and (2) reproductive lifespan. These two life-history events are affected by a third: age at sexual maturation (menarche). Individuals reaching sexual maturation earlier tend to reproduce earlier. Also, because age at menarche is uncorrelated with age at menopause, earlier age at menarche results in a longer reproductive lifespan (Ellis, 2004; Borgerhoff Muldor, 1989).

However, earlier age at menarche – and a faster life-history approach – is not always beneficial. As stated earlier, an individual's ability to develop “embodied capital” often results in better survival of offspring. In humans, for example, early pubertal and reproductive development can have distinctly negative effects. Early development can di-

vert an individual's resources away from growth before the skeleton has had a chance to fully mature. Early reproduction can also result in reduced metabolic resources available for the gestational development and subsequent nurturing of offspring (Allal, Sear, Prentice, & Mace, 2004). Adolescent mothers, on average, tend to be smaller than adult mothers and convert less of their pregnancy weight gain into fetal weight gain (Garn, Pezick, & Petzold, 1986), lack the full pelvic capacity of adults (Moerman, 1982), and have higher rates of stillbirth, premature delivery, retardation, congenital abnormalities, and low birth-weight than their adult mother counterparts (Black & DeBlassie, 1985; Furstenberg, Brooks-Gunn, & Chase-Lansdale, 1989; Luster & Mittelstaedt, 1993). From a life-history perspective, it appears that girls who mature earlier sacrifice offspring quality in favor of longer reproductive lifespans and larger quantities of offspring.

On the other hand, older mothers – through the development of embodied capital – tend to have acquired a more comprehensive skill-set before having children. Older mothers have more cognitive, survival, mate selection, and parenting skills (Bogin, 1999; Lancaster, 1986; Surbey, 1998). This is clearly demonstrated by lower rates of divorce and single motherhood, more capable parenting, and higher education and economic outcomes among adult mothers (Black & DeBlassie, 1985; Furstenberg et al., 1989; Luster & Mittelstaedt, 1993). Most importantly, children of adult mothers have better social developmental, cognitive, behavioral, and survival outcomes than children of young mothers (Black & DeBlassie, 1985; Brooks-Gunn & Furstenberg, 1986). This distinction between the competence of older and younger mothers has been documented in a variety of animal species (for a review see Promislow & Harvey, 1990). Overall, earlier pubertal and reproductive development often leads to a short-term reproductive strategy, whereas later reproduction leads to a long-term reproductive strategy, as well as greater fitness of offspring (Ellis, 2004).

Keeping the above information in mind, several questions come to mind. When *should* individuals reach sexual maturity? When should one stop utilizing energy for growth and skill development and begin using it for reproductive effort? And finally, what environmental cues and early life experiences trigger that change in energy distribution, leading individuals towards a specific life-history strategy?

Early childhood experiences (those occurring

in the first 5-7 years of life) serve as indicators of the availability and predictability of resources in one's life and environment. These experiences also serve as indicators of the availability and duration of interpersonal relationships. Early childhood experiences deeply impact how one allocates energy and reproductive effort as an adult (Belsky et al., 1991). Essentially, Belsky and colleagues draw on the concept of a sensitive period (the first 5-7 years of life), wherein individuals learn and develop reproductive strategies, to explain how different childhood environments lead to different reproductive strategies as adults.

Ellis (2004) suggests that paternal investment during childhood and beyond also plays a distinctive role in the onset and timing of pubertal development. He draws on the theories of Draper and Harpending (1982, 1988) to explain that the development of a girl's reproductive strategy is particularly sensitive to the role her father takes in the family, as well as her mother's sexual attitudes and behaviors, during early childhood. Ellis discusses the idea that cues about paternal investment are supplied by both an individual's father and mother. The most important cue appears to be father presence versus father absence. Other important cues include: regularity of father-daughter interactions, stability and quality of father-mother relationship, mother's attitudes toward men, and mother's sexual and repartnering activities. These cues transmit reproductively relevant information to young girls.

Ellis et al. (1999) found that girls whose fathers spent more time engaging in their children's care had later pubertal timing, that father-daughter affectionate-positivity was associated with later pubertal timing, and finally, that more supportive father-mother relationships were associated with later pubertal development. Furthermore, Tither and Ellis (2008), through a genetically and environmentally controlled sibling study, found that younger sisters in biologically disrupted families experienced menarche significantly earlier than younger sisters in non-disrupted families. In this particular study, younger sisters (who had greater exposure to father absence than their older sisters) went through menarche approximately 3-4 months earlier than their older sisters. In contrast, younger sisters in non-disrupted families went through menarche 1-2 months later than their older sisters. Tither and Ellis explain that girls who experience disrupted family environments (due to divorce, lack of paternal interaction, and unreliable paternal care) come to understand that male parental investment is not integral to reproduction. These girls

end up developing in a way that accelerates pubertal maturation, speeds up the onset of sexual activity, and leads to fairly unstable pair bonds. Finally, Ellis and Essex (2007), in a longitudinal study of family environment and sexual maturation, found that paternal investment and interaction predicted lower levels of pubertal maturation in daughters, when measured in the seventh grade. Clearly, the presence or absence of a father, in addition to the level of paternal care and interaction, serves as a cue for how likely one is to find and retain a long-term mate, as well as how integral a long-term mate is to reproduction and the raising of offspring.

Sex Ratio and Pubertal Maturation

As research on sex ratio has shown, sex ratio serves as an indicator of one's marital and mating opportunities, similar to the way father presence or absence indicates future marital and mating opportunities. Skewed sex ratios have been shown to impact marriage rates, rates of out-of-wedlock births, and rates of paternal investment (Fossett & Kiecolt, 1991; Barber, 2001; Kruger, 2009). Furthermore, experimental studies of sex ratio have shown that manipulating one's perception of the local sex ratio impacts the effort individuals make towards attracting possible mates (Griskevicius et al., in press), as well as whether individuals prioritize mating over a career (Durante et al., in press). Essentially, mating choices appear to be shaped by sex ratio cues, which serve as indicators of the availability of potential mates.

Research has shown that female-skewed sex ratios make women more likely to take a fast life history approach, reproducing earlier and quicker, without the aid of a long-term mate. Females that were raised in disrupted families without consistent paternal investment take a similar life history approach, in that they mature, engage in sexual activity, and reproduce at earlier ages. While no known research has explored the role that sex ratio may play in the timing of pubertal maturation, I argue that sex ratio may serve as an indicator of one's long-term mating potential in the same way paternal investment does. Life history theory predicts that, in female-skewed environments where the availability of long-term mates for females is limited, women will take a fast life history approach. This would mean earlier age at menarche, earlier age at reproduction, and a focus on quantity over quality of offspring. Women should experience earlier age at menarche because (1) it lengthens their

reproductive lifespan and (2) energy put into embodied capital would be better spent on intra-sexual competition for mates and reproductive effort.

DISCUSSION

While no correlational or experimental research has examined the relationship between sex ratio and pubertal maturation, there are potential benefits of such research in the fields of both biology and psychology. A large body of research reveals that early pubertal maturation in girls is associated with a number of negative biological and social outcomes. Specifically, early-maturing girls are more likely to develop breast cancer (e.g. Kelsey, Gammon, & John, 1993), ovarian cancer (e.g. Wu et al., 1988), and uterine cancer (Marshall et al., 1998); are at higher risk of mood disorder, body image issues and substance abuse (e.g. Ge, Conger, & Elder, 1996; Graber, Lewinsohn, Seely, & Brooks-Gunn, 1997); and have higher rates of spontaneous abortion, stillbirth, teen pregnancy, and low birth-weight babies.

An understanding of the role that sex ratio plays in pubertal timing could have implications for topics such as racial and socioeconomic disparities in incarceration rates. Incarceration rates in communities of color and poor communities often lead to female-skewed sex ratios in those populations (Sampson, 1995), which results in faster life history strategies and perhaps earlier pubertal maturation. This pattern may be cyclical – with fast life history strategy in one generation leading to unstable pair-bonds, less paternal investment, and eventually fast life history strategies in the next generation.

Given that sex ratio is impacted by a variety of factors – including examples such as the aforementioned incarceration rates and the gender preferences of countries like China – it seems imperative to understand whether skewed ratios affect pubertal timing. Further research into sex ratio and pubertal timing could help us understand the biological and psychological implications of skewed sex ratios. Those who make policy decisions, or influence cultural choices, will have more information on the potential negative effects of the skewed sex ratios that follow from their decisions.

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