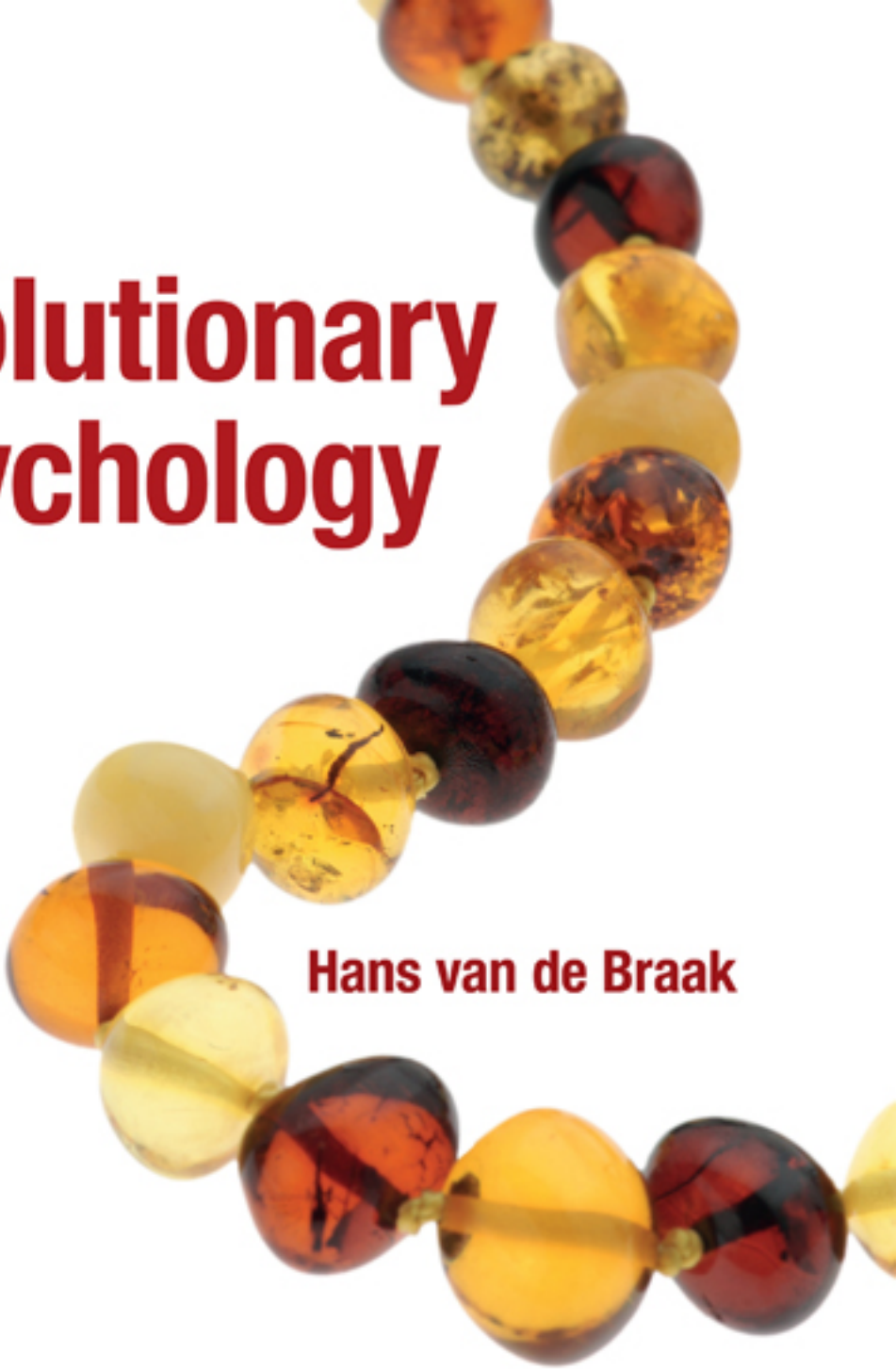
Evolutionary Psychology



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ALWAYS LEARNING

PEARSON

Evolutionary Psychology

Trivers argued that it is the relative parental investment of the sexes in their offspring that controls the operation of sexual selection. The sex which invests the most will be selective about whom they accept as a mate, and the sex which invests the least will compete among themselves for a mate. The greater parental investment by females represents the limiting resource with the result that the competition for mates of the limiting sex increases. But animals live in different circumstances: in some species both parents provide parental care (e.g. swans, modern humans), while in other species only females care for their offspring (e.g. elephant seals, gorillas). How much would the strength of sexual selection differ in these situations? How can the difference be explained?

The different strength of sexual selection

The ability of males to control the access of rivals to potential mates is an important factor that accounts for the different strength of sexual selection (Emlen and Oring 1977). This control can be direct by the physical herding of potential mates. In many ungulates, such as antilopes and gazelles, females and young aggregate into small herds which enables a better detection and avoidance of predators. The reasons for herding are unrelated to reproduction, but one result is that it increases the male potential for control of multiple mates. Control can also be indirect by managing the resources that are needed for successful reproduction. For example, humming birds depend on nectar feeding. When nectar production by flowers is high, territorial defence becomes feasible. Females rear the young alone but need a reliable source of nectar. That is why males allow females to nest within their territory, but aggressively exclude all rivals.

Control is largest when a polygynous male monopolises multiple females, as in elephant seals. His monopoly implies that he will prevent other males from reproduction. In this one-male, multi-female mating system, the male defends the herd and mates with females who care for the offspring. In this kind of mating system, sexual selection is strongest because the more females a male can control, the more intense the fights with rivals, and the greater the differences in the body sizes of the sexes. The strength of sexual selection is weakest in the monogamous mating system. In this system, each sex has one mate for life. Small or absent differences in body sizes of the sexes indicate the lesser strength of sexual selection. In monogamous species, such as albatrosses, swans, gibbons or modern humans, the males are not excluded from reproduction as in one-male, multi-female mating systems.

To summarise, females differ from males, first, because they have few, large gametes and, second, because they invest heavily in offspring. This explains why the female sex is the limiting resource for reproduction in the male sex, and why this sex competes strongly over mates. Thus, sexual selection solved the problem of the limiting female resource. This process of sexual selection is stronger in one-male, multi-female mating systems than in one-male, one-female mating systems because the polygynous male has a greater degree of control over the access to females.

4.4 Mating systems in human evolution

We have seen above that the strength of sexual selection depends on the kind of mating system. We will now focus on the origins of human mating systems. What kind of mating systems do primates have? And which mating systems were relevant

in the evolution of humans? Modern humans tend to live in pairs, but how did we end up in this mating system? Did early *Homo sapiens* have a one-male, multi-female system as did gorillas? Or a multi-male, multi-female system like chimpanzees who are promiscuous, that is, have sex with different partners?

What is a mating system?

Mating systems can be defined according to the number of mates that sexes have. Other criteria might be the duration of the bonds between sexes, the ability to control access to mates, and the means through which such control may be achieved. Stephen Emlen and Lewis Oring (1977) proposed an influential classification of mating systems, based on the degree of monopolisation of mates. Their classification was predictive, based on the following logic as summarised by Shuster and Wade (2003):

- Males compete with one another for access to mates.
- Like competition for scarce resources, male reproduction is limited by the spatial and temporal availability of sexually receptive females.
- The strength of sexual selection depends on the rarity of receptive females in relation to the abundance of competing males (so-called 'operational sex ratio').
- Sexual selection favours male traits that allow them to find and monopolise mates.
- Ecological constraints on male monopolisation attempts lead to a species-specific pattern of male–female associations, called a 'mating system'.

polygyny
one male-male, multi-female mating system in which multiple females mate with a single male.

serial monogamy
pairs that mate and raise offspring cooperatively, but then choose to mate with new partners.

Emlen and Oring (1977) made predictions about the kinds of mating systems that resulted from the reproduction and ecology of females. For example, we may predict that the one-male, multi-female mating system is likely to evolve when females form dense clusters and their offspring don't need male parental care. On the other hand, when females are scattered due to widely dispersed food resources, or when young need care from both parents, one may expect that a one-male, one-female mating system will evolve. Now that we know what mating systems are and how they allow us to make predictions, we need to know what kind of mating systems primates have (Box 4.2 Mating systems in primates).

BOX 4.2 Mating systems in primates

- The term ***monogamy*** (Greek *monos* = one; *gammos* = marriage) refers to a one-male, one-female mating system in which each sex has a single mate for life. Among primates, monogamy occurs in gibbons, lemurs, tamarins, marmosets and humans. Humans tend to be monogamous, but the pattern of marriage, divorce and remarriage suggests **serial monogamy** whereby men and women have successive partners over their lifespans (Fisher 1993).
- The term ***polygyny*** (*polus* = many; *gunē* = female) refers to a one-male, multi-female mating system in which multiple females mate with a single male. This system is common in baboons, gorillas, orangutans, and occasionally in humans. In orangutans, single males defend a group of females and their offspring, distributed over a large area. This variant is known as 'exploded' polygyny.
- The term ***polygynandry*** (*polus* = many; *gunē* = female; *andro* = male) refers to a multi-male, multi-female mating system in which both sexes are variable in their mate numbers. In this system, sexual relationships are promiscuous, that is,

short-term and indiscriminate with different mates. This mating system is common among macaques, many baboons and chimpanzees. In chimpanzees, several related males cooperate to defend a group of widely distributed females and their offspring. This system of polygynandry is also known as multi-male polygyny.

- The term ***polyandry*** (*polus* = many; *andro* = male) refers to a mating system in which multiple males mate with a single female. Polyandry is a rare mating system among mammals. It has, for example, been recorded that people in Northern India and tamarins sometimes engage in polyandry. Figure 4.1 depicts the mating systems that prevail in primates.

How did human mating systems evolve?

polygynandry
multi-male, multi-female mating system in which both sexes have a variable number of mates.

polyandry
one female, multi-male mating system in which multiple males mate with a single female.

polygynamy
mating system in which the home range of one male overlaps those of several females.

Many human cultures allow polygyny, but for the vast majority of people, monogamous relationships are the norm. Only a minority of wealthy, powerful men have the means to acquire and maintain multiple wives. How did human mating systems evolve? As humans are primates, we assume that primate models provide important insights about the origins of human sexuality. In order to reconstruct how human mating systems evolved, we focus on the phylogeny of humans and other primates. Recall, a phylogeny is the genealogical history of a group of organisms, represented by its hypothesised ancestor–descendant relationships. The diagram in Figure 4.2 shows the hypothetical stages in the evolution of the mating systems in humans and African apes, based on a reconstruction by Bernard Chapais (2008).

Chapais (2008, 2010) argues that the common ancestor of chimpanzees and humans probably formed large multi-male, multi-female groups where males stayed in the group after puberty, and females emigrated to other groups at sexual maturity. Polygyny, or one-male, multi-female mating groups emerged later due to males who monopolised a small number of females within large multi-male, multi-female groups. Instead of spatially separate one-male, multi-female units as in gorillas, it is more parsimonious to suppose a group structure with members of both sexes. In several monkey species (e.g. baboons, proboscis monkeys), polygynous units are also nested within larger multi-male, multi-female groups.

Precursors of the genus *Homo* had a mating system which consisted of males living with a small number of females within a large multi-male, multi-female group. The transition from polygynous units to monogamous pairs would require a reduced number of females associated with each male and gradually replace the prevailing mating system of polygyny. The tendency of men and women to form long-lasting relationships for the production of offspring would then be present in the earliest members of the genus *Homo* (around 2–2.5 mya). Since then, most humans lived in monogamous families while a minority lived in polygynous families.

Two hypotheses about the emergence of monogamy

In polygynous species, the maximum reproductive success of males is larger than in monogamous species. The question is: why would males switch to a lower level of sexual competition and a lower rate of reproduction? That is, for most males the switch meant a higher rate of reproduction because most had zero success in a polygynous system as opposed to at least some success with monogamy.

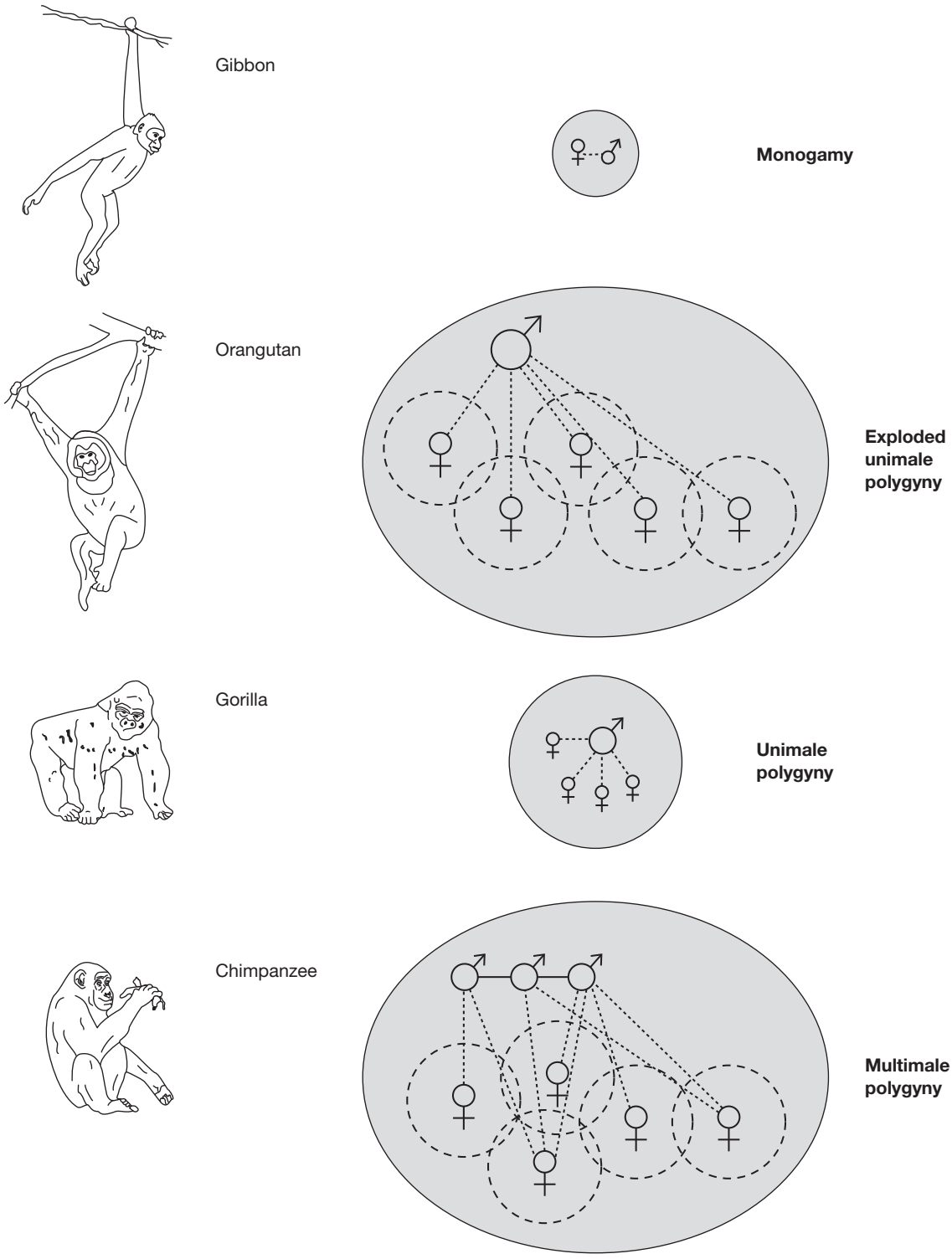

Figure 4.1 Mating systems in primates

Source: Lewin and Foley (2004)

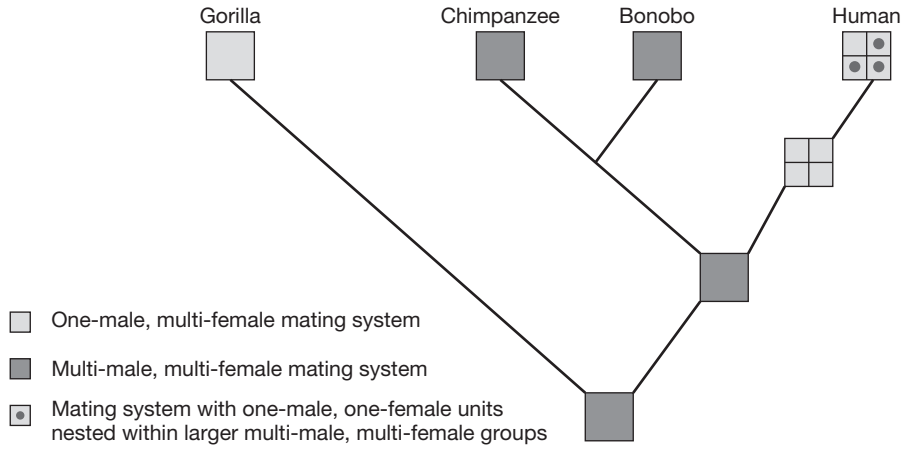

Figure 4.2 Hypothetical stages in the evolution of the mating systems in humans and African apes

Source: Dixson (2009)

lactation
the synthesis and secretion of milk by a mother's mammary glands.

How do we explain the emergence of monogamous relationships between males and females? This is mostly explained as a matter of parental cooperation: both sexes form a breeding unit based on sexual division of labour. This parental cooperation hypothesis has two major correlates which receive empirical support (Aiello and Key 2002). The first correlate is that the costs of maternal care are disproportionately high in the human species compared with other primates. The costs of gestation and **lactation** are not very different, but what differs substantially is the cost of provisioning food. Whereas weaned chimpanzees are largely self-sufficient in acquiring food, human babies grow over a longer period and need longer care before they are independent.

The second correlate is that the helping father reduces the maternal costs significantly. Patterns of food provisioning in hunter-gatherers confirm that mother's relatives, older offspring as well as the father may help with provisioning food. Thus, the bond between mother and father would be a parental partnership. However, the idea that women gathered plants and fruits while men hunted for meat to provision their wives and offspring, came under attack. Behavioural ecologists pointed out that hunters did not necessarily favour their wives and children but frequently gave away a large part of their catch. Successful hunters enjoyed high prestige from their generosity among allies and females which made hunting part of a male's mating effort rather than a parental effort (Hawkes 1991, 2002). So, male help in raising the offspring does not necessarily imply that monogamy emerged for reasons of paternal care.

A general principle derived from the comparative analysis of primates is that stable breeding bonds between individuals, whether monogamous or polygynous, are in the first place mating arrangements rather than parenting partnerships. Brotherton and Komers (2003) conclude that in most species which mate monogamously, paternal care evolved after pair-bonding was developed. This would explain why paternal care is absent in many mammals that mate monogamously. Paternal care was therefore not a necessary condition for the evolution of pair-bonding. In other words, male care originated as a mating strategy to monopolise one female, the same strategy that harem-holding primates practise with regard to multiple females.

The parental cooperation hypothesis implies that monogamy emerged as males refrained from monopolising females and shifted to assisting in maternal care for the offspring. An alternative explanation would be that monogamous pairs replaced the prevailing one-male, multi-female mating system because the costs of polygyny became too high. Most primate species, including our closest ancestors, indeed show intense competition for females. In particular polygynous males, in monopolising the reproductive capacity of females, leave the other males no mating opportunities. This is in sharp contrast to extant human hunter-gatherer societies, which have an egalitarian structure. How can we explain this shift towards a lower level of sexual competition?

Chapais (2008) advanced the hypothesis that any tool made of wood, bone or stone whose original function was to dig up roots or kill animals, could be used as an effective weapon against monopolising males. The capacity to throw weapons from a distance would equalise the distribution of females among males and lower the costs of competition for females. When armed males formed coalitions, it would be very costly to a dominant male to monopolise several females. According to this reasoning, polygyny would give way eventually to monogamy. Thus monogamous relationships were not the product of selection pressures favouring paternal care and pair-bonding but the byproduct of too costly polygyny and the rise of projectile technology. The costly polygyny hypothesis is therefore a more parsimonious explanation than the parental cooperation hypothesis. Monogamy did not evolve as a result of specific selection pressures but by the constraining of polygyny.

Humans are indeed better at throwing projectiles (e.g. stones, spears) than other primates, an ability that required whole-body anatomical changes and evolved in early *Homo* (Bingham 1999, 2000). Although this novel remote-killing capability may have arisen for other reasons such as deterring predators or hunting prey, it could also be used against bullying and dominating behaviour within groups. This hypothesis about the suppression of monopolising males is a specific version of a more general hypothesis which explains the egalitarian character of hunter-gatherer societies as a response to intimidating individuals and too much hierarchy (Boehm 1993).

Human sexual dimorphism

It is very likely that *Homo sapiens* evolved from a polygynous hominid ancestor who shifted from a one-male, multi-female to a one-male, one-female mating system about 2–2.5 mya. As monogamous males have a lower reproductive rate than polygynous ones, we may expect a marked reduction of sexual dimorphism, reflecting the change in mating system. Sexual dimorphism refers to systematic differences in body-form between individuals of different sex but of the same species. In monogamous species, males and females have more or less the same body size, but in polygynous species the difference is greater because males need to fight off competitors.

Dixson (2009) suggests several sexually dimorphic traits which indicate that our human ancestors were polygynous, such as body weight, body composition and body height. Sexual difference in body weight is mostly present in primates which have a polygynous mating system in which male competition for access to females is intense (e.g. gorillas). Selection for a larger male body size has also occurred among some monkey species which have a multi-male, multi-female mating system (e.g. macaques). In monogamous primates, the body size of males and females is almost equal (e.g. gibbons). Humans are sexually dimorphic in body size with an adult