

Human Sexuality: The Evolutionary Legacy of Mating, Parenting, and Family Formation

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Ascribing universal characteristics to human sexuality is rife with contention due to both methodological and ideological disagreements, as well as debate over what is ‘typical’ given variation in its expression. For example, Margaret Mead’s investigation into the sexual lives of Samoan adolescents during the 1920s found that teenagers engaged in pre-marital sex, often having multiple partners before marriage. The results, presented in *Coming of Age in Samoa*, were heavily criticized both by scientists for being too subjective and by religious organizations that claimed Mead was attempting to legitimize her own beliefs on sexuality.¹ Nonetheless, Mead’s pioneering work galvanized a growing number of researchers, who began to systematically investigate sexual and reproductive behaviour by way of time-intensive, cross-cultural inquiry. Yet, while long-studied, how best to characterize human sexuality remains challenging.

Given human placement in the primate order, we approach mating, parenting, and family formation from a comparative perspective to better understand the physical and behavioural traits that are either shared across or distinct from our closest living relatives. We will additionally draw on examples from contemporary small-scale societies, also referred to as traditional societies. Small-scale societies are not relics of the past, but they do exemplify a more representative, diversified, and inclusive view of human courtship, marriage, and family life, and thus provide valuable insights into human sexuality. Mating, parenting, and family life have changed substantially in just the last few centuries through industrialization, globalization,

¹ Margaret Mead, *Coming of Age in Samoa: A Psychological Study of Primitive Youth for Western Civilization* (New York: William Morrow, 1928); Paul Shankman, *The Trashing of Margaret Mead: Anatomy of an Anthropological Controversy* (Madison, WI: University of Wisconsin Press, 2009).

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and the shift from a subsistence-based to a cash-based economy. For example, small, nuclear families consisting of parents and their dependent children are the norm today in the developed world. Yet for most of human history, as well as in contemporary small-scale societies, they are not.² Rather, patterns of mating, parenting, and family formation occurred in a much broader social context and were both varied in their expression and flexible to situational needs.

This chapter reviews what can be gleaned about human sexuality from the evolutionary and ethnographic record. We cannot, of course, observe what ancestral human sexuality was like since it leaves neither fossil nor archaeological evidence. However, inferences about how humans mated, consorted, parented, formed partnerships, and aggregated into families can be drawn from two large and growing bodies of work. The first are anatomical and biological indicators of ancestral mating patterns inferred from fossil evidence as well as observations from non-human primates. The second is ethnographic research across an array of contemporary human societies, which highlights variation in mating, marriage, and family structure. Together, biological indicators and cross-cultural patterns shed light on the legacy, constraints, and possibilities carried forward into the diverse and variable expression of human sexuality today.

Ancestral Human Mating Systems

Chimpanzees, the great ape genetically most closely related to humans, have long been assumed as the behavioural model best resembling mating and childrearing patterns of the deep human past going back more than 4 million years. Chimpanzees live in multi-male/multi-female polygynandrous (both sexes mate with multiple partners) groups. However, the assumption that our ancestors lived in polygynandrous groups has more recently ceded to debate about whether they instead were organized in polygynous, gorilla-like harems, or had a hamadryas baboon-like structure with a single male and his consorts living within a larger group. These differences in group structure directly affect the possible kinds of relationships that can form between individuals of the same and opposite sex. Despite debate over the specific social organization from which the

² Karen L. Kramer, 'The Human Family: Its Evolutionary Context and Diversity', *Social Science* 10, no. 6 (2021): 1–17.

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hominin line (all modern humans, our immediate ancestors, and extinct human species) developed, most researchers agree that group living and multi-male/multi-female societies are ancient features of human sociality.

Differences between males and females within and across species offer insight into ancient and contemporary selection pressures. Sexual selection is a widely recognized evolutionary force that influences behavioural and physical traits across animal taxa. Anatomical and biological features are less plastic than cultural traits and as such hint at ancestral selection pressures and the mating patterns that underlie them. Three traits are commonly examined in reference to primate breeding systems: sexual dimorphism, testis size, and concealed ovulation. Each provides evidence that helps to explain current mating patterns.

Sexual dimorphism refers to male and female differences in size or appearance, other than differences in the sexual organs themselves. Although many exceptions exist, across primates, and mammals generally, sexual dimorphism is correlated with breeding systems. For example, monogamy is associated with low rates of inter-male competition, as with our lesser-ape relatives the gibbons, and minimal differences between males and females in body weight and canine tooth size (used for fighting among primate males, not for eating meat).³ In contrast, in species that have polygynous mating systems, inter-male competition is high and size differences tend to be much more pronounced. In polygynous primates, competition among males to take over and maintain a harem can be intense, and stakes are high since winners have much to gain. Among mountain gorillas, dominant males monopolize sexual access to a group of females and perform up to 70 per cent of all copulations.⁴ Gorillas exhibit high levels of reproductive skew, that is, variation across individuals in reproductive success, and males are nearly twice the size of females.⁵ For primates who live in multi-male/multi-female groups, such as chimpanzees, body size dimorphism tends to be intermediary between monogamous and polygynous species.⁶

3 Alexander H. Harcourt, Paul H. Harvey, Susan G. Larson, and Roger V. Short, 'Testis Weight, Body Weight and Breeding System in Primates', *Nature* 293 (1981): 55–7.

4 Tara S. Stoinski, Staceu Rosenbaum, and Katie Fawcett, 'Patterns of Male Reproductive Behaviour in Multi-Male Groups of Mountain Gorillas: Examining Theories of Reproductive Skew', *Behaviour* 146 (2009): 1193–215.

5 Steven R. Leigh and Brian T. Shea, 'Ontogeny and the Evolution of Adult Body Size Dimorphism in Apes', *American Journal of Primatology* 36 (1995): 37–60.

6 Alan F. Dixson, *Sexual Selection and the Origins of Human Mating Systems* (Oxford: Oxford University Press, 2009).

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Given the relationship between size dimorphism and mating systems, what evidence of sexual dimorphism is there in the hominin anatomical record? The general consensus is that height dimorphism was greater in the past and has diminished over time. *Australopithicine* (fossil hominins who lived from about 4 to 2 million years ago) males are estimated to be in the order of 50 per cent taller than females, and in *Homo erectus*-grade species (fossil hominins from about 2 million to 40,000 years ago), males are about 25 per cent larger. It is important to note, however, that determining size dimorphism from fossils is intensely debated due to differences in researcher interpretations, in part because isolated finds do not represent the actual distribution of a trait in a population. What can be measured with greater certainty is stature dimorphism in contemporary humans, among whom males are on average between 5 and 10 per cent taller than females, depending on population. This is often interpreted to indicate that size dimorphism has decreased over the course of hominin evolution as inter-male competition relaxed in conjunction with a prevalence of monogamy.

When the reduction in stature dimorphism occurred in the past, and its mating system implications, however, are not fully understood. Most researchers agree that humans today express relatively small size differences not only in stature, but also in other measures of body size when compared with closely related polygynandrous and polygynous species. For example, human dimorphism in weight averages about 1.15 (in other words, males are about 15 per cent heavier) than females, while the chimpanzee estimate is 1.3 and orangutans and gorillas are near 2 or more.⁷ Although body weight dimorphism is slight in modern humans compared with these species, it is double that for monogamous gibbons, who exhibit very little difference in weight by sex (1.07).⁸ These comparisons suggest that modern humans are less dimorphic than polygynandrous and polygynous species, but more dimorphic than expected for a monogamous species.

Added complexity arises when attempting to ascribe meaning to size dimorphism. Males may compete for female favour in other ways besides physical contest. Focus on body size dimorphism as an indicator of the

7 J. Micheal Plavcan and Carl P. van Schaik, 'Intrasexual Competition and Canine Dimorphism in Anthropoid Primates', *American Journal of Physical Anthropology* 87 (1992): 461–77.

8 Lesley A. Willner, *Sexual Dimorphism in Primates* (London: University College London Discovery Press, 1989).

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intensity of inter-male competition may significantly underestimate the many and particularly human ways that males may compete, such as through wealth, intelligence, social reputations, and political power. While the attenuation of body size differences is often used to signify a reduction in male competition, male reproductive skew, and polygyny, it may instead indicate an evolutionary shift from physical to social forms of competition.

Testes size, as an indicator of sperm production and competition, is another commonly used metric of a species' mating system. Large testes relative to body size is positively correlated with the frequency that females mate with multiple partners, with males responding by producing and delivering more sperm to outcompete other males. Adjusting for body size, human testes are smaller than those of polygynandrous chimpanzees, yet are similar relative to polygynous gorillas.⁹ At the same time, human testes are somewhat larger than those of other monogamous primates.

While testes size is a predictor of the extent to which females mate with multiple partners, it cannot discriminate between monogamy and polygyny because in both cases females mate with a single male, resulting in relatively low sperm competition.¹⁰ Thus, the ratio of testes to body size complicates a simple story of ancestral mating derived from sexual dimorphism alone because human values are within the range of variation found among gorillas and orangutans – great ape species with polygynous mating systems. Therefore, the tempered interpretation is that human testes size is consistent with a pairbonded polygynous species.

Human females also lack obviously visible or easily detectable signs of ovulation, particularly in comparison to the conspicuous sexual swellings of, for example, chimpanzees and baboons.¹¹ Several functional arguments have been proposed to explain this phenomenon, called concealed ovulation. In many primate species, female receptivity to sexual advances is limited to oestrus, when females are ovulating. In chimpanzees, oestrus swellings are an unambiguous sign of the potential for conception and concentrate the

⁹ Geoffrey A. Parker, 'The Evolution of Expenditure on Testes', *Journal of Zoology* 298 (2016): 3–19; Harcourt et al., 'Testis Weight'.

¹⁰ Robert D. Martin and Robert M. May, 'Outward Signs of Breeding', *Nature* 293 (1981): 7–9.

¹¹ Kelly Rooker and Sergey Gavrilets, 'On the Evolution of Visual Female Sexual Signaling', *Proceedings of the Royal Society, B: Biological Sciences* 285 (2018), <https://doi.org/10.1098/rspb.2017.2875>; Birgitta Sillén-Tullberg and Anders P. Moller, 'The Relationship between Concealed Ovulation and Mating Systems in Anthropoid Primates: A Phylogenetic Analysis', *American Naturalist* 141 (1993): 1–25; Beverly I. Strassmann, 'Sexual Selection, Paternal Care, and Concealed Ovulation in Humans', *Ethology and Sociobiology* 2 (1981): 31–40.

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attention of multiple males during the short window of fecundity.¹² Concealed ovulation, however, limits information about fecundity to males, and even to females themselves. One common explanation for concealed ovulation and the constant sexual receptivity of women is that these traits interacted to favour monogamy. If males do not know when females are fecund, they are more likely to be continuously attentive, favouring monogamy through mate defence and/or paternal care.¹³ Concealed ovulation might also ease tensions by dampening inter-male competition, and is thought to facilitate the formation of stable pairbonds within multi-male /multi-female societies.¹⁴ Yet, it is increasingly evident from comparative study that concealed ovulation is not only characteristic of humans, but also of many polygynous female primates who likewise do not display overt signs of ovulation.¹⁵

In sum, the preceding biological traits, when interpreted singly, prompt different perspectives on ancestral mating in humans. For example, while men are larger on average than women, weight and canine tooth dimorphism are slight compared with that of polygynous gorillas and are more comparable to monogamous gibbons.¹⁶ These differences suggest diverging sexual selection histories among the great apes (gorillas, orangutans, chimpanzees, and humans) with respect to male reliance on physical competition for reproductive success. Yet, while size dimorphism may suggest an evolutionary attenuation of male–male competition, testes size suggests that if there was a trend towards pairbonding, it may not have been expressed as fastidious adherence to monogamy. Relative testes size implies that sperm competition is lower than expected for a promiscuous primate, but higher than for a monogamous species. Human testes size (accounting for body size) is more similar to gorillas who live in polygynous societies. While concealed ovulation was once thought to be a human-specific adaptation that coevolved

12 Barbara B. Smuts and Robert W. Smuts, 'Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications', *Advances in the Study of Behavior* 22 (1993): 1–63.

13 Ryan Schacht and Adrian Bell, 'The Evolution of Monogamy in Response to Partner Scarcity', *Scientific Reports* 6 (2016), <https://doi.org/10.1038/srep32472>.

14 Frank W. Marlowe and J. Colette Berbesque, 'The Human Operational Sex Ratio: Effects of Marriage, Concealed Ovulation, and Menopause on Mate Competition', *Journal of Human Evolution* 63 (2012): 834–42.

15 Birgitta Sillén-Tullberg and Anders P. Moller, 'The Relationship between Concealed Ovulation and Mating Systems in Anthropoid Primates: A Phylogenetic Analysis', *American Naturalist* 141 (1993): 1–25.

16 J. Michael Plavcan, 'Implications of Male and Female Contributions to Sexual Size Dimorphism for Inferring Behavior in the Hominin Fossil Record', *International Journal of Primatology* 33 (2012): 1364–81.

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with monogamy, it is common among anthropoid primates who express different breeding systems.

If the story thus far seems somewhat unclear that is because it is unsettled. Nonetheless, when moving beyond the interpretation of traits singly to viewing them as a suite of interrelated attributes, some general claims can be made. The lack of dramatic size dimorphism and large testes size to body size appears to rule out an ancestry of early humans living in highly promiscuous societies. Yet because sexual dimorphism and testes size relative to body size are larger than expected for a strictly monogamous species, it also suggests that if early humans were monogamous, it was imperfect.

Living in Multi-Male/Multi-Female Societies

Although societies composed of multiple males and females are found among a few other primates, including chimpanzees and some baboons, several features distinguish male and female relationships in human communities.

First, human societies can be generally described as composed of adult males and females living in pairbonded family units that are embedded within larger groups. This represents no small evolutionary or social feat, and it cannot be stressed enough how unusual it is in animal societies for sexual boundaries to be, in general, amicably respected. Explanations usually given as to why this rarely occurs in other species centre on rivalries between males competing for females prohibiting social cohesion.

Second, in all human societies, pairbonds are socially recognized through marriage unions. Those marriage unions express a wide range of configurations that vary across groups and the individuals within a society. Some marriages are monogamous (one male/one female), others are polygynous (one male/multiple females), and some are polyandrous (one female/multiple males). In each of these marriage systems, males and females are pairbonded.

Third, across human societies, men, women, and children perform different tasks, target different resources, and share the fruits of their labour. Although this takes many forms, and details vary widely across cultures, the age and gender division of labour is foundational to human subsistence and childrearing. While the age and gender division of labour is not unique to humans, the combination of individuals pursuing different subsistence activities, cooperating in joint activities, and sharing childcare, food, and other resources in humans is unmatched when compared with other primates. The

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division of labour and the complementary inter-reliance of men and women, and adults and children affect many aspects of male–female relationships.

Fourth, adults often maintain lifelong relationships with their natal families and move easily between neighbouring groups. This fluidity rarely occurs among other great apes. For example, among chimpanzees, individuals who attempt to emigrate from other troops are met with violence and sometimes death. Explanations for why humans cultivate social bonds across multiple groups have centred on building networks to exchange food, raw materials, labour, information, and marriage partners.¹⁷

In sum, social organization with respect to men and women is novel in the hominin line in several notable ways. Humans came to live successfully, for the most part, in communities of coresidential households and in socially recognized monogamous, polygynous, or polyandrous pairbonds. Human social organization is also unusual in that family groups are integrated through cooperation and that men and women maintain ties with their natal group and can fluidly move between communities.

Human Mating Cross-Culturally

Frank Boas, a pioneer of early anthropology, and a teacher and mentor to Margaret Mead, noted the following: ‘Courtesy, modesty, good manners, conformity to definite ethical standards are universal, but what constitutes courtesy, modesty, good manners, and definite ethical standards is not universal. It is instructive to know that standards differ in the most unexpected ways.’¹⁸ Societal norms become internalized through the process of enculturation, which establishes informal guidelines for appropriate behaviours. As the preceding quotation suggests, though, what is considered appropriate varies widely across groups, indicating a broad range of norms across human societies. For example, in many industrialized nations, the nuclear family with a husband/wife pairbond at the centre is the assumed norm. Yet the nuclear family is just one of many sexual and household arrangements, and is likely a recent norm. The human family exhibits remarkable flexibility within and across populations in ways that differ

17 Karen L. Kramer, Ryan Schacht, and Adrian Bell, ‘Adult Sex Ratios and Partner Scarcity among Hunter-Gatherers: Implications for Dispersal Patterns and the Evolution of Human Sociality’, *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372, no. 1729 (2017), <https://doi.org/10.1098/rstb.2016.0316>.

18 Franz Boas, forward in Mead, *Coming of Age in Samoa*, xiv.

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from the nuclear family model.¹⁹ For instance, in the United States, 18.6 per cent of households were nuclear in 2020, down from 40 per cent in 1970.²⁰

Across the animal kingdom, species-typical labels (e.g., monogamy, polygyny, or polygynandry) are regularly applied to describe male–female mating interactions. But no simple or single designation characterizes humans. Instead, diverse mating systems are variably present both across and within societies. Representative data from a range of societies, known as the Standard Cross-Cultural Sample, show that polygynous marriage is allowed in most societies (about 85 per cent).²¹ Within these societies, however, the majority of marriages are monogamous.²² For example, among the Savanna Pumé, South American hunter-gatherers, while polygyny occurs (20 per cent of women and 11 per cent of men are polygynously married at some point during their lives), most marriages are monogamous, and this is consistent with other similar groups.²³ Nevertheless, over the life course, individuals often re-enter the marriage market due to asymmetries in the cessation of fecundity (women cease being fertile around the age of forty-five; men’s fecundity also declines with age, but somewhat later), divorce, and spousal death. This results in serial monogamy, where both men and women have multiple partners over their adult lives.

Marriage occurs in all human societies as a socially recognized union that separates some – a couple or a small group – from other members of a society. Although marriage is often thought of as the institution that legitimizes sexual activity, it might be more aptly seen, at least historically, as the institution that confines it. As a universal human trait, marriage publicly acknowledges who has sanctioned sexual access to whom, with divorce often resulting from extra-marital relationships. Many exceptions exist.

19 Kramer et al., ‘Adult Sex Ratios’; Rebecca Sear, ‘The Male Breadwinner Nuclear Family Is Not the “Traditional” Human Family, and Promotion of This Myth May Have Adverse Health Consequences’, *Philosophical Transactions of the Royal Society, B: Biological Sciences* 376, no. 1827 (2021), <https://doi.org/10.1098/rstb.2020.0020>.

20 U.S. Census Bureau, *Current Population Survey, Annual Social and Economic Supplement*, 2021.

21 George P. Murdock and Douglas R. White, ‘Standard Cross-Cultural Sample’, *Ethnology* 8 (1969): 329–69.

22 Mark V. Flinn and Bobbi S. Low, ‘Resource Distribution, Social Competition and Mating Patterning in Human Societies’, in *Ecological Aspects of Social Evolution: Birds and Mammals*, ed. Daniel I. Rubenstein and Richard W. Wrangham (Princeton, NJ: Princeton University Press, 1986): 217–43.

23 Kramer et al., ‘Adult Sex Ratios’.

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Amazing, from a comparative primate perspective, is that men largely recognize the sexual exclusivity of other men and their partners and respect the bounds of a pairbond. If they did not, humans could not have transitioned to living in multi-level societies, where biological families exist within extended families, which exist within kin groups, and kin groups within communities.

While pairbonds and marriage are acknowledged in all societies, sex and parenthood are not necessarily restricted to marriage. In some societies, pre- and extra-marital relations must be clandestine because they are punishable transgressions if individuals are caught. In other cases, uncommitted sexual liaisons are socially permissible, which generally fall under two well-documented ethnographic contexts. The first occurs prior to first marriage when adolescent girls are in a life stage when they have a low probability of conceiving and are given freedom to explore different pre-marital relationships. For example, among the Makushi of Guyana, sexually mature adolescents engage in pre-marital sex,²⁴ an opportunity for young people to learn about mutual mate choice and to identify possible long-term mates. Once married, however, conventions abruptly shift, and sexual fidelity is generally expected.

Socially sanctioned sex outside marriage also occurs in the context of either partible paternity or spouse sharing under certain situations. For instance, among some lowland South American Indigenous groups, married women may have extra-marital partners.²⁵ This most commonly occurs where more than one man is perceived to contribute to a baby's development. While these relationships are not formalized through marriage, these non-spousal fathers customarily protect and invest in children. In other societies, both men and women may maintain several sexual partners at the same time. Historic ethnographic accounts of the Inuit (Arctic hunter-gatherers), for example, describe 'wife swapping' among monogamous couples.²⁶ Husbands and wives both consent to these relations, the duration of which varies, but often results in long-term social and sexual partnerships. In other cultural situations, extra-pair relationships are clandestine because of the

24 Ryan Schacht, 'Cassava and the Makushi: A Shared History of Resiliency and Transformation', in *Food and Identity in the Caribbean*, ed. H. Garth (London: Berg, 2013), 15–29.

25 Stephen Beckerman and Paul Valentine, eds., *Cultures of Multiple Fathers: The Theory and Practice of Partible Paternity in Lowland South America* (Gainesville, FL: University of Florida Press, 2002).

26 Arthur J. Rubel, *Partnership and Wife-Exchange among the Eskimo and Aleut of Northern North America* (Fairbanks, AK: University of Alaska Press, 1961).