Pair Bonds and the Evolution of Monogamy

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Abstract

Long-term and exclusive pair bonding has often been seen as central to the evolution of a human way of life. Its emergence may be linked to aspects of human life history such as the lengthy dependence and slow development of infants and children requiring novel levels of biparental care. A comparative phylogenetic approach allows testing of functional explanations of pair bonding across species, informing our models of hominin evolution. For slowly reproducing primate species, social monogamy imposes fitness or opportunity costs on males in particular. The evolution of such a reproductive strategy for males requires explanation.

Keywords

evolution; hominins; life history; monogamy; pair bonds; parental care

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Long-term and exclusive pair bonding has often been seen as central to the evolution of a human way of life. Its emergence may be linked to aspects of human life history such as the lengthy dependence and slow development of infants and children requiring novel levels of biparental care. A comparative phylogenetic approach allows testing of functional explanations of pair bonding across species, informing our models of hominin evolution (Dunbar 2010; Lukas and Clutton-Brock 2013; Opie et al. 2013; Sillén-Tullberg and Møller 1993).

Nesting and the raising of young together is a feature of 90 percent of bird social systems, often described as “social monogamy” (Palombit 1999), which implies that partners of both sexes may seek matings outside the pair—extra-pair copulations (Martin 2013, 60). Among mammals such pairing arrangements are much rarer and are found in some 3 percent of species (Martin 2013, 59). This reflects the fact that mammal mothers are solely responsible for provisioning the young, leaving males free to increase their fitness by finding extra matings.

For roughly 230 primate species, the proportion increases to around 15 percent with species-specific or obligate monogamy, while some quarter of species show facultative monogamy as part of variable systems (Opie et al. 2013: Dataset S1). While pair bonds are often equated with monogamy and sexual exclusivity, among several species they occur in contexts of polygyny (males mating other females) or polygynandry (both males and females mating other partners) (Palombit 1999). In the case of human culture, pair bonding appears universally regardless of whether the marriage system is polygynous, monogamous, or polyandrous. A whole suite of emotional states and behaviors, known as “falling in love,” appears designed to maintain long-term pair bonds (Dunbar 2010). Similar emotional and behavioral mechanisms may underpin pair bonds in other species.

For slowly reproducing primate species, social monogamy imposes fitness or opportunity costs on males in particular. The evolution of such a reproductive strategy for males requires explanation. Early attempts to model human evolution in terms of a "sexual contract" argued that man the hunter coevolved paternal provisioning in exchange for exclusive sexual access to his mate, to assure him of paternity certainty (see Hrdy 2009, 146–51, for discussion). But there are plentiful examples among ape relatives, such as polygynous gorillas or monogamous gibbon species, where males have high confidence of paternity yet offer little care for offspring apart from protection. At the same time, several baboon species, with promiscuous mating contexts, have significant male care (e.g., not only protection but also carrying among chacma baboons). This has led to the argument that mating effort may be as strong a motivation for infant care in primates as paternity.

The unusual aspect of human pair-bonded monogamy is its context within large multimale– multifemale groups. Deacon (1997) pointed to the "dilemma" inherent in maintaining long-term exclusive pair bonds in settings of such social complexity. Given a hunter-gatherer-style sexual division of labor, males and females would typically be apart for lengthy periods each day, which makes it harder for mates to monitor each other—a particular problem for males because of paternity uncertainty (Dunbar 2010). For Deacon, symbolic markers generated through ritual and ceremony would have been the only means to represent "contracts" in the eyes of the community; so public acknowledgment of pair bonds was a major selection pressure for the emergence of symbolism and language.

Long before any symbolic contractual form, the evolution of pair bonds may have been implicated in increased brain sizes across species. The mean brain volumes of pair-bonded species of birds, carnivores, artiodactyls, and bats are significantly larger than those of non-pair-bonded species (Dunbar and Schultz 2007). There are two main reasons why pair bonds would be cognitively demanding and hence be selective for larger brains. First, each partner must judge the likelihood of cooperation and reliability in the other because defection could severely reduce reproductive success; and, second, each partner needs to coordinate activities and behavior with the other in raising their young. In the case of primates, brain size measured by neocortex volume relates to measures of social complexity including group size. This indicates that anthropoid primates began to use the kinds of intelligence evolved in pair-bonded relationships in a wider set of social relationships, creating bonds of friendship as intense as mated pairs among nonprimate species. Within primate taxonomic groups, pair-bonded species show bigger neocortex volumes for group size than polygynous or polygynandrous species (Dunbar 2010).

Hypotheses for the evolution of pair bonds

There is some dispute over the fundamental causes of pair-bonded monogamy in mammals and primates (see Opie et al. [2013] vs. Lukas and Clutton-Brock [2013]). It is probable that pair bonds evolved for different reasons among mammals in general, compared to socially complex primates. There are three major hypotheses for the evolution of pair bonds: first, for mate defense, allowing a male to guard access to a female to ensure paternity certainty, so-called male-biased pair bonding; second, to protect offspring from infanticide or predation, which is strategic for both sexes; and, third, for biparental care, which is more likely to be a female strategic priority or female biased.

Where females are widely dispersed, at low density for reasons of foraging competition, males may have no choice but to guard one female, having no opportunity for monopolizing more females. In analysis of 2,545 mammal species, monogamy arose among species where females were too widely spaced for males to guard more than one at once, supporting mate defense as the fundamental cause, while paternal care appeared as a consequence and not a cause of social monogamy (Lukas and Clutton-Brock 2013). When it comes to primate species, however, socially complex group living such as is characteristic of the evolution of monkeys, apes, and hominins makes mate defense less likely to be the main cause. In an analysis of 230 primate species, across prosimians, Old and New World monkeys and apes, Opie et al. (2013) found incidence of infanticide to be most likely to precede social monogamy and therefore to be the driving force in its evolution. Paternal care again was a consequence of monogamy, which was associated with a shift to discrete home ranges. Male infanticidal strategies are liable to have arisen in primate evolution owing to the slow life history of primates, with long periods of breastfeeding making infants extremely vulnerable and difficult to protect in social groups.

Among lesser apes, gibbons, and siamangs, which are generally monogamous, males appear most eager to maintain contact with females, suggesting that mate defense, besides reduction of infanticide risk, remains a significant factor (Dunbar 2010; Palombit 1999). In the larger communities of great apes, females became more interested in relationships with males as "hired-gun" protectors against infanticide risk and also sexual harassment (as occurs with orangutans and chimpanzees). In the common ancestors of panins (chimpanzees and bonobos) and hominins, female–female bonding and coalitions may have become increasingly important to counter the risk of aggression from multiple males in large communities (Dunbar 2010).

When did pair bonding start in human evolution?

Some have argued that pair bonds with significant monogamy extend back to early hominins (e.g., Lovejoy 2009). Evidence in *Ardipithecus ramidus*, one of the earliest bipeds, suggests significant reduction in sexual dimorphism with feminization of male canines compared to apes. However, the more advanced hominin *Australopithecus afarensis*, dating half a million years later and a more probable general ancestor for genus *Homo*, retains high sexual size dimorphism. With australopithecines showing similar sex size dimorphism to that found in orangutans and gorillas, pair-bonded monogamy appears unlikely in these hominins.

In general, substantial size dimorphism in primates is associated with male competition and polygyny, but a tendency to monomorphism is not simply associated with monogamy (Plavcan 2012). There is a statistically weak indication that size dimorphism is reduced in early African *Homo erectus* through disproportionate increase of size among females. The larger brain and body size of this species implies shifts in life history from previous apelike patterns toward lengthier infant and juvenile dependency, slower maturation, and longer life span. Heavier reproductive costs for females could only have been met with support from others. Hrdy (2009) and Isler and Van Schaik (2012) hypothesize that cooperative breeding was vital from this stage, leading to developments in cognition, intersubjectivity, and prosocial emotions. Great ape mothers are constrained in opportunities for allocare by the fact that they do not usually live with close female relatives, so they are hyperpossessive, saddled with hands-on care of an offspring until it has been weaned. Genus *Homo* mothers may have solved this conundrum by staying close to their own mothers and/or by drawing on help from older daughters. If mothers have reliable others to help take care of weanlings, they would be able to reduce the length of breastfeeding and start the next reproductive cycle sooner, leading to the "stacking" of dependent offspring (Robson, Van Schaik, and Hawkes 2006). The impact on humanlike life history includes the evolution of childhood—a period when the juvenile still has immature dentition and needs adult help with finding food—and increased survival rates for weanlings, which enables later maturation and longer life spans. In particular, mothers with longer-living mothers as helpers would improve their reproductive rate, hence selecting for postreproductive life spans.

Cooperative breeding strategies among related females would affect males. Increased female reproductive rates reward a male strategy of staying in a pair bond with greater fitness; a male then contributes to his own reproductive success by reducing female interbirth interval and improving offspring survivorship further through care like provisioning. The outcome of female kin-bonded cooperative breeding with emergent male investment (even at the level of mating effort) would be humanlike stacked reproduction with several immature offspring produced within a few years. This contrasts with the very lengthy interbirth intervals of great apes. While older siblings contributed as "helpers at the nest," new forms of sibling relationship could now emerge. With brothers and sisters of similar age that are able to stay within the same communities, brothers could act as protection for sisters against aggressive males. Increasing selection for social tolerance, with more sophisticated forms of cultural transmission, would further reduce the success of aggressive male strategies.

Among primates, the family of small-bodied New World monkeys, callitrichids, including marmosets and tamarins, offers the closest analogy for a cooperative breeding system. Because they produce twins, they have a relatively high reproductive rate, like humans; also like humans, they have concealed ovulation with receptivity throughout the menstrual cycle, with a tendency to reproductive synchrony; and their mating system is flexible but characterized by facultative monogamy, with high levels of male care, again comparable to humans (Dunbar 2010). Callitrichids are not significantly encephalized—a difference from the genus *Homo*—but they are notably prosocial compared to other monkeys and great apes.

Hrdy and colleagues have argued that the major changes in evolution of the life history and psychology of the genus *Homo* resulted from the combination of great ape cognition with a cooperative breeding system. In line with the cultural intelligence hypothesis, increased social tolerance and prosociality—something found among small-brained callitrichids—supports greater cultural transmission. The costs of the initial expansion of brains in genus *Homo* (from ca. 2 million years ago) could be met through allocare strategies, involving both female (and male) kin and some degree of male care, similar to the facultative or variable monogamy seen among callitrichids. The emergence of culturally contracted pair bonds in humans may belong to the later stage of encephalization in *Homo* beginning around 800 thousand years ago, accelerating from 300 thousand years ago. Dunbar observes: "the evolution of pair-bonding is dependent on having a large brain to manage the relationships involved, rather than pair-bonding having evolved to facilitate the rearing of large-brained offspring" (2010, 165). In this view, a phase of cooperative breeding early in genus *Homo*, with emergent male investment, would underpin the cognition needed for subsequently evolved pair bonding. This places humanlike pair bonds late in human evolution, where they are associated with the onset of language and symbolism and when neocortex volumes indicate the increased size of social groups.

Human sexual traits and mating systems

Human sexual characteristics such as women's sexual cycles and signals—concealed ovulation and extended receptivity—and men's relative testis size have been related to the evolution of human mating systems. Humans are not the only primates who lack visible signs of ovulation; they compare in that respect with callitrichids, as noted, as well as with hanuman langur monkeys (*Semnopithecus entellus*), a species with high rates of infanticide, besides others. It has been argued that concealed ovulation combined with sexual receptivity throughout the cycle selects for more assiduous male attention, so promoting pair bonds. In this view, because the male has no indication of the precise time of female fertility, his best strategy is to guard his mate throughout her cycle. Once she is pregnant, he has confidence of paternity and is more likely to invest in offspring. An alternative hypothesis argues that ovulation concealment has the effect of paternity confusion and is adaptive for females where they face a risk of infanticide. Sillén-Tullberg and Møller (1993) performed phylogenetic analyses across anthropoid primates (using the method of parsimony) to test whether the evolutionary change from visible signals of ovulation to loss of any signal evolved in certain mating systems. They found that, in virtually all contexts, when ovulatory signs were lost the ancestral mating system was not monogamous. This supports the second hypothesis of paternity confusion to protect against infanticide. However, they also found that, once ovulation concealment had evolved, monogamy was more likely to evolve subsequently, so there is a relationship between concealed ovulation and the evolution of pair bonds. This analysis needs to be repeated with more recently developed phylogenetic methods to confirm the result.

Women's continuous sexual receptivity throughout the cycle with no clearly defined "estrus" has an impact on the operational sex ratio between males and females (i.e., the number of male days vs. female days when potentially fertile sex can occur). Marlowe and Berbesque (2012) argue that this has had the effect of reducing the intensity of male–male competition in the evolution of human mating systems. Across primate species operational sex ratio predicts the degree of sexual size dimorphism—an index of mate competition. But humans do not conform to this formula. It is a discrepancy that could be explained by women's continuous availability, yielding many more possibly fertile days.

Alan Dixson (2009) has shown that human male characteristics such as testis size, dimensions of the sperm-carrying duct, size of sperm vesicles, and, critically, sperm midpiece size all fall into the range typical for primate mating systems where males are not in direct multimale competition. This means that they resemble pair-bonding marmosets and gibbons, or harem-living gorillas and gelada, more than macaques, plains baboons, and panins (Martin 2013, 68). Nevertheless, given extended receptivity, with concealed and unpredictable ovulation, women are well designed for discreet extra-pair copulation. In earlier studies of British postgraduate couples in stable pairs, Robin Baker and Mark Bellis (1989) showed that sperm ejaculate volume increased if a man had been away and unable to mate-guard his partner for several days, which suggested that this was strategic in case of sperm competition.

That monogamy may be an outcome of male competition is suggested by Blurton Jones and colleagues' (2000) analysis of pair-bond stability among hunter-gatherer groups. Examining divorce rates among the Hadza, !Kung (or Ju/'hoansi), Ache, and Hiwi, they found that male mating opportunities were the best predictor of desertion. The cost to offspring in terms of "father effect"—a measure of how the father's presence improves child survival—had no impact. This undermines the assumption that pair bonds evolved for paternal support of offspring. Blurton Jones and colleagues suggest that women may have had an interest in a "conventional solution" to male contests over sexual access as a means of reducing time disruption and risks of aggression. This hypothesis compares to Deacon's (1997) view of symbolic contracts required to remove sexual conflict in large-scale multimale–mutlifemale group contexts.

Are women more likely to be monogamous?

Using mathematical models, Gavrilets (2012) investigated the male "dilemma" of a switch from mate competition into provisioning mate and offspring instead. The problem is the risk of losing paternity to freeriders. Female choice for provisioning males—most likely formerly low-ranked males—is seen as critical if pair bonds are to evolve. While females are not expected to become completely faithful to provisioning males, a level of fidelity would emerge in the balance between selection for "good genes" of high-rank males (who do little provisioning) and the need for care and provisioning. Resistance by females to aggressive, dominant male strategies is likely to evolve in conditions of increasing egalitarianism typical of hunter-gatherer economies. This would promote investor male strategies.

Behavioral ecologists such as Hrdy, Gowaty, Borgerhoff Mulder, and Scelza emphasize the flexibility and opportunism of women's mating strategies. These have challenged the assumptions based on early sexual selection theory that males can always gain fitness via additional matings but females have little to gain. Factors that may lead to more multiple mating by women include social contexts with female kin acting in support, with either uxorilocal postmarital residence patterns or women's ability to visit kin regularly. Partible paternity belief systems, for example, may foster sex with multiple partners in predominantly matrilineal systems of descent. Pair bonding with monogamy may also follow a premarital phase of life history with several partners—a typical hunter-gatherer pattern (Scelza 2013). Once women marry, the strategic reasons for their having affairs include cultivating back-up mates in case of death or desertion and seeking "good genes" or gaining the benefits of extra gifts and investment. A woman may also be asserting her own choice after an initial arranged marriage at a young age, a pattern found with the Himba, which typically leads to divorce and remarriage (Scelza 2013).

Relating the emergence of monogamy to a wider "deep structure" of human society, Chapais (2013) compares human and extant nonhuman primate societies to model possible evolutionary sequences. He notes the character of human monogamous stable pair bonds in relation to strong bonds between human groups, where kin ties are traced on both male and female sides, with connections between kin and affines. He also notes female choice as a significant factor in mobilizing systematic male provisioning. Recognition of kin on both sides—maternal and paternal—could have given female hominins increased leverage in resistance to unrelated and potentially aggressive males, shifting the dynamic of male competition from "the arena of physical dominance to the arena of economic competence" (Chapais 2013, 62). The outcome would come to resemble typical hunter-gatherer bride-service economies. This suggests that a focus on female strategic alliances, which have tended to be neglected in the past in favor of male alliances, may be the most fruitful area of future research on the origins of human society.

SEE ALSO: Fire, early human use of; Brain Evolution and Energetics of Encephalization; Social Brain Hypothesis; Infanticide; Partible Paternity; Marriage: Approaches from Evolutionary Ecology; Cooperative Child Rearing: The Evolution of Alloparenting in Hominins; Fatherhood, Biosocial Perspectives on; Parental Effort and Investment; Grandmother Hypothesis, Grandmother Effect, and Residence Patterns; Sexual Dimorphism in Hominin Ancestors

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