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MEN AND REPRODUCTION
Perspectives from biological anthropology

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Introduction
In 1840, Charles Darwin recorded the following observations of his first-born son, William Erasmus (Darwin Correspondence Project n.d.):

May 10th. I made loud snoring noise, near his face, which made him look grave & afraid & then suddenly burst out crying. This is curious, considering the wondrous number of strange noises, & stranger grimaces I have made at him, & which he has always taken as good joke. I repeated the experiment.

May 13th. Unexpectedly I came to him, with my back to him, & then stood motionless,—he looked very grave & surprised, & would almost have cried had I not turned round, when his face relaxed into smile. These vague fears, curious.—

Whatever you think of these observations—curious insights, charming science, odd parental emotional distance—they help initiate our foray into biological anthropology perspectives on men and reproduction. For while Darwin was a product of the social and historical moment, his writings were sometimes deeply personal and reveal a profound meaning attached to his own family life (Desmond and Moore 1994). The evolutionary approach that Darwin pioneered is central to biological anthropology. He integrated comparative nonhuman animal research, physiological studies, cross-cultural data, insights from animal domestication, and field observations and experiments to advance a theoretical understanding of natural selection and sexual selection. He showed that this theoretical and empirical work applied to humans too: Humans had evolved, shaping characteristics such as violent behavior, voices, and emotional expressions.

To bring Darwin’s outlook into the present, he would marvel at how much more we now know about men and reproduction. Fossil, archaeological, genomic, physiological, cross-cultural, and increasingly sophisticated (e.g., experimental, statistical, big data) social behavioral research provides remarkable insight into men and reproduction today. Ancient and contemporary DNA shows that some modern humans interbred with and inherited small portions of our genomes from Neanderthals and Denisovans, with genetic material from a finger bone in present-day Russia pointing to the direct product (a daughter) of a Neanderthal mother and Denisovan father (Warren 2018). Large demographic databases reveal age-specific male fertility, also showing that in the waning number of countries permitting polygynous marriage, older
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Men have more kids than in socially monogamous societies (Schoumaker 2019). Brain imaging and hormonal studies reveal how fathering a child can influence a man’s physiology, from activation of the ventral tegmental area to altering his testosterone level (e.g., Feldman 2019; Gettler 2014; Gray et al. 2017; Rilling and Mascaro 2017).

Our aim in the present chapter is to share an accessible and current overview of men and reproduction from a biological anthropology perspective. This means first discussing an integrative evolutionary approach that features life-history theory and highlights distinct but complementary insights concerning adaptive function, phylogeny (evolutionary history), development/life course, and proximate mechanisms (like brain activation and hormones). We advance a model of men and reproduction that places key features of male fertility scheduling (i.e., number and timing of childrearing) and paternal investment in adaptive and phylogenetic scope. We discuss key processes by which males develop the means to reproduce: Developmental influences that include enculturation in reproductive behavioral norms, and more immediate adult social success and mating opportunities. We also highlight the effects of reproduction on men themselves, in addition to influences on their children and others such as reproductive partners.

Theoretical background

Male (and female) reproductive strategies are influenced by a series of trade-offs, which influence the allocation of resources across several domains (e.g., time, energy, food). The most notable trade-offs are between somatic effort (investment into growth and maintenance of the physical body, immune system, etc.) and reproductive effort (investment in the production of offspring), which is further subdivided into trade-offs between mating effort (acquiring and maintaining relationships with reproductive partners) and parental effort (direct investment in offspring) (Low 1978; Trivers 1972). These trade-offs, the central elements of life-history theory, shape the allocation of resources that influence many evolved life-history traits, such as the timing of sexual maturation, age at first birth, the number of offspring an individual has, and how much is invested in each.

Compared to other mammals, primates tend to have slower life histories, experiencing longer lives, later ages at first reproduction, and longer interbirth intervals (Zimmerman and Radespiel 2015). Paternal care has evolved independently several times among primates (Fernandez-Duque et al. 2009) and is associated with earlier weaning and shorter interbirth intervals (Opie et al. 2013; West and Capellini 2016). These characteristics, part of our primate heritage, have been taken to an extreme in humans, which exhibit extensive male care that is highly variable within and across societies. Human children exhibit periods of dependency that are longer than interbirth intervals so that human mothers (unlike most primates) typically have several dependent offspring at once. As a result, women need assistance, from fathers, kin, and potentially other male figures, in order to successfully raise offspring, so that human reproduction is sometimes characterized as cooperative breeding (Hrdy 2009; Kramer 2010; see also Crittenden and Herlosky in this volume). Male care is often indirect, in the form of provisioning and protection, with men in many societies having minimal interactions with children until after they are weaned (Gray and Anderson 2010).

The trade-offs outlined above suggest that men, more than women, face trade-offs between mating and parental effort, and to some extent must “decide” on whether to maximize offspring quantity (maximum mating effort, minimal parental effort) or quality (fewer offspring, with greater investment in each) (see Gray and Anderson 2010). High levels of parental care are expected to be favored in socioecologies in which male care helps offspring survive to reproduce. If male care has minimal impact on offspring outcomes, or if its absence is read-*
ily replaced by other allomothers (such as kin, or support from state-level organizations), then men may minimize parental involvement. The level of parental commitment among men is thus influenced by the opportunity costs of foregoing reproductive opportunities with other potential mates, and by the level of support anticipated from the mother as well as extended kin networks (Anderson and Starkweather 2017; Starkweather 2017). These factors contribute to the variable and facultative levels of male parental investment observed across contemporary human socioecologies.

Life history allocation approaches are concerned with optimization and ultimate causation measured as survival and reproduction. However, as ethologist Nikolaas Tinbergen (1963) showed, there are four major problems of behavior: Adaptation (function), phylogeny (evolutionary history), proximate causation (neurobiology), and ontogeny (change across the life course). These four approaches provide complementary rather than competing explanations of behavior. While a full review of all mechanisms, development, phylogenetic history, and ultimate functions related to male reproduction is beyond the scope of this chapter, we hope this synthesis will equip readers with an interdisciplinary understanding of the complementary explanations for how and why human males seek mates, father and nurture children, get jealous, cooperate, compete, and ultimately change in the varied ways that they do so. In addition, we use life-history theory to contextualize how human males may shift strategies over their life course, in response to intrinsic and extrinsic stressors.

**Model of men and reproduction**

Figure 3.1 provides a conceptual model of men and reproduction. This model serves as an organizing structure for the remainder of the chapter material (e.g., subheadings) and for a body of work that can be integrated within the scope of men and reproduction. While focusing at the moment on male fertility patterns and paternal contributions, subsequent sections consider...
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Contributors to and consequences of male reproduction. The directions of arrows in the figure point to a conceptual flow—from drivers of reproduction to its effects.

Contributors to male reproduction

Fertility patterns

Human male reproductive scheduling differs from that of our primate cousins, including the apes to whom we are most closely related (see Muller and Emery Thompson 2012). Perhaps the most immediately informative contrast is between male reproductive scheduling of the few quantitative human hunter-gatherer demographic studies and wild ape paternity patterns. Contemporary hunter-gatherers live in socioecological circumstances more similar to those of our ancestors in which key patterns of reproduction evolved (Marlowe 2005). However, these diverse hunter-gatherer populations have long cultural and demographic histories, with access to technologies (food processing, metal, phones) and medicines that foragers 200,000 or 2 million years ago lacked (e.g., Kelly 2013; Marlowe 2005). So, while hunter-gatherer data can inform evolutionary models of human reproduction, they should not be mistaken as “living fossils” suspended in some past, “traditional” time.

Hunter-gatherer males tend to have first reproduction in their early to mid-twenties, have around five to six children spaced three to four years apart, and most typically have their last offspring in their forties, though for some men fertility continues into later ages (Blurton Jones 2016; Hewlett 1991; Hill and Hurtado 1996; Howell 2010). By contrast, wild chimpanzee males have peak age-specific fertility between ages 15–25 years, with a rare 50-year-old male father recognized at the upper boundary; among gorilla males, a majority of offspring were fathered by males 15–24 years of age (Langergraber et al. 2012). Wild chimpanzees also exhibit greater reproductive skew or variation among males compared with human foragers. Comparisons with other wild apes such as orangutans and bonobos (Surbeck et al. 2019) reinforce several key, putatively derived characteristics of human male reproductive scheduling: Later ages of reproductive maturation and first reproduction, less reproductive skew, higher fertility, and later age of last reproduction (see: Robson and Wood 2008; Smith 2018). In the course of humans evolving slower life histories, such life-history markers as first and last reproduction have been shifted toward older ages, compared with our closest primate relatives.

As humans migrated widely in concert with social, economic, and political transformations, those modal patterns of hunter-gatherer male reproductive scheduling have given way to greater variation in male reproductive timing (Bribiescas et al. 2012; Low 2015; Vinicius et al. 2014). As extreme ethnographic illustrations, Eurasian eunuchs were created as punishments or for celibate protective services by political elites; some men have had hundreds of children via the maintenance of harems or through sperm donation; and males from as young as ten years to as old as 90 or more have fathered offspring as lifestyle changes have helped fuel greater plasticity and potential in reproductive function (Betzig 1986; Gray and Anderson 2010). Less dramatically, systematic cross-cultural analyses have highlighted patterned variation in male reproduction across hunter-gatherer, farmer, pastoralist, and other small-scale societies (Low 2015; Marlowe 2000; Kaplan et al. 2009). Such analyses show that most human reproduction occurs within long-term partnerships like marriage (Gray and Garcia 2013). A key constraint on men’s reproduction is access to a mate, with the accrual of adequate status and family resources often necessary before being able to initiate reproduction. Men tend to be older than partners, with age discrepancies minimized in socially monogamous societies but amplified when polygyny is more prevalent, as older polygynous men frequently marry much
younger women. Genetic data align with ethnographic and demographic reproductive patterns, revealing lower Y chromosome (male) measures of variation compared with mtDNA (female), and highlighting Y bottlenecks reflective of restricted male mating opportunities (Karmin et al. 2015).

National and international data also offer insight into male reproductive scheduling (Gray and Anderson 2010; Schoumaker 2019). These data are more often on a larger social scale (e.g., country) than earlier anthropological scholarship focused on small populations like foragers or rural farmers, but they also ensure relevance today of biological anthropological approaches to male reproduction. One of the best online sources is Our World In Data (https://ourworldindata.org/fertility-rate). This site integrates data from a variety of key resources such as the World Health Organization with a focus on female fertility parameters, but with some extrapolation to male fertility feasible. Global average fertility is 2.4 children born per woman. A key pattern is that fertility has fallen considerably in recent decades, with around one-half of all countries now at below-replacement levels. Some of the key variables driving fertility declines include increasing educational attainment, especially among females; access to contraception to achieve lower-fertility goals; and cost/benefit changes to having children, with less economic contribution and more expense for school (Sear et al. 2016; Shenk et al. 2013). An evolutionary perspective underscores the power of sexual motivation to acquire life’s ultimate currency—reproductive fitness, or children—but that fertility behavior reflects complex biocultural processes.

**Paternal contributions**

Besides a focus on male reproductive scheduling as a central concern in our model of men and reproduction, let us turn to what men contribute to reproduction. Men’s contributions can run a gamut, from sperm to non-genetic physiological influences (e.g., epigenetics and non-genetic male effects), protection to resource provisioning, direct childcare to social and moral training. While evidence for non-genetic maternal effects is established (e.g., via intrauterine nutrition and stress physiology), evidence for parallel paternal effects is more controversial and uncertain (Baxter and Drake 2019). Some nonhuman experimental evidence makes plausible paternal effects, though the bulk of human research is based on cross-generational correlational designs (Soubry et al. 2014).

One key issue theoretically and in various social contexts is the distinction between biological/genetic and social fatherhood. DNA-based paternity testing enables directly assessing paternity. In nonhuman primates like baboons and chimpanzees that exhibit some slightly elevated likelihood of preferential associations between biological fathers and offspring in multi-male, multi-female social systems, the relationship and proximity cues between a male and female mate are central to such associations (Buchan et al. 2003; Sandel et al. 2020). In humans, male kin vigilance over a mate’s sexual fidelity (e.g., Strassmann et al. 2012), a man’s own vigilance and assessment of a mate’s fidelity via relationship assessments (e.g., Anderson et al. 2006; Daly and Wilson 1988), and phenotypic resemblance between a man and offspring (Alvergne et al. 2014) are primary means by which biological paternity might be inferred. Men’s sexual jealousy can vary across social contexts and is enhanced with higher male investment and lower prevalence of extramarital sex (SceIza et al. 2019). Genetically based paternity testing enables direct evaluation of biological paternity. Given a variety of social contexts in which men value genetic contributions over say adoption or stepfathering (see Inhorn in this volume), genetic contributions are distinct and can guide practical and legal decisions about men’s obligations to a given child.
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Mating opportunities

The basic life history trade-off between mating and reproductive effort, outlined earlier, ignores the possibility that caring for offspring can be a criterion of mate selection, weakening the trade-off. While traditional perspectives on parental care focused on offspring well-being as the key outcome, human males can use their potential and/or demonstrated ability to provide for offspring as a strategy for attracting and retaining mates (Anderson et al. 1999a, 1999b). Under this framework, a man’s investment in biological children through a current mate functions as both parental effort and mating effort. Once the relationship with the mother has ended, his investment in the child is solely parental effort and declines from previous levels as he allocates resources into new mating relationships. While models of male care frequently assume that men’s primary reason for investing in children is to positively impact children’s well-being, the trade-off model raises the possibility that male care also impacts the man’s ability to attract and retain a mate. Consider a widespread form of male care in contemporary societies: Child support paid by men to children they no longer live with. Men who pay “pre-divorce” levels of support may have fewer resources to allocate to new relationships. Consistent with the trade-off model, men in the United States who pay child support are less likely to have a subsequent child with a new partner. However, consistent with the idea that paternal care may be an attractive feature to potential mates, men who pay child support are more likely to subsequently remarry than men who do not pay child support (Anderson 2011). The trade-off model also helps explain the “puzzle” of stepfathers, who help raise children who are genetically unrelated to them; by helping to raise a woman’s child from a previous union, a man is investing in his relationship with her, and increasing the possibility that he will have future children with her (Anderson 2000). Men’s level of investment in children is thus facultative, and highly dependent on the status of their relationship with the child’s mother (Scelza et al. 2020).

Another factor that is likely to influence a man’s investment in offspring is his perception of whether he is actually the father of his putative offspring. Because of internal fertilization and gestation, women (at least until the advent, late in the twentieth century, of assisted reproductive technology) are certain they are the mothers of their children, while men always face the potential that another man fathered the child they thought was theirs. Data on actual nonpaternity rates are scarce, but suggest that fewer than 2% of men unknowingly raise children who are not theirs (Anderson 2004). Rates of nonpaternity likely vary both within and across cultures, as the costs and benefits of extra-union sexual liaisons, for both men and women, vary. For example, among the Dogon of Mali, nonpaternity is less common among practitioners of religions that restrict women’s sexuality and freedom of movement (Strassmann et al. 2012), while among the Himba of Namibia, a society that grants women greater sexual autonomy, nonpaternity rates are higher (Scelza 2011). Regardless of whether he is actually the father, a man’s perception of his paternity may have important implications for his level of investment in the child. Men with low paternity confidence are more likely to withhold investment, both before and after birth, resulting in an increased likelihood of elective abortion (Anderson et al. 2006, 2007). Among children born to unmarried women in the United States, men who do not legally acknowledge paternity and are not named on the birth certificate are probably men with low confidence in paternity. If the father is not named on the birth certificate, the baby is more likely to be low birth weight and premature, and more likely to die in infancy (Anderson 2017; Ngui et al. 2014). While acknowledging that paternal involvement is influenced by a complex suite of factors, including social inequalities, structural racism, adverse childhood experiences, and historical trauma, an evolutionary approach suggests that male investment in offspring is facultative and multifactorial, with trade-offs playing an important role that is sometimes underappreciated.
**Paternal contributions**

In a multi-faceted evolutionary model of human reproduction, the likely earliest social service provided by ancestral males was the protection of offspring (Gray and Crittenden 2014). This could have been protection against predators and/or against other males. Opie et al. (2013) argue that the risk of infanticide led to paternal care in primates: Male care shortens lactation duration, reducing the length of the period when infanticide from non-paternal males is most likely. Phylogenetically closer to home, male chimpanzees, who are not thought of as highly involved fathers due to their promiscuous mating system, nonetheless preferentially spend time with infants they have fathered, but only during the first six months of life when infants are most vulnerable to infanticide (Murray et al. 2016). Many human male secondary sexual characteristics, such as facial hair, deep voices, large body size, upper body musculature, and enhanced oxygen-carrying capacity, appear to function in contexts of male–male competition, whether by direct fighting (for which muscle and aerobic capacity are advantageous) or as visual signals (of age and social dominance, perhaps evolved in multi-scale social contexts) (Grueter et al. 2015; Puts 2010). That is evidence that could also be relevant to protection, as males might seek to prevent other males from accessing a current mate. Or in a gorilla-like model, ancestral hominin males might have tried to protect their young, nursing genetic progeny from being injured or killed (infanticide: See Rosenbaum et al. 2018) by an unrelated male challenger. The ethnographic and demographic evidence of the salience of male protection is difficult to accurately discern among recently studied hunter-gatherers or other smaller-scale societies, perhaps in part because projectile weapons mute earlier and more direct relevance of protection. That said, stories from small-scale societal narratives (Scalise-Sugiyama 2014) and historic research (e.g., bride capture) hold some relevance for protection.

Paternal contributions like protection arose in mosaic fashion among our ancestors (Gray and Anderson 2010; Gray and Crittenden 2014). In one view of how variable mammalian male reproductive behavior could be classified, Kleiman and Malcolm (1981) contrasted indirect (protection, resource provisioning) and direct (proximity, holding, interacting with) care. Taking up that view, a potential human paternal contribution is provisioning. In hunter-gatherer societies, this usually focuses on obtaining game meat by hunting, with debates over how much of that resource acquisition is driven by family provisioning (parenting effort) versus signaling to and sharing with non-family members for political or sexual benefits (mating effort) (e.g., Marlowe 1999). In non-forager contexts, this is the equivalent of male breadwinning or earning a paycheck to invest in a mate and their offspring. Besides day-to-day relevance, male resource provisioning can also be of significant impact at a man’s death (e.g., willing land or other inheritance) or other children’s landmarks (e.g., supporting costs of education or paying costs of a dowry or brideprice) (Gray and Anderson 2010). In an evolutionary scope, much of the material resource focus of provisioning took on new significance with the domestication of plants and animals and enhancement of material transfers like land or livestock.

Men can also provide direct childcare such as watching or holding a young child (Hewlett 1992; Marlowe 2000). In an evolutionary model, direct paternal care is likely preceded by male–female reproductive associations, given that comparative approaches typically recognize the formation of long-term bonds as a necessary but insufficient requirement for paternal care (Lukas and Clutton-Brock 2013). The proximity between mates can facilitate the father’s involvement, though fathers may be just one class of caregivers among a network that includes maternal grandmothers, older siblings, and others (Hrdy 2009; see Crittenden and Herlosky chapter). Among hunter-gatherers, a father’s direct childcare like supervision or carrying may aid his mate’s foraging budget (e.g., if slower dependents can be left with father, or if he carries...
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(a child). Data on direct childcare across societies recognize that other caregivers like maternal grandmothers often provide more such care than fathers (e.g., Kramer and Veile 2018). However, hunter-gatherer fathers tend to provide more direct childcare than fathers in farmer or pastoralist societies (Marlowe 2000), and in social contexts characterized by nuclear households without other available family caregivers fathers may be expected to provide more such care (Shwalb et al. 2013; Starkweather 2017).

Fathers can also support children’s social and moral development. This can include telling stories with moral lessons or other core societal meanings embedded in them (Boyette and Hewlett 2018; Scalise Sugiyama 2017). This may also entail sharing information about a paternal legacy (e.g., family history), religious beliefs, or other key facets of identity. In some societies, this is manifest in sex-specific ways, with fathers helping their sons learning a trade or preparing for sex-differentiated roles like in adolescent rites of passage (Scelza 2010; Schlegel and Barry 1991).

Developmental influences

Human male reproductive behaviors can exhibit high within-species variation (both within and across societies), which in turn can affect and be affected by a host of social and biological factors. Patterns of paternal investment can vary by sex ratio (Schacht and Borgerhoff Mulder 2015), residential status (Gray and Brown 2015), and economic change (Schacht et al. 2018), among other major factors. It is possible that some of this behavioral plasticity is an adaptive response to early developmental environments (Del Giudice 2018). Cues of environmental quality (e.g., mortality risk, pathogen load, nutrition availability, alloparental care, maternal attachment style, and sex ratio) during development may modulate an organism’s “pace of life” and adult life history strategy (Quinlan 2010). Males who have adapted to what was perceived as a high-risk (i.e., high mortality) environment may be more likely to pursue a fast life history strategy (mating effort expressed as aggression, less stable pair-bonding, less paternal investment, higher rates of male–male competition, earlier age at first reproduction) than a male raised in a more stable environment (Del Giudice et al. 2015). In addition, childhood ecology (Kuzawa and Fried 2017; Magid et al. 2018) and social circumstance (Gray et al. 2020; Sarma et al. 2018) can potentially shape future allocations to reproductive physiology and behavior.

Social success

Apart from developmental influences, adult social status is related to men’s reproductive potential. Men’s social status can be determined by both physical (finances, land, food) and “information goods” (leadership style, respect, neural capital) (Henrich and Gil-White 2001), in addition to contrasts between dominance (e.g., strength, physical aggression) and prestige (freely conferred status contingent on physical or informational resources). Evidence points to common properties of high-ranking individuals (i.e., leaders): Enhancing collective action, providing counsel and expertise, and garnering respect (Garfield et al. 2016). Data from small-scale societies indicate that men with more resources and status tend to have more mating opportunities and offspring (von Rueden and Jaeggi 2016). In large nation-states, men’s resources like wealth are associated with higher fertility, in part because lower-income men are less likely to find long-term mates (Fieder et al. 2011; Nettle and Pollet 2008). Male physical traits such as deep voices, facial hair, and upper-body musculature appear to have been driven more by male–male competition than female choice, in part based on sex differences in perceptions of these traits today (e.g., beards signal social dominance more than attractiveness to women) (Geary 2010; Puts 2010). A large literature indicates that female choice of men draws on traits indicative of
long-term compatibility (e.g., similar religious affiliation and kindness) and capacity to invest in her and future offspring (e.g., Gray and Garcia 2013; Sugiyama 2015).

Consequences of male reproduction

Effects on fathers

What are the consequences of reproduction on men? Given space constraints, we identify many key potential consequences in Table 3.1. This is not an exhaustive set of impacts of reproduction on men, nor is the research foundation on which this tabular summary is based. Many of these effects relate directly to potential influences of fathering on men’s changing social behavior (time with male friends versus family), physiology (hormones, brain activity), and health-related outcomes, including a primary currency: Survival/mortality. An emphasis is given to a transition to first-time fatherhood, given that life-history transitions may be most marked at that time. Note that any such potential consequences must be placed in a socioecological context given the recognized variation cross-culturally and historically in reproductively relevant male social behavior, in lifestyle variables, and in other key variables like institutions (e.g., for paternity leave or expectations about work). Such context-dependent complexities play out in the testosterone literature (see Gray et al. 2020), for which investigations into male testosterone variation in the context of variable mating and parenting effort have been undertaken in varied social contexts internationally. Yet in that testosterone literature, like any other facet here, there are methodological strengths (e.g., the value of longitudinal or experimental work: See Gettler et al. 2011) relative to cross-sectional designs to discern causality, among other key research design considerations (such as sample size, health measures, sampling, etc.).

In addition to these life course–related influences of fatherhood on men, we highlight two other evolutionary consequences of reproduction on men’s anatomy and physiology. The first is the consequence of limited ancestral sperm competition pressures on male reproductive anatomy and physiology. Sperm competition refers to competition between gametes of different males to fertilize a given egg and is amplified when a female mates with multiple males around the time of ovulation. By a variety of measures such as relative testis size, sperm quality and quantity, and size of seminal vesicles, humans exhibit traits consistent with male ancestors predominantly mating with a single female around the time of conception (as opposed to multi-male mating) (Dixson 2009). Moreover, men’s reproductive function evidences diminished function with advancing age—in sexual desire, erectile function, testosterone level, sperm quality and quantity, etc.—which appears to reflect diminished maintenance support for reproduction at later ages (Bribiescas 2018; Gray et al. 2019). An interpretation is that these age-related changes in male reproductive function accord with ancestral male-specific fertility patterns touched on earlier, like those modeled among hunter-gatherers. The point is that ancestral male reproductive patterns have shaped today’s men—in their reproductive function broadly, including how that changes with advancing age.

Effects on others

Paternal care can have consequences for their mates and other adult caregivers. As cooperative breeders (Hrdy 2009), human fathers may represent the “first-line” of available allomaternal caregivers which also can include maternal kin, siblings, and unrelated caregivers (see: Crittenden and Herlosky in this volume), although this varies cross-culturally (Gray and Anderson 2010). Paternal care may be particularly important during critical periods such as peri-pregnancy and lactation (Marlowe 2003) when maternal energy requirements are higher (Butte and King
**Table 3.1** Impacts of fatherhood on men

<table>
<thead>
<tr>
<th>Domain</th>
<th>Sample finding</th>
<th>Theory/rationale</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td><strong>Behavioral time</strong></td>
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<tr>
<td>allocation</td>
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<tr>
<td><strong>Work hours</strong></td>
<td>Work hours often stay same or ↑</td>
<td>Many impacts with invested care, especially of first child care, indicating importance of providing</td>
<td>Gray and Anderson (2010)</td>
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<tr>
<td><strong>Male–male bonding</strong></td>
<td>Time with male friends or playing team sports ↓</td>
<td>Trade-offs of male coalitions and intimate family life</td>
<td>Knoester and Eggebeen (2006)</td>
</tr>
<tr>
<td><strong>Direct childcare</strong></td>
<td>↑ activities, though contingent on context</td>
<td>New child and new demands</td>
<td>Craig and Mullan (2011)</td>
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<tr>
<td><strong>Sleep</strong></td>
<td>Potential disruptions</td>
<td>New child and shifts to sleep patterns</td>
<td>Knoester and Eggebeen (2006)</td>
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<tr>
<td><strong>Relationship quality</strong></td>
<td>Often ↓ in fathers, though less than in mothers</td>
<td>Less time and attention between parents</td>
<td>Kluwer (2010)</td>
</tr>
<tr>
<td><strong>Sexual function</strong></td>
<td>Often ↓ partnered behavior</td>
<td>Mating/parenting trade-offs and sexual conflicts relevant</td>
<td>Gray et al. (2015)</td>
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<tr>
<td><strong>Brain activity</strong></td>
<td>↑ activity in hippocampus, hypothalamus, anterior cingulate cortex, etc.</td>
<td>Sensory, motivational, and cognitive appraisals of paternal stimuli</td>
<td>Rilling and Mascaro (2017)</td>
</tr>
<tr>
<td><strong>Ventral tegmental area</strong></td>
<td>↑ activity aligned with fathers' parenting behavior</td>
<td>Fathering can be emotionally rewarding</td>
<td>Mascaro et al. (2013)</td>
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<td><strong>Hormones</strong></td>
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<td><strong>Testosterone</strong></td>
<td>Often ↓ with involvement in intimate family life</td>
<td>Aligns with mating/parenting allocations</td>
<td>Gray et al. (2020)</td>
</tr>
<tr>
<td><strong>Oxytocin</strong></td>
<td>Often ↑ with direct care</td>
<td>Proximate mechanism and bonding</td>
<td>Feldman (1999)</td>
</tr>
<tr>
<td><strong>Prolactin</strong></td>
<td>Mixed findings</td>
<td>Might align with paternal feelings and behaviors</td>
<td>Gettler et al. (2012)</td>
</tr>
<tr>
<td><strong>Immune function</strong></td>
<td>No relevant research</td>
<td>↑ paternal care means ↓ allocation to immune system</td>
<td>Gray and Anderson (2010)</td>
</tr>
<tr>
<td><strong>Microbiome</strong></td>
<td>No relevant research</td>
<td></td>
<td></td>
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<tr>
<td><strong>Telomere length</strong></td>
<td>Sperm telomere length may ↑ with age</td>
<td>Causality uncertain, as is relation to fathering</td>
<td>Eisenberg and Kuzawa (2018)</td>
</tr>
<tr>
<td><strong>Body composition</strong></td>
<td>Some evidence ↑ fatness, in part due to ↓ activity</td>
<td>Context-dependent lifestyle variable shifts</td>
<td>Garfield et al. (2015)</td>
</tr>
<tr>
<td><strong>Health status</strong></td>
<td>Positive and negative influences</td>
<td>High burdens for young dependents may lessen</td>
<td>Bartlett (2004)</td>
</tr>
<tr>
<td><strong>Mental health</strong></td>
<td>Positive and negative influences (e.g., anxiety)</td>
<td>Disruptive but rewarding challenges to fathering</td>
<td>Garfield et al. (2006)</td>
</tr>
<tr>
<td><strong>Depression</strong></td>
<td>Patterned depressive symptoms many samples</td>
<td>Reflective of sex- and context-specific challenges</td>
<td>Gray et al. (2018)</td>
</tr>
<tr>
<td><strong>Mortality</strong></td>
<td>Marriage and lower mortality but less clear fathering effects</td>
<td>Variety of lifestyle and social factors covary w/ fathering</td>
<td>Modig et al. (2017)</td>
</tr>
</tbody>
</table>
In this view, fathers (and male provisioning) act as an energetic buffer during costly periods of female reproduction and human development, increasing paternal inclusive fitness by reducing the mortality of their progeny and/or boosting the fertility of their mate. Paternal care can aid mate retention and enhance a mate’s fertility by reducing the interbirth interval, among other key consequences (e.g., Marlowe 2001; Winking and Koster 2015).

**Effects on children**

Paternal care can have consequences for offspring. Paternal absence in early childhood (likely as an indicator of environmental stability and reliable allocare) has been predicted to be associated with a fast life-history pace for females (i.e., early menarche, insecure attachment style, and earlier age of reproduction) (Belsky et al. 1991; Ellis 2004), suggesting men’s reproductive strategies may influence their children’s reproductive behaviors. However, empirical support for this model is mixed and has received the most support in WEIRD (Western, educated, industrialized, rich, and democratic) populations (Sear et al. 2019). The relatively few studies among non-White samples show weaker support for the model or even delayed puberty associated with paternal absence (Anderson 2015; Sear et al. 2019). Other potential effects of fathers’ presence and involvement include offspring survival, physical growth and health, socioemotional development, social success, and reproductive transitions (Boyette et al. 2018; Gray and Anderson 2015).

**Conclusion**

As described above, human males display a remarkable degree of behavioral plasticity in reproductive strategies. Variation in ecology, culture, sex ratio, mortality rates, and costs of mating effort all ultimately influence how a man reproduces. While the degree of investment may be variable within and between populations, intensive paternal care (compared to other primates) is a hallmark of our species. The eventual emergence of fatherhood during human evolution, when coupled with cooperative breeding, was likely a contributing factor in the evolution of modern human life-history traits. Moreover, the transition to fatherhood can have profound effects on men, their offspring, and other caregivers. Charles Darwin experienced this milestone firsthand, as he interacted with his newborn son, also serving as an anecdote in biological anthropology perspectives on men and reproduction.

**References**


Men and reproduction


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