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Evolution of Long-Term Pair-Bonding in Humans

Kelly Rooker and Sergey Gavrilets
University of Tennessee, Knoxville, TN, USA

Synonyms

[Evolution of mating systems](#); [Human evolution](#); [Social monogamy](#)

Definition

Long-term pair-bonding occurs when one breeding male and one breeding female share a common territory, associating with each other for more than just one breeding season regardless of whether or not they currently have any offspring together. In humans, long-term pair-bonding can occur via monogamous or polygamous relationships.

Introduction

Humans have previously been called the “uniquely unique species” (Alexander 1990). Despite there being many different factors contributing to this uniqueness (e.g., the large brain), one of the most important is humans having a multi-male, multi-female social organization and a long-term pair-bonding mating system (Flinn

et al. 2005; Geary and Flinn 2001; Hill et al. 2011). Most species living in groups composed of multiple males and multiple females are promiscuous, while most pair-bonded species live in groups comprised of only one male and one female. There are no primates other than humans where multiple reproductive pairs live together (de Waal and Gavrilets 2013). Nuclear and extended families, as well as parental investment in offspring, are characteristics found in all human societies (Geary and Flinn 2001); such characteristics clearly set humans apart from their African ape ancestors (de Waal and Gavrilets 2013; Flinn et al. 2005). The question then is how could humans have evolved such a unique combination of social organization and mating system.

In fact, long-term pair-bonding in humans has always been considered an evolutionary mystery. Why is this practice so common in human societies around the world? How did long-term pair-bonding first evolve in humans? What were the evolutionary pressures making it beneficial to humans? Although these questions have all been asked repeatedly for decades, even centuries, there has yet to be any real consensus on their answers. Still, much progress has been made.

Monogamy and pair-bonding often get used interchangeably, but “monogamy” can mean many different things. For instance, *cultural monogamy* refers to human institutions such as marriage. *Sexual monogamy* is in reference only to sexual relations; one male and one female will mate exclusively with one another, but have no or

few interactions outside of that sexual intercourse. Similarly, *genetic monogamy* is when all offspring produced by one male or female in that pair have that same mother and father. Rates of genetic monogamy can be tested in the field by looking at the genetic makeup of all offspring produced (Reichard and Boesch 2003).

Finally, there is *social monogamy* or what is more commonly called *pair-bonding*. In social monogamy, one male and one female exclusively assort with each other. This assortment is not just in terms of copulations or the genetics of their offspring, but also in terms of with whom they live, where they sleep, and most generally where they spend their time (Reichard and Boesch 2003). In other words, under social monogamy, one breeding male and one breeding female will share a common territory, associating with each other for more than just one breeding season, regardless of whether or not they currently have any offspring together (Lukas and Clutton-Brock 2013).

It should be noted that many researchers do not restrict the word “pair-bonding” to involving *only* one male and one female. Rather, the term is often used more broadly to describe any lasting reproductive relations between particular males and females. For example, in polygyny where one male is having such lasting reproductive relations with multiple females, some would say that male is just having multiple distinct pair-bonds occurring simultaneously (Reichard and Boesch 2003). Using this terminology, humans as a whole are very much considered having long-term pair-bonds since every known human society has practiced either polygamy or monogamy (and hence long-term pair-bonding) (Chapais 2008). Considering only the raw number of human societies throughout the world (vs. also the populations of each of these societies), only about 17 % of such societies practice social monogamy. The vast majority of the rest (>80 %) practice polygyny. Even among the polygynous societies though, only a small minority of the men in each are actually polygynous; most males lack sufficient resources needed to support multiple female mates (Reichard and Boesch 2003).

True genetic monogamy is rare in humans, even in the socially monogamous cases (Reichard and

Boesch 2003). However, despite the widespread prevalence of extra-pair matings, there still has yet to be a human society with sexual promiscuity as the main form of mating system (Chapais 2008). Hence, for the rest of this entry, “long-term pair-bonding” will be synonymous with “social monogamy,” thus including both monogamy and polygamy. For cases where one male and one female *do* remain exclusive with each other, this entry instead refers to these as *strict monogamy*.

In addition to all these different types of monogamy, the word “monogamy” can also imply differences in duration. *Long-term monogamy* implies the one male and one female which form a pair will remain together across many breeding seasons. *Life-long monogamy* is then a different term used to describe when a male and female’s long-term monogamy in fact lasts for the rest of their lives. Conversely, *short-term monogamy* refers to monogamy that typically lasts for only one breeding season or year; one male and one female will be monogamous to each other, but only within that limited amount of time. Cases where pairs practice short-term monogamy throughout their lives, but in each instance of short-term monogamy have a different partner, are instead referred to as practicing *serial monogamy* (Reichard and Boesch 2003).

For example, many species of birds will be monogamous throughout each breeding season (or other period of time), but then each individual will have a different mate come next breeding season (Reichard and Boesch 2003). This means such birds are monogamous *within* breeding seasons, but not monogamous *between* breeding seasons (i.e., serial monogamy). In addition, human societies where divorce is common, as well as remarriage for both men and women following divorce, have mating systems resembling serial monogamy (Reichard and Boesch 2003).

Monogamy from a female’s perspective often makes a lot of sense. In eutherian mammal reproduction, only females must go through the costly periods of internal gestation and lactation (Opie et al. 2013). Not only are such activities quite energetically expensive for females, they make predation, death, and other injuries to the female more likely. In addition, due to relatively long

gestation and lactation periods, female eutherian mammals are also much more limited than males are in the quantity of offspring they are able to have in a lifetime. While males are limited only in the number of copulations they are able to obtain with fertile females, females have their main constraint as time (Kappeler 2013).

In a monogamous mating system, having a male remain with/around a female could help the female in any number of ways, be it protection of her and/or her offspring/resources, help in securing meat or other valuable resources, and/or help in caring for any offspring produced from the union. All of these would help loosen the female's main constraint (time) either by allowing a female's interbirth interval to be shortened (e.g., by a male helping with parental care of the older offspring), improving her health which leads to longer times of fertility (e.g., by provisioning the female with valuable foods), and/or lengthening her life and hence her fertile period (e.g., by protecting her from other males or predators) (Kappeler 2013).

On the other hand, of critical importance when considering the evolution of long-term pair-bonding is why *males* would ever play their role in a socially monogamous mating system. In eutherian mammals, males have much greater potential for producing more offspring throughout their lives than females (Kappeler 2013), due to the aforementioned female traits of internal gestation and lactation (Opie et al. 2013). This means that males mating with only one female throughout their lives are sacrificing all that "extra" reproductive potential. Thus, for long-term pair-bonding to evolve, there would have to be some fitness compensation present to make up for that loss in male reproductive potential (Kappeler 2013). The rest of this entry is primarily concerned with considering the many possible forms of such "fitness compensation."

Although certainly not prevalent, long-term pair-bonding is widespread throughout the animal kingdom. Long-term pair-bonding is most notably found in birds and mammals. Among mammals, about 3 % of species practice long-term pair-bonding (Kleiman 1977). Even the newer, upper estimate of 9 % of mammals practicing

social monogamy (Lukas and Clutton-Brock 2013) pales in comparison to the 90 % of birds estimated to practice social monogamy. However, these 3–9 % of mammal species are found in many different clades of mammals, and long-term pair-bonding is believed to have evolved independently upward of *sixty* different times in mammals (Lukas and Clutton-Brock 2013).

Such pair-bonding in mammals may appear to be strictly behavioral, but neurophysiology has also been shown to play a role. Certain neuropeptide pathways (e.g., oxytocin, arginine vasopressin, and prolactin) have been shown to have been co-opted to form pair-bonding reward pathways in several species of monogamous mammals, including primates (Lovejoy 2009). Compared to birds, social and genetic monogamy in mammals are tightly correlated, meaning mammals' rates of extra-pair copulations are relatively low (Lukas and Clutton-Brock 2013).

Rates of long-term pair-bonding of course vary significantly among mammal species. While some mammalian orders contain zero socially monogamous species, about 29 % of primate species are socially monogamous (Lukas and Clutton-Brock 2013). In addition, primates are unique among mammals in that social monogamy has evolved independently in every major primate clade, and there are relatively few transitions away from monogamy once it has evolved (Opie et al. 2013).

Among just anthropoid primates, long-term pair-bonding is believed to have evolved independently seven different times, three in Platyrrhini (New World monkeys) and four in Catarrhini (apes and Old World monkeys). Indeed, socially monogamous species among anthropoid primates today include species as varied as New World monkeys (e.g., marmosets, tamarins), Old World monkeys (e.g., De Brazza's monkeys, Sumatran surilis), and apes (e.g., gibbons, humans) (Sillen-Tullberg and Moller 1993). Despite social monogamy not being ubiquitous among primates, its widespread prevalence indicates there must be some significant benefit to species practicing social monogamy. Although this entry focuses on humans, many of the hypotheses and ideas presented below could similarly apply to many of these other primate species as well.

It is the aim here to first discuss the transition *to* long-term pair-bonding: what were human societies like prior to long-term pair-bonding becoming the norm? Second, the many hypotheses which have been given to explain the evolution of long-term pair-bonding in humans will be discussed. Then, both empirical and theoretical work will be looked at as they pertain to each of these hypotheses. Finally, other work which takes a broader look at the question of long-term pair-bonding in humans will be discussed.

Pathways for the Transition to Monogamy in Groups

Part of the debate surrounding the evolution of long-term pair-bonding in humans is over the ancestral social organization and mating system of genus *Homo*. Were human ancestors monogamous? Or promiscuous? Did they live solitary? In one-male groups? Or in multi-male, multi-female groups? These ancestral-state questions are still very much debated, with many researchers having wildly different, and often directly contradicting, views (Duda and Zrzavy 2013).

Humans, and many other primate species, are group living. Such groups of individuals come in various sizes, but all with their associated benefits and costs (Hill et al. 2011). For instance, groups afford members protection against both predators and other groups. Such protection could come from group members' alarm calling, alerting other group members of some impending danger, or in the form of an alliance against a predator or invading group. Groups can also facilitate resource sharing, whether it be with meat, other valuable foods, or other resources. Individuals in groups are better guaranteed a steady supply of nourishment, with food sharing in groups especially helping with food/resource scarcity in the event of a drought or other severe ecological conditions. In the case of species with alloparenting, group living can help with child-rearing and allowing females to have more offspring than they would be able to otherwise. Finally, group living may also help with acquiring mates. By living in groups with at least one male and one

female, potential mates are always nearby and mating attempts likely easier to facilitate (Flinn et al. 2005).

On the other hand, group living can also come with potential costs to all group members, primarily from ecological competition (for resources, mates, etc.) (Hill et al. 2011). Living in groups can result in conflict between group members. Such conflict can be energetically costly to those group members, even resulting in injury or death if fighting is the outcome. Living in close proximity to others can increase theft of resources, food, mates, etc., making group members expend more energy and time guarding such resources and again potentially fighting over them. Finally, visibility by a predator, disease, and other parasites becomes more prevalent when living in the higher population densities that come with groups. Such risk would be absorbed by all group members, not only potentially resulting in increased susceptibility to predation, lasting disability, and death but also potentially in loss of resources and other vulnerabilities (Flinn et al. 2005).

Humans' closest living relative, the chimpanzee, is certainly a group-living species. Chimpanzees live in highly promiscuous multi-male, multi-female societies. Most evidence does not point to monogamy being the ancestral state of the chimpanzee-human last common ancestor. Rather, their ancestral state was likely some type of promiscuity, with monogamy in humans being a derived trait. However, this broad framework still leaves much room for debate in terms of what that ancestral human social organization, and resulting mating system, specifically looked like (Chapais 2013). The following are the four main pathways which have been proposed for such an ancestral state.

Promiscuity

First, the *Pan*-human last common ancestor could have been very much like *Pan* (chimpanzees and bonobos). In this case, the ancestral state for *Homo* would be individuals living in fully promiscuous (i.e., with no stable mating bonds) multi-male, multi-female groups. From this backdrop, humans would have retained this multi-

male, multi-female social organization, but then evolved to a socially monogamous mating system from the promiscuous *Pan*-like one (Chapais 2013).

Harems

An often-favored alternative to the above is if the *Pan*-human last common ancestor had a harem-style mating system, similar to that of gorillas. In this case, the social organization would have consisted of groups made up of one male with many females (his “harem”) and then lone roaming males outside of any group. The one male in the harem would mate with all of the females in the harem and also provide protection/guard them, while the roaming males got few, if any, copulation opportunities. From this backdrop, humans would have reorganized into a social organization consisting of multiple males and multiple females making up any one group while still keeping their long-term pair-bonding structure (Chapais 2013). Evidence for this pathway includes humans’ *australopithecine* ancestors having large body size sexual dimorphism (larger than either chimpanzees, modern-day humans, or later human ancestors), which is indicative of fierce one-on-one male competition, as seen in gorillas (Geary and Flinn 2001). In addition, one mathematical modeling approach found this pathway to be the most likely one leading to humans (Nakahashi and Horiuchi 2012).

Multilevel Societies

A third alternative discussed is the idea of multilevel societies. Here, the chimpanzee-human last common ancestor would have lived with a social organization and mating system similar to hamadryas baboons. Under this framework, males still have harems (i.e., groups made up of one male and multiple females, all of whom that one male mates with and protects), but then multiple harems live together in larger groups, often referred to as “clans.” Under this backdrop, these larger groups would already be practicing long-term pair-bonding. However, from this humans could have even evolved strict (one-male, one-female) monogamy, since “clans” could contain “harems” of one male and precisely one

female. If the size of the male harem was reduced to only female per male, strict monogamy would be the effective result (Chapais 2013).

Strict Monogamy

Finally, although considered unlikely by many, it is also possible that strict monogamy was the ancestral mating system for humans. Similar to gibbons and other primates with such monogamy, monogamous pairs would have been spaced out geographically and not had any kind of group social organization. What evolved from this backdrop would then be the group social organization: monogamous pairs moving closer to each other, ultimately forming multi-male, multi-female groups while still retaining their monogamous mating system. Again, although this pathway is certainly a logical transition, there is little evidence supporting the chimpanzee-human last common ancestor being strictly monogamous (Chapais 2013; Sillen-Tullberg and Moller 1993).

Hypotheses for the Evolution of Social Monogamy

Regardless of from where exactly it came, there is no doubt that long-term pair-bonding evolved at some point in humans’ past. Similar to the debate over the ancestral state of *Homo*, there is also much debate over how long-term pair-bonding first evolved in humans. Again, there have been many different hypotheses proposed, some directly contradicting each other, and relatively little headway made in finding concrete answers as to which hypothesis is the most likely. Despite no consensus after decades of research, progress has still been made. Note some hypotheses presented below are unique to humans, while others are more widely applicable to many primates or even mammals in general. Some hypotheses are also highly dependent on one or more of the pathways discussed above, while other hypotheses could still be possible regardless of the specific pathway from which early humans evolved. Also note that some hypotheses below only work with regard to strict monogamy (these

will be noted), while most do not specify the type of long-term pair-bonding needed.

In general, all the hypotheses discussed below can be grouped into four main categories. The first is ecological. This hypothesis has gained much support for the evolution of social monogamy among nonhuman mammals, but is widely discredited as being a factor in the evolution of social monogamy in humans. The second group of hypotheses include those having to do with protection, of either the offspring, the mate, or one's self. The third group of hypotheses relates to food: provisioning of the mate, the offspring, or in cooperation. Finally, the fourth group of hypotheses involves conflict, either strictly between males fighting over mates, group-related, or among siblings produced by the same male. It should be noted that most of these hypotheses are not mutually exclusive, but rather two or more could have simultaneously contributed selection pressure to the evolution of long-term pair-bonding in humans.

Ecological Hypothesis

The first hypothesis discussed here is the "ecological" hypothesis (Komers and Brotherton 1997). Females are assumed to be solitary and relatively spaced out geographically (due to ecological competition), while males are roaming, looking for mates. However, because of the females' geographic spacing, it may become increasingly lucrative for a male to stick to just one female's range. Doing so will save males' energy resources expended in searching for females and also better guarantee males a mate. If they instead wandered, males would have to travel long distances between females with no guarantee of, first, even finding another female, and, second, her desiring to mate with said male once found (Komers and Brotherton 1997).

A recent study found the most likely ancestral state for all nonhuman mammals is solitary females and roaming males with overlapping ranges (Lukas and Clutton-Brock 2013). They then found social monogamy to have evolved in nonhuman mammals under conditions involving intense female-female competition, low female density, and where breeding females were

intolerant of sharing their ranges. Under these conditions, males would likely be unable to defend access to more than one female. Among all nonhuman mammals, socially monogamous species today do in fact live at significantly lower densities than solitary species, even after controlling for body size differences and despite the fact that both socially monogamous and solitary species share similar home-range sizes (Lukas and Clutton-Brock 2013).

Although considered by many to be a favored hypothesis for the evolution of social monogamy in nonhuman mammals, this hypothesis is much less accepted with regard to human evolution since humans did not likely come from solitary ancestors. Each of the three pathways which assume humans had non-strictly monogamous ancestors (i.e., three of the four discussed above) all centers on early humans living in groups of more than two individuals (Kappeler 2013). However, it is certainly possible that changes in early human dietary patterns (even within groups) lowered female densities, making it much harder for one male to guard multiple females. In this way, a transition from polygyny to strict monogamy could still have been facilitated in humans under the ecological hypothesis (Lukas and Clutton-Brock 2013).

Protection Hypotheses

The following three hypotheses all deal with protection as the main selection pressure on early humans for the evolution of long-term pair-bonding.

The first hypothesis under this category deals with protection of one's offspring, namely, protecting them against the risk of infanticide. Infanticide, the practice of killing an infant not one's own prior to it being weaned, has been widely documented across primates (van Schaik and Dunbar 1990). In most instances, infanticide is committed by a new alpha male who has just taken over a group. By killing any infants not his in the group prior to their weaning, he is forcing their mothers to return to fertility sooner, increasing the probability of him having offspring with one or more of those ex-mothers and hence increasing his overall fitness. Such evolutionary

benefit for males has already been well-established (van Schaik and Dunbar 1990).

Having an offspring killed in its first year of life is clearly very costly; the biological mother and father would each get zero fitness benefit from the said offspring, despite the mother (and possibly the father as well) investing much time and energy into the pregnancy and early life of the offspring. As such, it may behoove the father to stick around that offspring up until the point it gets weaned in order to protect it from any infanticidal attacks by other males. In doing so, such a male has effectively formed the groundwork for having a pair-bond with the mother of his offspring (van Schaik and Dunbar 1990).

Infanticide is quite common among primates, in large part due to altriciality (and in turn long durations of lactation), which makes the infants more susceptible to having infanticide committed against them (Opie et al. 2013). These facts would hold for humans as well. In addition, Opie et al. found that in primate phylogeny, infanticide by males typically precedes social monogamy (Opie et al. 2013). They concluded that not only is social monogamy in primates much more likely to evolve in the presence of high male infanticide, once social monogamy *does* evolve, it is more likely for there to be a subsequent decline in the amount of male infanticide than an increase in the level of polygyny (Opie et al. 2013).

There is still much debate over the role of infanticide in the evolution of long-term pair-bonding in nonhuman mammals. Contrary to the Opie et al. work discussed above, other prominent researchers (Lukas and Clutton-Brock 2013) found “the available evidence suggests that male infanticide is unlikely to be the principal mechanism for the evolution of social monogamy in mammals.” Despite finding rates of male infanticide among socially monogamous species (9 %) to be lower than rates among solitary species (27 %), they concluded from their analysis that this difference was most likely due to “an independent evolution of the two traits” (Lukas and Clutton-Brock 2013).

One key factor considered there was that in most socially monogamous mammals, the duration of female lactation does not typically exceed

her gestation period. However, it is in cases where such lactation duration *does* exceed gestation length that a benefit would be expected for males killing other males’ offspring (Lukas and Clutton-Brock 2013). This is because female mammals will not typically have two unweaned offspring concurrently. Hence, if lactation duration exceeds gestation length, there is benefit to the male in killing one offspring, so the next (his) can be born sooner and the female will still only have one unweaned offspring at any given time (Opie et al. 2013).

For example, in modern-day humans, one study found 50 % of nursing women to return to normal estrous cycling within 10 months of giving birth and 100 % of the women by 20 months, while the cross-cultural average age of weaning in humans is 30 months (Quinlan 2008). In chimpanzees, offspring are typically weaned around 4 years of age, while females on average only have one offspring every 5 years, meaning female chimpanzees will also only have one offspring to care for at a time (Pillsworth and Haselton 2006).

The second hypothesis under the category of protection deals with mate guarding or a male protecting his mate. In most formulations, this hypothesis centers on the idea of paternity certainty. After mating with a female, males can either stay around that one female (“guarding” her) or leave her in search of new mates. By guarding her, a male can prevent other males from mating with that female (which can increase his fitness by reducing or eliminating completely any sperm competition), as well as offer protection to her physical well-being (discussed later). Roaming males attempting to copulate with a guarded female normally face a high cost-to-benefit ratio in any fight with a male guard, and the guards typically win these fights (Reichard and Boesch 2003).

In general, a male must choose between acquiring *more* mates and increasing his paternity certainty with *one* mate. If conditions make the latter more important to a male’s fitness than the former, one could expect pair-bonding to evolve, as the male constantly remains near his one mate to help ensure paternity certainty, which would increase his fitness (Hawkes 2004). However, note that

mathematical models of this hypothesis have not supported mate guarding as a strong enough selection pressure for long-term pair-bonding to evolve (e.g., see Gavrillets (2012)).

Among socially monogamous species, levels of mate guarding vary drastically. Kokko and Morrell (2005) constructed a theoretical model and found that males will evolve to guard little if females are either very faithful or very unfaithful. The intuition behind this finding is again that in gaining paternity, males face a trade-off between having more mates and increasing paternity certainty in their one mate. Hence, if a female is highly faithful, her mate would be able to gain more mates by guarding little, with little risk to the paternity certainty of his mate's offspring. Similarly if a female is highly unfaithful, her mate would likely have little to lose by trying to gain more mates by guarding little since even if he spent his time/energy instead guarding her, she would likely still sneak copulations outside this mating bond. In addition, Kokko and Morrell found that attractive males are predicted to guard less, with the intuition being they are more likely to find *more* mates, and hence paternity certainty becomes less crucial in the trade-off (Kokko and Morrell 2005).

A related hypothesis to mate guarding, involving the direct physical protection of one's mate mentioned earlier, is the bodyguard hypothesis (Chapais 2008). Rather than paternity certainty being the driving selection force behind the evolution of long-term pair-bonding, it could instead be physical protection of the female. If a group is such that a female must be constantly worried about harassment/violence from other males, her (and her future offspring's) fitness would be increased by having the male stick around her. However, in doing so he would also be increasing his paternity certainty, especially if the harassment she was receiving was sexual in nature, meaning the mate guarding and bodyguard hypotheses are largely indistinguishable (Chapais 2008).

The last hypothesis in this category deals with protection of one's self, namely, against the threat of sexually transmitted diseases (STDs) (Kokko et al. 2002). This hypothesis hinges on the fact that STDs were increasingly problematic among

early humans, as group size and population density increased (i.e., as humans became increasingly ecologically dominant). As these STDs became more widespread and lethal, the costs of having sexual relations with multiple partners greatly increased. If such costs increased sufficiently enough, it could have been better in terms of a male's fitness to have *fewer* mates rather than more. If that was the case, individuals would have switched to a strategy favoring remaining faithful to one or two mates rather than promiscuity, and hence long-term pair-bonding could have evolved (Kokko et al. 2002).

In addition, using the same reasoning, STDs could influence female choice. A female may view a dominant male, or a male who has mated with many females, as too risky to mate with due to the threat of getting an STD from him. Hence, females may actively begin rejecting mating with such males. Mathematical models have supported this hypothesis as a way for mating systems to change and long-term pair-bonding to become more prevalent (Kokko et al. 2002).

Provisioning Hypotheses

These next three hypotheses all fall under the category of food or other provisionings as the key selection pressure on the evolution of long-term pair-bonding in early humans.

The first hypothesis under this category, food-for-sex, deals with males provisioning their mates or, in particular, males provisioning females in exchange for copulations. As hunting became more important in early human history, and also the nutrients obtained from meat more valuable, females could increase their fitnesses by mating with males in order to obtain more high-benefit foods or other valuable resources. Females were able to increase their fitnesses through such beneficial provisionings, while males increased their fitnesses by increasing their likelihoods of obtaining mates. Provided such benefits were strong enough, and these exchanges consistently occurring between the same male and female, long-term pair-bonding could ultimately be selected for (Reichard and Boesch 2003).

Such exchanges of important foods for copulations are routinely seen in the genus *Pan*

(chimpanzees and bonobos). “Important foods” include meats and fruits high in fats and/or proteins, as well as foods requiring increased search time (Lovejoy 2009). Looking at primates, there is an association between the evolution of social monogamy and a reliance on relatively scarce foods (Lukas and Clutton-Brock 2013). Fruit, compared to foods like gum, bark, and fungi, offers much higher nutritional value while also being a more limited resource. Indeed, fruit constitutes a main part of the diet in about 90 % of socially monogamous primate species and only 28 % of solitary primate species. Conversely, foods like gum, bark, and fungi constitute the main part of the diet in about 40 % of socially monogamous primate species and 78 % of solitary primate species (Lukas and Clutton-Brock 2013).

In addition, a hypothesis related to both the above and the ecological hypothesis, the resource defense hypothesis, posits that social monogamy could have evolved from a male defending a highly valued (e.g., due to food resources) territory, able to keep all intruders out. In this case, a female may want to remain in that territory permanently, not so much because of the male himself, but because of the valuable territory he is able to control (Reichard and Boesch 2003).

The next hypothesis in this group, paternal care, looks at a different type of male provisioning, this time to his offspring (Benshoof and Thornhill 1979). Parental investment is any expenditure benefiting an individual’s offspring at some cost to that individual (even if just an inability to invest that energy into other fitness components) (Quinlan 2008). Offspring fitness is increased when a male is around to help provision the said offspring. Provided this helping male is indeed the offspring’s biological father, the male will be helping his own fitness as well (Wittenberger and Tilson 1980). 59 % of socially monogamous mammal species have been found to have regular carrying or provisioning of offspring by males, whereas only *three* nonmonogamous mammal species have such carrying or provisioning (Lukas and Clutton-Brock 2013). Mammals in particular may require the extra help from offspring provisioning because of that special energy-intensive (i.e., 670 kcal/

day in humans) lactation period in a female mammal’s life (Quinlan 2008).

In addition, some researchers believe that as the human brain got bigger and human infants became increasingly dependent on others (altricial) during the early years of their lives, mothers were no longer able to care for their offspring alone (Benshoof and Thornhill 1979). For instance, children cross-culturally consume more calories than they produce until at least age fifteen; contrast this with chimpanzees who typically produce more calories than they consume by age five (Conroy-Beam et al. 2015). Over the past 4 million years, human ancestors underwent a doubling of the length of their developmental period (Geary and Flinn 2001). Among modern-day hunter-gatherers, females on average have one child every 3–4 years, meaning most women will have multiple dependent offspring to care for at the same time, unlike in chimpanzees and other primates (Pillsworth and Haselton 2006). In addition, parental investment in offspring does not just stop; rather, it often continues all the way through to become “grandparental investment” (i.e., alloparenting) (Conroy-Beam et al. 2015).

If more than one adult was needed to care for an offspring, fitness-wise it made sense that that “other adult” would be the offspring’s biological father, since no other adult (besides the mother) would have as much genetic material invested in the offspring. As hunting became more important in the early human diet, males (the hunters) were increasingly needed as meat providers. Hence it could have been some combination of increasingly altricial offspring, the importance of hunting, and bipedality (meaning humans were more easily able to carry offspring and/or the provisionings) that could have helped long-term pair-bonding to evolve, provided paternity certainty was sufficiently high (Benshoof and Thornhill 1979). However, two separate phylogenetic analyses suggest that paternal care is more likely to be a secondary adaptation occurring either with or after the evolution of long-term pair-bonding, rather than a main driver of this evolution (Lukas and Clutton-Brock 2013; Opie et al. 2013).

The next hypothesis under this category, related to both parental investment and food-for-sex, is that of economic interdependence (Conroy-Beam et al. 2015). Much research has gone into the evolution of a division of labor among early humans, namely, why, how, and when did men and women become solely responsible for specific and different tasks or chores. The economic interdependence hypothesis hinges on the fact that, on average, men have more strength/endurance needed for hunting large game than women do. In addition, during pregnancy and lactation, women are already expending more energy in their daily lives than men and would likely encounter increased risk during large-game hunts (Conroy-Beam et al. 2015). For example, a pregnant female requires 8–10 % more in caloric intake than a nonpregnant female and a lactating female about 26 % more (Pillsworth and Haselton 2006).

Under this hypothesis, males and females would then engage in economic partnerships, whereby each sex would focus on that resource acquisition they could accomplish most efficiently. Hence, males would provide meat for a female and her offspring, and the female would share with him the foods she had produced or gathered. Not only does this give females easier access to valuable meat, it also provides males with protection in the event that he is unsuccessful in hunts (Conroy-Beam et al. 2015).

A related idea to this involves the idea of cooking (Wrangham et al. 1999). Cooking food is beneficial in terms of (1) calorie intake, (2) protection from disease or other sickness due to food poisoning, and (3) increasing the edible range of plant foods through digestibility. While men went out to hunt, women were left at the camp and hence became in charge of cooking. While males relied on women then for the cooked food each night they came back to camp, women in turn also relied on the men to help protect these valuable cooked foods as well as any foods which had already been gathered but yet to be cooked. It is in this way that such a relationship benefited both the male and female and could have fostered the formation of long-term pair-bonds (Wrangham et al. 1999).

Once producing one's own food became prevalent among early human societies, there were two main strategies each individual could adopt, producing vs. scrounging. An individual following the producing strategy would be focused on producing his/her own food and then storing such food for later consumption. On the other hand, an individual following the scrounging strategy would instead not be focused on producing his/her own food, but rather finding already-produced food elsewhere. Since females were naturally less mobile (due to the demands and restrictions of pregnancy, lactation, and parental care) and males naturally stronger, a logical division of labor resulted where females followed the producing strategy and males the scrounging strategy. However, this means males were often stealing already-produced foods from females, making it in females' best interests to "buy protection" in any way they could. Since one such form of payment could be the female giving one male her exclusive reproductive rights, long-term pair-bonds could have evolved under this selection pressure (Wrangham et al. 1999).

Conflict Hypotheses

Finally, this last category of hypotheses all deals with conflict as the main selection pressure for the evolution of long-term pair-bonding in early humans.

The first hypothesis in this category, one specifically relating to humans, has to do with the idea of leveling (Chapais 2013). As tool and weapon use became increasingly common across early humans, male size/strength dimorphism became less important in fights. Just because an alpha male is bigger and stronger than a lower-ranked male does not necessarily give that alpha male an advantage in a physical confrontation if the lower-ranked male has more and/or better tools/weapons available to him than the alpha male (Chapais 2013). This meant that any fights between two now-evenly-matched males were much more costly to both males involved and also more likely to end without a winner despite the larger cost involved. Hence, it was harder and more costly for an alpha male to protect any "harem" of females, making pairs of one male

and only one female increasingly common until only strict monogamy was left (Chapais 2008).

Males fighting over mates can be very costly to a group as a whole. If males' time and energy are being spent in intragroup conflict, there will be less time and energy available to devote to intergroup conflict. As such, this second hypothesis under the category of conflict predicts that groups with more monogamous pairs will be more successful in the long term than promiscuous groups which routinely have intragroup fighting over mates. This hypothesis posits that since cooperation is key to early human survival and long-term pair-bonding supports such cooperation, long-term pair-bonding could have been able to evolve (Chapais 2013).

There is little doubt that cooperation is in fact key to early human survival. Humans are a cooperative group-living species, and coalitions are often formed in human social competition (Geary and Flinn 2001). Among contemporary hunter-gatherers, cooperation is shown in ways far exceeding that of other primate species. Such examples include sharing food across all members in the group, groups having high levels of alloparental offspring care, cooperative hunting or other food acquisition strategies, construction and maintenance of living spaces, transportation of children or resources, contribution to public goods, etc. (Hill et al. 2011).

There is some evidence for this hypothesis from the palaeontological record (Lovejoy 2009), albeit rather controversial. Fossils 4.4 million years old of *Ardipithecus ramidis*, a species occurring relatively soon after the hominin/chimpanzee split, indicate reduced sexual size dimorphism and reduced upper canine teeth size, both of which are indicative of a decline in male-male conflict (Lovejoy 2009). *Homo erectus* appeared about 1.5–2 million years ago with males about 20 % heavier than females (similar to the sexual dimorphism seen in today's humans). Contrast this with the 60 % heavier males found in the *Australopithecine* species from up to 5 million years ago (Geary and Flinn 2001). If reduction in intragroup conflict was a driving force behind early human evolution, it would be expected that related characteristics like sexual dimorphism

would evolve quickly in humans' ancestral line. The above fossil record provides support for this idea.

One intriguing alternative related to this hypothesis is if long-term pair-bonding evolved via cultural evolution (i.e., as an institution via marriage) instead (Henrich et al. 2012). This means that instead of relying on the evolution of *gene(s)* relating to long-term pair-bonding, it is instead *cultural* traits (norms) that are important in this evolution. Humans and their ancestors are still sexually dimorphic in size (as discussed above), an indication that the species should perhaps not be considered genetically monogamous and that it is culture playing the crucial role instead (de Waal and Gavrilets 2013). However, note these cultural hypotheses would be operating on a much shorter time scale than the genetic hypotheses (i.e., tens of thousands vs. hundreds of thousands of years) (Fortunato and Archetti 2010).

Henrich et al. question how one-male, one-female (strict) monogamy came to be when approximately 85 % of societies (meaning raw number, not considering each society's population size) in the anthropological record allow for polygyny. They reason that strict monogamy was favored by cultural evolution because of how much it benefits groups (i.e., cultural group selection). Similar to the above *gene* evolution, because of those benefits, groups with strict monogamy would do better in the long term than their counterpart groups with polygamy (Henrich et al. 2012).

So where do such benefits come from? As already discussed, monogamy can lower male-male competition within a group; it can also reduce the number of unmated males within the group. This is true regardless of the mating system of the comparative group (i.e., promiscuous vs. polygynous). Having fewer unmated males within a group can reduce crime rates (for murder, rape, assault, robbery, etc.) and other personal abuses which are harmful to groups. Males low enough in rank/status that they get no mating opportunities will have essentially zero fitness and thus, evolutionarily, nothing to lose. This creates males who are more willing to take risks in order to get copulations and hence creates

conflicts within their groups (Henrich et al. 2012). Again, groups who impose long-term pair-bonding as the social order will do better than those that do not. Under this hypothesis, even if selection on the actual genes is not strong enough to produce long-term pair-bonding, such evolution is still possible, just considering instead evolution on the related cultural traits.

Finally, the last hypothesis considered here deals with conflict between a male's various offspring, especially if produced by different females (Fortunato and Archetti 2010). As it became the norm for humans for property and/or other resources to be passed on to the next generation, more clearly defined familial lines became increasingly beneficial. A father's fitness can be decreased by having to split his wealth (resources) among the more offspring he would have by having more mates. Strict monogamy would allow male/female mating bonds to be stable over time and hence all the male's resources to be given to his offspring, all full siblings. In this way, strict monogamy could simply be a strategic behavior on behalf of males and females in allocating their resources to the next generation (Fortunato and Archetti 2010).

In particular, Fortunato and Archetti (2010) constructed a mathematical model and found two conditions which would make strict monogamy (or "monogamous marriage" in their words) the most beneficial cultural mating system. First is when there is unigeniture, meaning only one offspring inheriting all of a parent's wealth, and second is when women are more faithful in a monogamous bond than a polygynous one. If the latter is the case, while men would still have that fitness loss from not mating with more than one woman, they *would* get a benefit from that one woman being more faithful than otherwise (i.e., increased paternity certainty). Note the female of this long-term pair-bond would also benefit, in that her male mate would be investing his resources exclusively in her children for the next generation (Fortunato and Archetti 2010).

This hypothesis could help explain why monogamous marriage is so common in societies with intensive agriculture (e.g., plow or irrigation agriculture of much of Europe and Asia, as

opposed to hoe agriculture or pastoralism of much of sub-Saharan Africa). In intensive agriculture, land is often the limiting resource, so splitting land among multiple heirs can only go so far. Hence, this hypothesis would be predicted to have much greater selective pressure under intensive agriculture than other forms of agriculture (Fortunato and Archetti 2010).

Comparative Work

Most of the research discussed above focuses on only one of these hypotheses. There is relatively little comparative work done pitting such hypotheses against each other. One exception to this is Gavrilets (2012). In this paper, Gavrilets constructed models for several of the above hypotheses in order to look at how long-term pair-bonding could have evolved in early humans' past. In particular, he found that long-term pair-bonding was rarely predicted to evolve in (1) the baseline scenario ("communal care"; males allocate some amount of effort toward helping *all* offspring in their group), (2) with mate guarding, (3) with food-for-sex, and (4) with "mate provisioning" (equivalent to the food-for-sex hypothesis except males are only able to provision one female and females to be provisioned by one male) (Gavrilets 2012).

However, long-term pair-bonding *was* able to evolve provided two things were present: (1) inequalities between males in their fighting abilities (i.e., rank among males in a group) and (2) differences in females in both "faithfulness" (how faithful any given female will be to her mate) and choosiness (for a male who will provision her more). These results imply that it is likely that more than just mate guarding or food-for-sex is needed in order for long-term pair-bonding to evolve. Not only is male rank important (since lower-ranked males may initially be the only ones who do better pursuing a pair-bonding mating strategy), but females' ability to choose mates (namely, those who provision more and/or provide more care) is also important in allowing long-term pair-bonding to evolve (Gavrilets 2012).

The above study looked at individual fitnesses, meaning how different mating systems could have evolved by benefiting the individuals within such a system (Gavrilets 2012). Another theoretical study instead took a group selection approach, looking at how different mating systems could have evolved by benefiting *groups* as a whole (Nakahashi and Horiuchi 2012). These authors constructed a mathematical model looking at the evolution of the alpha male strategy, as well as female mating and grouping strategies. In particular, they found that a human-type mating system (i.e., one in which groups consist of multiple females and multiple males, male-male competition is weak, and there is no female promiscuity) can evolve when having a larger group is beneficial (e.g., in defense against other groups) and when the cost of female promiscuity is large (e.g., due to the many types of human venereal diseases) (Nakahashi and Horiuchi 2012).

Conclusion

Despite all the research and curiosity surrounding the evolution of long-term pair-bonding in humans, few concrete answers have yet to be obtained. In particular, there is still debate over the ancestral mating system in early humans, as well as the main selection pressure(s) resulting in humans switching their mating system to one of long-term pair-bonding. Indeed, researchers still contradict each other over whether the chimpanzee-human last common ancestor had a promiscuous mating system (like chimpanzees), a harem-style polygynous mating system (like gorillas), or multilevel societies (like hamadryas baboons). Many of the hypotheses for the evolution of long-term pair-bonding in humans have more support under only one of these mating system ancestral states, making this a related, and equally important, research question.

In terms of how long-term pair-bonding evolved and whether strict monogamy was a culturally and/or genetically evolved trait in humans, these are both still very much unanswered research questions. Many different researchers have contributed much to this ever-growing

body of literature spanning over a century, but few agreed-upon answers have yet been obtained. Some hypotheses have certainly gained more support throughout the years than others, but there are still so many being actively considered. The time is ripe for researching human origins, and progress will likely be made in this upcoming decade. Being human, it is only natural to ask the question of from where did this species come and to investigate those traits that make humans the “uniquely unique species” (Alexander 1990). The human universal of forming long-term pair-bonds is just one such trait.

Cross-References

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- ▶ [Australopithecus Group](#)
- ▶ [Biparental Care](#)
- ▶ [Breeding Systems](#)
- ▶ [Ecology of Pair-Bond Stability](#)
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- ▶ Sexual Size Dimorphism
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- ▶ Social Monogamy
- ▶ Social Monogamy (Versus Genetic Monogamy)
- ▶ Why Humans Are Unique

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