
Loss of Oestrus and Concealed Ovulation in Human Evolution

The Case against the Sexual-Selection Hypothesis

by Bogusław Pawłowski

The assumption that absence of oestrus and of manifestations of ovulation is specific to humans has given rise to various proposals of a role for selection pressures in the evolution of these features in the form of sexual selection or other behavioural adaptations. Analysis of the sexual behaviour of nonhuman primates and humans indicates, however, that constant receptivity is not unique to humans and that human sexual behaviour is not independent of the phases of the menstrual cycle. Quantitative differences in the distribution of sexual behaviour between humans and the nonhuman primates in question may be the result of many morphological, ecological, and cultural factors of which those differences are side effects. In the case of the postulated selection pressures on the disappearance of visual manifestations of ovulation, the rather unlikely chimpanzee model of anogenital swelling in the early Hominidae may be replaced by an early-hominoidal model in which the swelling was relatively small. Its reduction in anthropogenesis may have been caused by bipedal locomotion, the cost of water accumulation, hyperaemia of the area, and an increase in adipose tissue. Furthermore, olfactory communication in the context of sexual behaviour in the climatic conditions of the African savannah would have been sufficient for detection of the fertile periods of the menstrual cycle. Thus, assuming the existence of direct selection pressures on sexual behaviour in the Plio/Pleistocene evolution of the Homininae seems unjustified.

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The rich literature on the sexual behaviour of the Homininae (*Australopithecus* and *Homo*) emphasizes the uniqueness in this regard of *Homo sapiens* and attributes considerable importance to the role of sexual behaviour in the process of hominization and even in the evolutionary success of the species (e.g., Morris 1967, Alexander and Noonan 1979, Lovejoy 1981, Kourtovik 1983, Parker 1987, Turke 1988). The absence of signs of ovulation and the accompanying so-called constant receptivity in human females are considered fundamental. The uniqueness of their emergence in the evolution of the Hominoidea is assumed on the basis of the chimpanzee model. This assumption has produced many hypotheses as to the evolutionary causes of various forms of sexual signaling and behaviour allegedly characteristic of the Plio/Pleistocene evolution of the Homininae. The adaptive advantage of constant receptivity has been suggested to be greater cooperation within the group and reduction of competitiveness among males (Etkin 1963, Pfeiffer 1969, Fox 1972, Daniels 1983), the emergence of monogamy (Etkin 1954, Morris 1967, Lovejoy 1981), the intensification of paternal behaviour (Alexander and Noonan 1979; Symons 1979; Strassmann 1981; Turke 1984, 1988), the possibility of acquiring greater quantities of protein through males' hunting (Symons 1979, Hill 1982, Parker 1987), and the possibility of deceiving males as to their paternity (Benshoof and Thornhill 1979) and thus reducing the risk of infanticide on the part of males (Hrdy 1981). Other hypotheses include the concealment of ovulation from the female herself, supposedly to increase the effectiveness of deceiving males about females' fertility (Alexander and Noonan 1979), and, in an improbable scenario advanced by Burley (1979), females' conscious avoidance of the pain of childbirth by avoiding sexual contacts in the fertile, symptomatic phases of the menstrual cycle, with selection favoring females who were unaware of the moment of ovulation and therefore unable to avoid pregnancy. Still other hypotheses have treated the loss of oestrus as a side effect of, for example, the increase in androgen levels associated with endurance in walking and the pursuit of prey (Spuhler 1979) or of the lengthening of the period of female responsiveness in response to longer lactation (Kourtovik 1983).

The majority of hypotheses, however, assume the existence of sexual selection pressure for behavioural change. These can be criticized not only in terms of comparative data on the detailed level but also in terms of the mechanisms of behavioural selection proposed—many of which postulate the existence of behavioural rules that if valid should apply to other animals (especially nonhuman primates) as well. I shall concentrate here on questioning the correctness of the assumption that absence of oestrus and concealed ovulation in *Homo* are exceptional and showing that there are many environmental and cultural factors that may have influenced the forms of sexual signaling and behaviour in human evolution.

Loss of Oestrus as an Evolutionary Trend in Primates

Oestrus is a period of strong sexual drive in the female cycle in which the female accepts male copulation. It is very clearly marked in, for example, rodents, carnivores, and lemuroids. Because in many primates, despite the intensification of copulation in the ovulatory phase of the cycle, females also allow males to copulate in other phases, Chalmers (1979), Loy (1987, cited by Wallis and Englander-Golden 1992), and Martin (1990, 1992), among others, have maintained that oestrus does not occur in this order. If so, its absence in humans may differ from the situation of many other primates in degree rather than in kind. Detailed analysis of the differences is possible by comparative examination of the three indicators of female sexuality proposed by Beach (1976)—receptivity (readiness to copulate when copulation is initiated by a male), proceptivity (active encouragement of a male to copulate), and attractiveness (stimulus releasing sexual excitation in the male)—and one indicator for males proposed in this paper that Beach does not consider.

Research on the sexual behaviour of primates has shown that in at least a few species of the Cercopithecoidea and the Hominoidea females very rarely refuse copulation, and if they do it has to do with the particular male rather than with their hormonal state (having refused one, they immediately copulate with another) (Chalmers 1979, Keverne 1987). Female orang-utans (*Pongo pygmaeus*) (Maple 1980, Galdikas 1981), chimpanzees (*Pan troglodytes*) (Lemmon and Allen 1978), and bonobos (*P. paniscus*) (Badrian and Badrian 1984) copulate irrespective of the phase of the cycle. These data indicate that the loss of oestrus is a trend in some Haplorhini and not a change that occurred only in the Homininae. Thus, constant receptivity as defined by Beach (1976) is not a distinctive feature of *H. sapiens*, and hypotheses based on its species-specific character in the evolution of the Homininae are questionable. However, under another, less precise definition of receptivity, constant receptivity is understood as constancy of the female's sexual activity across her cycle. If receptivity is interpreted in this way, the parameters differentiating the Homininae from the rest of the primates should be constant proceptivity and attractiveness.

Although females of some nonhuman primate species are constantly receptive, there is a distinct fluctuation in the frequency of sexual behaviour relative to the phase of the female cycle that results in part from changes in proceptivity and attractiveness. Nonhuman primate females express increased interest in males when levels of estrogen and testosterone are high, that is, in the proliferative and ovulatory phases. This interest is manifested by approaching males, presenting the anogenital area, and encouraging them to copulate (Wallis and Englander-Golden 1992). In most primate species the most frequent initiation of copulation by fe-

males occurs in the proliferative and ovulatory phases (Saayman 1970, Nadler 1981, Nadler et al. 1986, cited by Wallis and Englander-Golden 1992). A similar pattern is found in the initiative of males, for which visual, olfactory, and behavioural signs in females constitute changes in their attractiveness. Research on human sexual behaviour has demonstrated fluctuations in proceptivity and attractiveness approximating those in the chimpanzee. Proceptivity in a woman is measured in terms of such criteria as sexual self-excitement, initiation of hetero- and homosexual behaviour, sexual fantasizing and thinking, sexual desire, and number of orgasms (table 1). Despite the fact that these studies were conducted among women from highly civilized cultures, the results indicate the dependence of proceptivity on the phases of the menstrual cycle much as in the nonhuman primates. Apart from male-initiated heterosexual encounters it is possible that the degree of sexual attractiveness of a woman might also be measured by the length of sexual intercourse in relation to the phase of the cycle, the increase in attractiveness being reflected in an increase in male sexual excitation and a reduction in the time required for ejaculation. Among rhesus monkeys, this latter time was found to be on the average 5.4 minutes in the proliferative phase and 12.5 minutes in the luteal phase (Wallen 1982), though, admittedly, under conditions of limited space the differences proved negligible (4.8 versus 6.3 minutes).

An indicator not considered by Beach but one of enormous importance for the analysis of sexual behaviour is the sexual excitability of the male. Dependent on the endogenic level of androgen, this indicator may explain the indiscriminate, intense sexual activity of young males or males with high testosterone levels. The highest frequency of copulation among baboons (Saayman 1970), macaques (Zhao 1993), and chimpanzees (Tutin 1979) was observed in young males, and, while the frequency of copulation increases in the ovulatory phase of the cycle in mature males, no such relationship exists in juvenile (juvenile and subadult) male baboons (Saayman 1970) or chimpanzees (Hasegawa and Hira-iwa-Hasegawa 1989, Wallis 1995). Thus females are constantly receptive and males alone are selective as to the choice of the period of copulation relative to their age and androgen level. An increase in this indicator may prevent the detection of changes in female proceptivity and attractiveness. If this indicator in humans differs from that in other Hominoidea and some Cercopithecoidea in that it remains high longer in relation to the length of the reproductive period and may inhibit the indicators of sexuality in women, it may be connected with an extended period of development. Delayed sexual maturity and longer duration of juvenile sexual behaviour in men are also suggested by the longer period of immaturity of the hormonal system regulating menstrual cycles and behavioural responses in young women—expressed in less frequent ovulation, lesser capacity for progesterone secretion of the corpus luteum and its lower level in saliva (Ellison et al. 1987, cited by Ellison 1991), and lower frequency of secretion

TABLE 1
Proceptivity, Attractiveness, and Intercourse Frequency by Phase of the Menstrual Cycle in Homo sapiens

	Phase of Menstrual Cycle					No Change
	Menstrual	Proliferative	Ovulatory	Luteal	Premenstrual	
Proceptivity						
Autosexual behaviour		+ (3)	+ (1, 2)		+ (3)	
Female-initiated sexual encounters		+ (1, 3)	+ (1, 2, 4)			(5, 6)
Sexual thoughts and fantasies	+ (9)	+ (4, 7, 8, 9)	+ (7, 16)		+ (7, 9, 16)	(5)
Sexual desire		+ (7, 10, 11, 12, 13)	+ (7, 11, 13)	+ (12)	+ (10)	
Number of orgasms			+ (4, 14)			
Other ^a			+ (15)			
Attractiveness ^b			+ (1, 2, 16)			
Intercourse frequency		+ (2 plus 10 of 12 studies collated by Hill 1988)	+ (6 of 12 studies collated by Hill 1988)	- (12 studies collated by Hill 1988)	+ (4 of 12 studies collated by Hill 1988)	

NOTE: +, increase in comparison with other (or, in the case of bimodal data, previous) phases; -, decrease in comparison with previous phase.

SOURCES: 1, Adams et al. (1978, cited by Hill 1988); 2, Harvey (1987); 3, Bancroft et al. (1983); 4, Matteo and Rissman (1984); 5, Spitz et al. (1975, cited by Hill 1988); 6, Persky et al. (1978, cited by Hill 1988); 7, Markowitz and Brender (1977, cited by Hill 1988); 8, Sanders et al. (1983, cited by Hill 1988); 9, Zillmann, Schweitzer, and Mundorf (1994); 10, Tinklepaugh (1933b, cited by Hill 1988); 11, McCance et al. (1937, cited by Hill 1988); 12, McCullough (1973, cited by Hill 1988); 13, Dennerstein et al. (1994); 14, Udry and Morris (1968); 15, Daly and Wilson (1983:318); 16, Englander-Golden et al. (1980, cited by Hill 1988).

^aE.g., increase in intensity of makeup.

^bAs measured by male-initiated encounters.

of this hormone in the luteal phase in women under 22 years of age than in women of similar height and weight between 23 and 35 (Thorne 1988, cited by Ellison 1991). This phenomenon may create a slight negative progesterone effect that influences proceptivity and attractiveness in young women. Thus neoteny and the lengthening of the period of endocrine-system immaturity in *H. sapiens* may disrupt the behavioural manifestations of the physiology of this system with regard to sexuality. This is significant for research on the sexual activity of women, where consideration of the ages of their partners (and, even better, the latter's androgen levels) would permit the identification of the male excitability factor that may mask the indicators of female sexuality. If the group of women under study has young male partners with very high levels of testosterone, fluctuation of the frequency of sexual activity in relation to the phases of the cycle may be impossible to record (as has been found in chimpanzees [Hasegawa and Hiraiwa-Hasegawa 1989, Wallis 1995]). This may be the reason that fluctuations in sexual activity are not recorded in female college students (although other reasons could be more frequent refraining from sexual contact at the time of increased probability of becoming pregnant or more frequent changing of partners). Young chimpanzees also copulate twice as often as mature animals (Hasegawa and Hiraiwa-Hasegawa 1989). Since in at least a few species of primates the indicators of sexu-

ality in both females and males show fluctuations dependent on hormone levels, an approximately similar distribution of sexual activity in females should be expected here.

Field data on all the nonhuman primates indicate the highest frequency of sexual activity in the ovulatory phase of the cycle. For many it increases in the proliferative phase and immediately before menstruation. This is consistent with the fluctuations of hormonal secretions and confirms the results of research on proceptivity and attractiveness. In chimpanzees (Wallis 1982, 1992), macaques (Herbert 1974, cited by Wallis and Englander-Golden 1992), and baboons (Saayman 1972), most copulation occurs at the time of anogenital swelling, that is, during the proliferative and, in particular, the ovulatory phase of the cycle. In primates in which there is no such swelling, the distribution of copulation is similar, that is, most sexual activity occurs in the ovulatory phase of the cycle. This is by no means to say that copulation is absent in the other phases of the cycle. Very convincing data in this respect are available for the gelada, in which Dunbar (1978) found a more even distribution of copulation during most of the cycle, and for the crab-eating macaque (*Macaca fascicularis*) (Noordwijk 1985), in which no relationship between the frequency of copulation and the degree of swelling was found. The stump-tailed macaque (*M. arcoides*), which does not display outward signs of ovula-

tion, also copulated throughout the cycle (Nieuwehuisen 1985, cited by Hrdy and Whitten 1987). This behaviour intensifies only slightly in the ovulatory phase of the cycle in the vervet monkey (*Cercopithecus aethiops*) (Andelman 1987) and the Geoffroy's tamarin (*Saguinus oedipus*) (Brand and Martin 1983). Copulation independent of ovulation or hormone levels has also been observed in the Japanese macaque (*M. fuscata*) (Nigi, Hayama, and Torii 1990). These data confirm that the absence of oestrus is quite frequent in the primate order; it seems to be the evolutionary trend in this group of animals (see Dunbar 1988, Martin 1992) and not a unique phylogenetic acquisition of the Homi-
 nae.

Hill (1988) collected data on 12 groups from ten research projects on the frequency of copulation in relation to the menstrual cycle and found that the number of sexual contacts decreased during ovulation (in relation to the preceding phase) in only three. Given that two of these three studies involved female college students, the decrease in the number of sexual contacts may be attributed to the desire to avoid intercourse in this period because of the fear of pregnancy. Where there is no hormonal contraception or fear of pregnancy, fluctuation of sexual activity in relation to the phases of the menstrual cycle is clearly observable. The greatest number of instances of sexual self-excitement in women (1.6 times more frequent than in the menstrual phase) was observed in the ovulatory phase of the cycle (Harvey 1987). A considerable increase in sexual contacts in the ovulatory phase and their decrease in the luteal phase was also recorded in lesbian women (Matteo and Rissman 1984).

The data presented by Hill (1988) also show that no decrease in the frequency of sexual contacts in the proliferative phase was recorded in any case and in ten cases a considerable increase was observed. It was in fact in the luteal phase that there was no increase in the frequency of sexual activity in any of the groups. In four cases the increase was recorded before menstruation, and these data correspond to the similar increase in the same phase of the cycle in macaques (Keverne 1976, cited by Chalmers 1979). This phenomenon is linked with the considerable decrease, just before menstruation, in the level of progesterone. This increase in sexual activity both in the ovulatory phase of the cycle and before menstruation is so characteristic of some primates (including humans) that Manson (1986) has proposed a bimodal curve for its distribution.

Harvey (1987) observed that women, similarly to men, show maximum initiative in heterosexual activity precisely during ovulation. She found a correspondence between the fluctuation of this behaviour and the fluctuation of estrogen levels across the cycle (increasing from menstruation until the ovulatory phase and then decreasing through the luteal phase until menstruation). It is interesting that the number of sexual contacts with other than regular partners is greatest in the ovulatory phase of the menstrual cycle (Bellis and Baker

1990), indicating an increase in the sexual indicators and in sexual excitability in this period.

The changes recorded in the indicators of sexuality and the uneven distribution of sexual activity across the menstrual cycle indicate that sexual behaviour cannot be considered independent of the physiological periodicity of functional changes in the endocrine-system glands associated with human reproduction. If the proliferative and ovulatory phases were considered together, the consistency in the distribution of sexual activity between, for example, chimpanzees or macaques and humans would be even greater. That selection has favored the intensification of sexual contacts before ovulation is biologically reasonable. The variability of gestation in the Anthropoidea (4%) is greater than in other mammals (including the Prosimii) (2.1%), and it may be suggested that either the spermatozoa of this group of animals are more vital (lasting longer than 48 hours) or ovulation is longer (although more frequent occurrence of multiple ovulations in a cycle and induced ovulations are other possibilities) (Martin 1992). These data indicate that hypotheses regarding the behavioural evolution of humans that emphasize the uniqueness of the absence of oestrus are debatable, however marked the phenomenon.

Ecological and Cultural Influences on the Distribution of Sexual Activity

When women subjects are unaware of the aim of the research on their sexual activity, they manifest a considerable increase in sexual excitability in the middle, premenstrual, and postmenstrual phases of the cycle, and otherwise their responses are the reverse (Englander-Golden et al. 1980, cited by Wallis and Englander-Golden 1992). Moreover, results corresponding to the expected bimodal distribution of sexual activity tend to be achieved when the data are collected soon after the events and not with retrospective data (Manson 1986). Even if objectively recorded, however, the independence of sexual activity from hormonal factors that is so often emphasized in research on the evolution of human sexual behaviour may have a variety of causes. Rather than requiring, as the majority of researchers propose, the pressure of sexual selection, it may be explained as the result of the influence of ecological and cultural factors.

Sexual behaviour is influenced by such living conditions as the space occupied and, in the case of social species, the isolation of the heterosexual couple. The area of the available space occupied by male and female rhesus monkeys (*M. mulatta*) significantly influences sexual activity (Wallen 1982), and spatial parameters of the environment influence the frequency and distribution of sexual activity in all apes (Graham and Nadler 1990). In limited space (a cage) the frequency of copulation has proved to be independent of the phases of the female's

cycle. Male gorillas, orang-utans, and chimpanzees caged with a female display increased frequency of sexual activity (e.g., chimpanzees [Butler 1974] and orang-utans [Heinrichs et al. 1970, cited by Butler 1974] copulate every day), but when the female decides on the male's access the frequency is comparable to that recorded under natural conditions (Graham and Nadler 1990). Thus, the reactions of males under such conditions are more strongly affected. The presence of other males (especially outsiders) stimulates greater sexual activity independent of the phase of cycle in both males (e.g., in the macaque and the gorilla) and females (e.g., in the langur and the gelada) (Zhao 1993). Under such conditions, accompanied by the weakening of other selective pressures, hypersexuality becomes adaptive. In the absence of selective factors distinguishing individuals in terms of fitness in acquiring food, avoiding predators, or adapting to climatic changes, increase in sexual activity and consequently fertility become decisive for individual fitness. No periodic changes in proceptivity and attractiveness were recorded in the stump-tailed macaque (Slob et al. 1978, cited by Hill 1988) and the pig-tailed macaque (*M. nemestrina*) (Easto and Resko 1974, cited by Hill 1988) under laboratory test conditions when the couple was isolated. Great differences in the frequency of sexual activity in the bonobo and the chimpanzee to the advantage of the bonobo may result from the time the two sexes spend together (nearly 100% in the bonobo and less than 40% in the chimpanzee) (after Wrangham 1993). Proceptivity and attractiveness are indicators of considerable importance under natural conditions, as their function is to reduce the physical distance between male and female, that is, to form couples (Hill 1988). Under conditions that require animals to spend most of their time together in limited space, the variability of these two factors loses its significance.

The decline in importance of many selective factors that once differentiated individuals in terms of fitness and the increase in group density and domestication may have played a considerable role in the evolution of human sexual behaviour. Confinement to a hut or shelter of some kind and the constant physical presence of an individual of the opposite sex may have flattened the curve of the distribution of sexual activity across the cycle in *H. sapiens* as in the other primates (e.g., talapoin, macaques, baboons, gorillas, orang-utans, chimpanzees [Keverne 1987]) living under similar conditions.

Hormonal physiological parameters in the women of hunter-gatherer and horticultural societies are different from those of Western women. A relatively low level of hormone production by the female gonads (Rosetta 1995) has been recorded in non-Western societies. Because of the hormonal conditioning of sexual behaviour, both the importance of this behaviour and its distribution across the menstrual cycle may be different in these societies. Research on !Kung San women (Worthman 1978, cited by Hrdy 1981) revealed that the frequency of copulation increases in the proliferative and

ovulatory phases and there is a link between increased level of steroids in the blood, frequency of sexual activity, and number of orgasms. The level of testosterone in Ache men is lower than in men of Western societies (Bribiescas 1994), and, more interesting, Ache who have recently shifted to agriculture display higher testosterone levels than those who remain hunter-gatherers. Thus the change of economy in the Neolithic may, through a change in hormone levels, have influenced some indicators of sexuality (e.g., male excitability) and thus caused the flattening of the distribution of sexual activity across the menstrual cycle.

The considerable influence of cultural factors on sexual behaviour is indicated by the fact that fluctuation of sexual activity with the phases of the menstrual cycle has been recorded in African-American female manual workers and not in educated European-American housewives (Udry and Morris 1968). Education of women and men has proved decisive in avoidance of sexual intercourse in the menstrual phase (Barnhart, Furman, and DeVoto 1995); a university degree is linked with less avoidance of sexual contacts in this phase and thus with a more even distribution of this behaviour across the cycle.

Another factor affecting the distribution of sexual activity across the menstrual cycle may be the culturally imposed weekly and daily rhythms associated with particular types of work. On working days, from Monday to Friday, the frequencies of copulation are similar and relatively low, whereas they increase considerably on Saturdays and almost double on Sundays (38.3% of copulations take place on weekends) (Palmer, Udry, and Morris 1982). This evolutionarily quite new seven-day periodicity may influence the distribution of sexual activity across the menstrual cycle, perhaps postponing its peak for a few days. A similar dependence of the intensity of sexual activity on the distribution of work time and time off was also found by Silber (1994).

Because research on the sexual behaviour of modern humans reveals its dependence on the phases of the menstrual cycle, this phenomenon must have been present in all the earlier stages of the evolution of the Homininae. It is very probable that because of the absence of hygiene inhibiting olfactory communication, the absence of clothing under African climatic conditions, the relatively high daily air temperatures, which facilitated evaporation and the reception of pheromonal signals, the necessity of greater involvement in the protection and acquisition of food at the expense of sexual activity, and the absence of many of the cultural factors influencing sexual behaviour, the periodicity of this behaviour was greater than the research on modern humans indicates and approximated that of other primates. The sexuality of *H. sapiens* calls into question both the view that a new type of such behaviour emerged as early as in the Plio/Pleistocene evolution of the Homininae and the attribution of substantial hominizing functions to this phenomenon. If differences are observed, they tend to be quantitative rather than quali-

tative in character, and they may be explained as side effects of certain ecological-cultural factors rather than in terms of the direct operation of sexual selection in the early stages of anthropogenesis. The development of tool making and use connected with encephalization and the use of fire and the construction of shelters also meant substantial liberation from the selective pressure of predation and climatic and alimentary factors. Only then could the fitness benefits of fertility associated with sexuality assume major importance. The excess of free time itself, accompanied by the implementation of effective technologies for food acquisition and the lengthening of the day because of the control of fire may have been very important elements in certain changes in sexual behaviour. Even in historical times the differences between societies (e.g., 6.8 sexual contacts per month for women between 20 and 24 in Bangladesh versus 9.5 for women under 25 in the U.S.A. [Udry, Deven, and Coleman 1982]) and between social groups (e.g., the aristocracy and the lower social strata) indicate that economic conditions and the amount of free time are very important in differentiating sexual behaviour as well. It is hardly surprising, then, that the distribution of sexual activity across the menstrual cycle may have been flattened more in some societies than in others.

The evolution of the Homininae was accompanied by considerable climatic change, which altered the physical environment in terms of both the daily and the annual cycle. The changing environment may have called for a more flexible behavioural response, and this may have led to greater independence of the functions of the endocrine system from the environment and somewhat relaxed the strict hormonal control of human behaviour.

Signs of Ovulation in the Evolution of the Homininae

The very fact of intensification of sexual activity in the proliferative and ovulatory phase of the menstrual cycle confirms the view that ovulation in humans is not completely concealed. The variation of proceptivity across the cycle indicates the existence of behavioural signaling of the fertile phase of the cycle. This behaviour is influenced by endogenic factors whose action was evolutionarily fixed as one of the mechanisms increasing the chance of conception. Because the signaling is not controlled by rational thought and need not be perceived as such, it may seem absent. In addition to behavioural signaling, there may be visual and olfactory signaling as well.

Visual signals of ovulation involving swelling of the anogenital areas are absent in modern humans. There would not be anything unusual about this—most primates, including most hominoids, lack such manifestations—if it were not for their occurrence in the chimpanzee, the model animal for the evolution of the

Homininae. This is the reason that hypotheses concerned with the disappearance of this feature in anthropogenesis are advanced.

Although concealed ovulation is to be understood as the absence of external signs of ovulation—visual ones such as swelling of the anogenital area and olfactory and behavioural signals—many writers, as Sillén-Tullberg and Møller (1993) point out, consider ovulation as concealed in the absence of its visual signs only. Because this phenomenon occurs very often in the primates (Dixson 1983, Andelman 1987, Sillén-Tullberg and Møller 1993), interpreting it as specifically human and connected with hominization seems unjustified. Ovulation is also concealed in the case of anogenital swelling in the bonobo, which lasts for 48% of the cycle although the ovulatory phase lasts only two to three days (after Wrangham 1993). It is not the absence of signs of the brief moment of ovulation that is the issue here but the possible evolutionary change in this signaling. The proponents of the view based on the chimpanzee model maintain that evolution inhibited or reorganized the once-distinct signals of the fertile phase of the cycle in the line of the Homininae. The question is whether such a change in fact took place in the evolution of the Homininae and, if so, whether its causes were connected with sexual selection and its effects were significant for social structure.

Adopting the chimpanzee model for many morphological and behavioural features does not mean that sexual swelling similar in intensity to that in the chimpanzee was present in prehomines. Dixson (1983) concludes that prehomines did not have this feature at all. In the Hominoidea swelling and reddening of the skin in the anogenital area in the proliferative and ovulatory phases of the cycle occur only in the chimpanzee. His proposal is accepted by Hrdy and Whitten (1987), who maintain that, given that the pink swelling is absent in the majority of primate species, this feature is the basic and original condition in the primates and the appearance of the sexual swelling in the Hominoidea is specific to *Pan*. It seems that although many changes are emphasized in modeling the evolution of humans, changes in the model species are too often neglected. Undoubtedly many changes have occurred in the genus *Pan* since it diverged from the line leading to *Homo*, that is, in the course of the past 5–7 million years. Chromosome analysis (Yunis and Prakash 1982) indicates the occurrence of a greater number of chromosome changes in the evolution of the chimpanzee than in humans. Considering the absence of visible remnants of this feature in *Homo* and assuming evolutionary specialization in the direction of multimale social structure in the chimpanzee after the divergence of the lines leading to *Pan* and *Homo*, it seems probable that this feature was absent in the prehomines.

Yet the occurrence of at least slight anogenital swelling in the evolution of the Hominoidea is indicated by its original presence in the Cercopithecoidea (Sillén-Tullberg and Møller 1993) and its vestiges in the pudendal-lip swelling in the ovulatory phase of the cycle in

the gorilla (Nadler 1981) and the swelling during pregnancy in the orang-utan (Galdikas 1981) in the same way as in the chimpanzee (Wallis and Goodall 1993).

If this feature occurred in the prehomines and its basic development is to be connected with the evolution of the line of *Pan*, slight anogenital swelling in the proliferative and ovulatory phases of the cycle would be a more appropriate model for this line. That the swelling was slight in the phylogeny of humans is substantiated by the cladistic analysis of this feature in the primates conducted by Sillén-Tullberg and Møller (1993), who postulate that the original state in the prehomines and all of the Hominoidea was only slight swelling and reddening of the anogenital area. Similarly to Dixson (1983), they tend to accept the idea that the extreme swelling of the anogenital area is specific to the chimpanzee.

The idea that there may have been some such swelling in the prehomines and the early Homininae is supported by the considerable length of the penis in *Homo*. The lengthening of this organ took place in the primates that have anogenital swelling—the chimpanzee, the stump-tailed macaque, the mandrill, and the yellow baboon (*P. cynocephalus*). In nonhuman hominoids lacking anogenital swelling—the gorilla, the orang-utan, and the gibbon—the penis is almost invisible. Swelling increases the depth of the vagina (at maximum swelling in the chimpanzee it increases as much as 52% [Dixson and Mundy 1994]), and proper penetration requires the longer penis. Dixson and Mundy report that in 11 chimpanzee males the length of the penis at erection was 11–19 cm, with an average of 14.4 cm, thus only slightly less than in *H. sapiens*. Yet, because of the evolution of bipedalism and the abdominal relocation of the female external genitals, the lengthening of the human penis does not need to be explained in terms of so great a swelling of the female as in the chimpanzee. Bipedalism itself seems an insufficient explanation for the 15–17-cm length of the erect penis (Imielinski 1985). With an average vagina depth of ca. 10–12 cm (Imielinski 1985), approximating that of the chimpanzee (ca. 12.5 cm [Gould and Martin 1981] or 12.6 + 1.69 cm [Dixson and Mundy 1994]), such a long penis is not indispensable. Therefore it is possible that its “extra” length is connected with the existence of slight swelling in an already bipedal female. The situation of the relaxation of the penis-elongation selection factor—that is, the retreat of swelling and a long penis—occurs in the stump-tailed macaque. What remains to be explained is the disappearance of relatively slight visual signs of ovulation in the Homininae, a vestige of which, in the form of periodic (estrogen-dependent) peripelvic hyperaemia, occurs in *H. sapiens* as well (Wallis and Englander-Golden 1992).

Irrespective of the model accepted for the prehomines (chimpanzee or gorilla, the latter proposed by Schröder [1993 a, b]) and on the assumption of the existence of anogenital swelling, the disappearance of this feature is usually explained in terms of sexual selection for a change in reproductive strategy. Certain features

of the evolution of the Homininae could, however, have influenced this feature.

Probably the simplest explanation is as a side effect of bipedalism. Erect posture changed the position of the female external genitals and concealed them between the legs, and thus swelling as a mode of signaling became useless (Tanner 1981). Selection may have favored females who did not have the periodic problems with bipedal locomotion caused by considerable anogenital swelling (Gallup 1982). However, the evolution of bipedalism was a long-term process. Despite some disagreement (see Kozieł 1994), it seems that the mode of locomotion of the first *Australopithecus* differed from that of the later forms and may have been intermediate between those of contemporary apes and of humans (McHenry 1991, among others). If swelling was less in the prehomines than in the chimpanzee, it would not have had so much influence on female locomotion.

In addition to bipedalism, which changed the position of the genitals, the change of the line of vision (males could no longer constantly see the female genitals) could have been another reason for the loss of functionality of this feature. The change of environment for a more open one in which the Homininae were subject to greater danger from predators may have increased the density of the population, and in such a case this feature may have lost its function of long-distance sexual signaling. At the same time, selective pressure toward an increase in the amount of adipose tissue and its reserves in the buttocks area caused the replacement of the sexual swelling, sensitive to the action of estrogen, by adipose tissue. The loss of functionality need not have caused the disappearance of this feature if the cost of maintaining it was negligible, but swelling increases the weight of a female (in *P. ursinus* by 8–10% [Bielert and Busse 1983, cited by Zinner, Schwibbe, and Kaumanns 1994] and in *M. nemestrina* by 17% [Dixson 1983]) and adds to the energetic cost of locomotion for at least several days. Other possible additional costs of anogenital swelling could have been specific to the line of the Homininae. In the new savannah environment the thermoregulatory system may have been modified in order to conserve water. Under such conditions swelling involves an additional cost (ca. 1.5 liter in the chimpanzee), and effective evaporation of sweat on the swollen area is hindered by its location in the area of humid vegetation in the savannah environment. Furthermore, because of the loss of hair and the risk of hypothermia at night (Pawłowski 1998) the loss of heat through the highly hyperaemic sexual swelling would have been a disadvantage.

If the slight swelling was present in the early Homininae, there may have been many physiological and morphological reasons other than sexual or social ones for its disappearance. The reduction of the anogenital swelling in the gelada (*Theropithecus gelada*) is considered to have been caused by its atypical way of feeding (most of the time in a sitting position) (Dixson 1983). The reduction of the sexual swelling in some species of macaques (Dixson 1983) cannot be linked to changes in

social and reproductive structure, for these were not altered.

Thus, seeking evolutionary explanations for the disappearance of this exaggerated feature in sexual selection and behavioural selection pressure that resulted in the emergence of new social structures seems inappropriate. There were many more fundamental adaptive changes, and they included changes (often as side effects) in the features just discussed.

Olfactory Sexual Signaling in Human Evolution

Although the evolutionary trend in the primates is the development of tactile-visual perception and selection oriented toward the development of parts of the brain unconnected with smell, olfactory communication persisted. Because of the limbic projection of the olfactory system and its closer connection than in the case of hearing and sight with the centers of emotion, signals perceived in this way are often subconscious (Stoddart 1990, Schleidt 1992). This may be the reason that this type of communication is underestimated. Recent research shows that *H. sapiens* cannot properly be described as a microsomatic creature (Schaal and Porter 1991). The actual sizes of the bulb in apes and humans are similar. Although the mucosa of the human nose have fewer receptor cells than those in the other mammals, the quantity of olfactory substances produced by humans is almost the largest of all the primates (Stoddart 1990). Did chemical signals perceived with the sense of smell and the odorless, nonvolatile ones perceived by the rudimentary vomeronasal organ (Stensaas et al. 1991, Cohn 1994) have any influence on the physiology of reproduction and reproductive behaviour in the evolution of the Homininae?

From the point of view of the number, size, and production of the sebaceous and apocrine glands, humans are the smelliest hominoids. Characteristically, the sebaceous glands are three times more active during puberty, when the apocrine and apoecrine glands develop, and their occurrence mainly in places such as the armpits, the areola mammae, and the navel, pubic, and anogenital areas indicates that their function is connected with reproduction (Stoddart 1990).

Homo, *Pan*, and *Gorilla* contrast with the other primates in having axillary organs (Cohn 1994), their location in the armpit being marked by perpendicular rows of hair with the accompanying sebaceous, apocrine, and eccrine glands. Here the odor involved in olfactory communication is produced and diffused with the cooperation of microorganisms. It is dissolved in the watery secretion of the eccrine glands, and it is similar for all three taxa (Montagna 1985). Spielman et al. (1995) maintain that chemical signaling by the axillary organ performs the same pheromonal function as in the other mammals. The secretion of pheromones by this area in an animal of partly or fully erect posture is probably

connected with the fact that it is situated close to the organ perceiving the signals (the nose). Compared with the anogenital area, the axillary organ is situated closer to the level of the receptor of olfactory signals in the bipedal *Homo* than in the gorilla and the chimpanzee, and for this reason it is best-developed in this species (Stoddart 1990). Because the armpit is almost closed, intensive sweating is irrelevant for thermoregulation, and the changes in the size of the axillary glands and the smell of the sweat of a woman in relation to the phases of the menstrual cycle (that is, to hormone levels) confirm their signaling, pheromonal functions (Mykytowicz 1985). The high development of the axillary organ in the majority of modern humans may be a form of compensation for the reduced role of vaginal pheromones. According to Tanner (1981), the concealed genitals and enlarged buttocks caused by bipedal locomotion prevented the spread of pheromones, and the considerable distance between the vagina and the nostrils of upright males resulted in a lower concentration of pheromones reaching the olfactory organs. This may have reduced the role of female pheromones in intersexual communication. Yet, the signaling persists, as the increase of estrogens in the proliferative phase of the cycle is accompanied by an increase in copulines (volatile fatty acids) whose production depends on the vaginal bacterial flora. The odor of vaginal secretions is perceived as pleasing only in the ovulatory phase of the cycle (Stoddart 1990).

That both pubic and axillary hair develop during puberty is a reflection of their function in olfactory communication. Hair provides an additional area for the activity of the microorganisms involved in producing the odor, and being springier than head hair it enhances the diffusion of the secretions. Its importance in disseminating chemical signals is indicated by the fact that after thorough washing of the armpit with soap the typical odor reappears within 6 hours in an unshaven armpit but only after 24–48 hours in a shaven one (Shelley et al. 1953, cited by Schaal and Porter 1991).

The perception of these chemical signals by the olfactory mucosa and the vomeronasal organ may be conscious and/or unconscious and may take a variety of forms. In the rhesus, swelling and reddening of the mucosa of the nose are as much dependent on hormones as anogenital swelling. The mucosa of the nose are stimulated by hormones, and the sympathetic nervous system is connected with changes in their sensitivity to odors. When the amount of estrogen increases during ovulation and pregnancy, swelling and reddening of the mucosa of the nose also occurs in women (Mykytowicz 1985).

Although the data on olfactory communication in connection with reproductive behaviour in humans are inconsistent, enough is known to demonstrate its influence on the menstrual cycle, sexual activity, and even mate selection. Among the evidence for this are the following findings:

1. The synchronization of the menstrual cycles of women living together (McClintock 1971, Graham and

McGrew 1980) and the fact that this synchronization has been found to occur in women whose upper lips were rubbed with diluted axillary secretion of another woman (Russell, Switz, and Thompson 1980, Preti et al. 1986, Stern and McClintock 1998).

2. The influence of the presence of a man on the length of the menstrual cycle, with occasional sexual contacts and celibacy being associated with increased frequency of irregular (Burleson, Gregory, and Treva-
than 1991) or nonovulatory cycles and greater regularity and shorter cycles with the influence of the male axillary secretion only (Cutler et al. 1986, cited by Stoddart 1990).

3. An increase in sexual activity under the influence of the axillary odor of a woman (Cutler 1987); here the pheromone involved seems to be androstenol, which has been found most abundant in the axillary secretions of women in the middle of the proliferative phase of the cycle (Stoddart 1990).

4. The influence of androstenol and androstenone on the assessment of the attractiveness of individuals (McCullough, Owen, and Pollack 1981, Filsinger, Braun, and Monte 1985).

5. The lowering of the threshold of sensitivity at the end of the proliferative phase and in the ovulatory phase of the cycle (Doty et al. 1981, cited by Stoddart 1990), when even androstenone is perceived more positively than in other phases (Grammer 1993). Reduction of the negative reception of this odor facilitates sexual activity.

6. The perception of pheromonal signals by men under laboratory conditions (Reynolds 1991). The odor associated with the vaginal secretion may be perceived consciously, and it has the greatest concentration of volatile free fatty acids and the most pleasing smell in the ovulatory phase of the cycle (Keith et al. 1975, cited by Wallis 1985).

7. The possibility that mate selection is linked with MHC (major histocompatibility complex)-dependent body-odor preferences associated with the immunological recognition of peptides (Wedekind et al. 1995). Women who do not use hormonal contraception perceive the odor of a man as more pleasing when his MHC differs more from their own.

Most of this research shows that olfactory communication in connection with reproductive behaviour is often subconscious. Thus periodic changes in the degree of attractiveness are rarely connected with periodic changes in this form of signaling. Greater importance is attributed to the so-called vomeroferrines, the chemical substances perceived by the vomeronasal organ, which influence electrical changes and the temperature of the skin. What is more, Montibloch et al. (1994) have demonstrated sexual dimorphism in the mode of reception of these signals.

If olfactory signaling influences reproductive behaviour in the contemporary civilized societies of *H. sapiens*, it must have been even more significant in the earlier stages of human evolution. The original reduction of olfactory signals may have been a side effect of erect

posture, which moved the receptor of these signals away from the anogenital area that was their main source. It was perhaps at this point, however, that the axillary organ shared with *Pan* and *Gorilla* became enlarged, and the fact of this enlargement is evidence of selection directed toward maintaining this signaling.

Under the conditions of the open savannah, with abundant sunshine, and the increased secretion of the olfactory glands caused by work, olfactory signaling was sufficiently intensive to perform its function. Increased body temperature allowed greater development of symbiotic microorganisms and increased enzymatic activity, increased secretion of the sebaceous glands (by 10% with an increase in skin temperature of 1°C), and more rapid volatilization of olfactory substances and greater effectiveness of olfactory stimulation (Schaal and Porter 1991). As the temperature of breathed air increases, the mucosa of the nose are altered, with qualitative changes in the perception of odors (Schaal and Porter 1991). With the increase in secretion of the axillary organ under hot savannah conditions, olfactory signaling could perform its communicative functions in the sexual context without any substantial change. More important, with selection directed toward increase in the significance of other forms of communication, these conditions did not require any proportional increase in olfactory signaling.

One factor that may have prevented more olfactory signaling in early forms of *Homo* is the greater density of the group connected with protection against predators and the need to stay close together during colder nights. Under conditions of increased radiation in open space under a cloudless sky, the temperature on the ground may have dropped at night to the point that the Homininae, who had little if any hair (Wheeler 1984), had to avoid excessive heat loss. One solution might have been gathering in groups as is done, for example, by contemporary Pygmies (Turnbull 1986). In such situations olfactory communication may have become too intense and selection may even have favored its reduction. Androstenone, perceived negatively by both sexes and linked with male rivalry and territoriality, may have prevented too close contact of individuals not just at night. A decline in the production of this pheromone may have attenuated antisocial, aggressive behaviour within the group. Yet the reduction of the role of the sense of smell with the parallel development of other forms of communication did not result in the loss of significance of this signaling. There seems to have been no selection directed against this mode of communication, especially since it was already weakened in *Australopithecus*. Despite the absence of visual preovulatory and ovulatory signs, olfactory communication was, together with behavioural signals, sufficiently strong to cause intensification of sexual activity in the fertile period of the cycle, as is the case in the gorilla and the orang-utan.

The reason olfactory signaling has such limited significance in human reproductive behaviour, especially where clothing is worn, may be weaker olfactory condi-

tioning in infancy. Olfactory experiences are well remembered and associated with the limbic structures of the brain, and good olfactory memory (Schleidt 1992), especially of odors perceived in childhood, must be significant for reproductive behaviour. Experiments on rodents have shown that the olfactory environment in the very early stages of life has considerable influence on later behaviour associated with olfactory communication (Fillion and Blass 1986). If "imprinting" of odors that influence later behaviour similarly occurs in humans, the abandonment of breast feeding, hygiene (often accompanied by deodorants and perfumes), separation of mothers from infants during sleep, and shaving of the axillary hair by nursing mothers may have considerably altered the conditioning of reactions to odors. In hunter-gatherer societies and even more in the earlier evolution of the Homininae, infants were in almost constant contact with their mothers. They were subject to olfactory conditioning all the time and not just during feeding as in contemporary clothes-wearing societies. Study of two-week-old infants revealed that if they were breast-fed they differentiated between the axillary odor of their mothers and those of other women (Cernoch and Porter 1985). Research on olfactory sensitivity to pheromones should perhaps take into consideration the type of feeding in infancy. It may be that the main function of the apocrine and sebaceous glands on the areola mammae, apart from protecting the skin against the caustic action of the saliva, is pheromone conditioning of infants. The plexus venosus areolaris raises the temperature of this area in relation to the rest of the breast, and this along with the higher temperature of the armpits may increase the rate of volatilization of the olfactory substances and thus their semiotic effectiveness (Schaal and Porter 1991).

In considering the earlier stages of human evolution it should be assumed that olfactory communication in the context of sexual behaviour played a greater role than it does in contemporary *H. sapiens*. Absence of intensive hygiene, the influence of pheromones secreted by the apocrine glands on the breast and by the axillary organ, and, to a certain extent, pheromones from the vagina of the nursing mother could have conditioned the imprinting of the attractiveness of these odors and sensitivity to them in the context of later sexual behaviour.

It must be borne in mind that, like the loss of oestrus, the diminishing significance of olfactory communication is an evolutionary trend in the primates. In the chimpanzee neither the amount of copulines nor their qualitative change in the course of the female cycle is a sufficient olfactory signal for males, for these do not vary enough by phase of the cycle (Fox 1982). Although individual variation of copuline production is considerable, it distinguishes sexually mature from immature females (Fox 1982). The fact that chimpanzee males inspect the vagina with their fingers, which they later smell and lick, shows that olfactory communication in the chimpanzee is also relatively weak but that males look for these stimuli (Nishida 1970, cited by Fox 1982). Thus the weakening of olfactory signaling is not simply

characteristic of the line leading to *H. sapiens* but an evolutionary trend in the Hominoidea.

Conclusions

Hypotheses of an evolutionary basis for the absence of signs of ovulation and for strong sexual selection due to loss of oestrus in human evolution are controversial. Constant receptivity is not species-specific, occurring in at least several other species of primates. It should not be attributed such evolutionary significance in the line of the Homininae, and it should not be the justification for the specific character of human social structure and reproductive strategy. As in the other primates, there is fluctuation in sexual activity with changes in proceptivity and attractiveness in the female cycle. The flattening of the curve of the distribution of sexual activity seems to be a definite evolutionary trend in many anthropoids. The differences in degree of the distribution of this activity between humans and the other primates can to some extent be explained in terms of the endocrinological, ecological, and cultural conditions. They need not be the product of specific selective pressure favoring a new type of reproductive strategy.

Similarly, the disappearance of visible signs of ovulation in the course of the evolution of the Homininae need not be associated, as in the other primates, with selection directed toward a new type of reproductive behaviour. Rather, it may be the consequence of the evolution of bipedalism and of environmental conditions. If hunter-gatherer societies and even Western ones have semiochemical and behavioural signaling that affect periodic changes in sexuality indicators and a bimodal distribution of sexual activity, this signaling must have been present to a greater extent in all the earlier forms of the Homininae. The absence of visual signaling of ovulation could have allowed these forms greater flexibility in the choice of a reproductive strategy adaptive under particular ecological and cultural conditions. Such behavioural adaptation was the effect of other evolutionary changes in this line (e.g., bipedalism, brain-size increase, the change in the rate of individual development) and not the direct cause of a change in social structure and the effect of sexual selection.

To attribute these very significant evolutionary changes in the process of hominization to sexual selection is questionable. The considerable flexibility of the species in terms of reproductive strategies demonstrates both the influence of various ecological factors on reproduction and the absence of evolutionary selective pressure toward rigid programming of these structures. It indicates that the sphere of sexual behaviour was never so significant in the evolution of the Homininae as to require selection for any strictly defined type of reproductive strategy in *Homo*.

The pressure of the changing environment in human evolution—climatic conditions involving the need to overcome various nutritional stresses, change in the dietary niche, and increased heat and later probably

cold—was more significant in the process of hominization than sexual selection and the often postulated change in reproductive strategy.

Comments

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Pawłowski correctly emphasizes that concealed ovulation and nonreproductive sex are not unique to humans and that chimpanzee-like anogenital swellings are unlikely to have occurred in ancestral Hominidae or Hominae. However, his claim that direct selection of sexual behavior was absent in early Homininae seems unjustified. First, phylogenetic analyses suggest that while concealed ovulation is likely to evolve in lineages with overtly polyandrous females, once evolved it seems to facilitate the evolution of social monogamy (Sillén-Tullberg and Møller 1993). The evidence for sexual behavior and social mating systems in hominids and extant human societies fits this scenario, although Pawłowski misses this point. Secondly, the claim of relaxation in sexual selection seems unjustified given current patterns of human sexual behavior.

While Pawłowski interprets intraspecific variation in copulation frequency as a cultural phenomenon, such variation is common throughout the animal kingdom (Møller and Birkhead 1992, Birkhead and Møller 1998). An important determinant of sexual behavior is spatial and temporal variation in its costs and benefits. Accordingly, within-pair copulation rates increase in social contexts where extra-pair copulations are frequent. Furthermore, males often retaliate with copulation in response to presumed extra-pair copulation by a mate (Birkhead and Møller 1992), even among humans (Baker and Bellis 1995). An increase in copulation frequency in Western societies may indeed be a cultural phenomenon in that culture alters the conditions for extra-pair copulations, thus altering the cost/benefit ratio for within-pair copulations.

Pawłowski neglects the role of sexual selection in the evolution of human sexual behavior. Theory predicts that the ecology and hence the habitats chosen by individuals of a particular species affect the social mating system and hence sexual selection (Emlen and Oring 1977). This long-standing tradition in behavioral ecology has gained considerable observational and experi-

mental support by providing links between habitat quality, resource abundance, and sexual behavior (reviewed in Andersson 1994). Rather than eliminating sexual selection, changes in resource abundance will affect the social and the genetic mating system and hence the associated social and sexual behavior.

“Cultural” explanations of human behavior erroneously lead to the assumption that current variations in sexual behavior, mate preferences, and reproductive success are cultural artifacts rather than examples of sexual selection in action. By “sexual selection” we mean nonrandom variation in mating success associated with variation in one or more phenotypic characters. There is ample evidence for such variation in humans, with features such as symmetry and wealth being associated with number of mates and sexual partners (e.g., Borgerhoff Mulder 1991, Thornhill and Gangestad 1994). Intense sexual selection is also associated with particular body odors, and the degree of female preference for these odors has been demonstrated to be related to proximity to ovulation (Gangestad and Thornhill 1998). This preference is perceived entirely at a subconscious level, and therefore any deliberate choice or policing activity influenced by culture is unlikely to have generated it and its mere existence is evidence for strong current (and hence in all probability past) sexual selection. Thus, it seems unlikely that the evolution of human sexual traits took place in a context devoid of sexual selection pressures. Although ovulation in humans may not be signaled visually as in many other primates, there is compelling evidence that modern women are able to signal ovulation by changes in asymmetry in soft body parts (Manning et al. 1996) and by changes in dress and behavior (directly related to salivary estradiol levels and hence stage in the menstrual cycle [K. Grammer, personal communication]). If phenotypic variation in these traits is associated with differences in mate choice or sexual behavior and if these differences are partly controlled by heritable variation, these recent findings provide further evidence for a current role of sexual selection in shaping female reproductive strategies.

Pawłowski discusses long- versus short-distance signaling in humans. Multiple signals are common in many signaling systems; different phenotypic features may be signaled by different signals, or a particular signal may give a partial indication of the individual's overall phenotypic character (Møller and Pomiankowski 1993). Such signals may interact in a number of ways and provide information about different features at different distances. Speculation about the role of different signaling systems must await studies of how these systems interact and the distances at which signals are perceived.

In conclusion, there is ample evidence to suggest that sexual selection currently acts on phenotypic variation in humans, although it remains undetermined whether such selection will result in microevolutionary change. We believe that progress in the understanding of loss of estrus and concealed ovulation will come from detailed

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studies of intraspecific phenotypic variation and its causes and reproductive consequences.

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Pawłowski states that “field data on all the nonhuman primates indicate the highest frequency of sexual activity in the ovulatory phase of the cycle.” Yet he questions the “assumption that the absence of oestrus and concealed ovulation in *Homo* are exceptional” and contends that the “absence of oestrus is quite frequent in the primate order.” Further, he concludes, “Research on human sexual behavior has demonstrated fluctuations in proceptivity and attractiveness approximating those in the chimpanzee.” How do these statements square with the evidence?

Studies of the common chimpanzee (*Pan troglodytes*) report that 94% to 96% of all copulations took place during or around the period of maximal swelling (reviewed in Takahata, Ihobe, and Idani 1996). Early reports on bonobos (*P. paniscus*) emphasized that copulations occurred throughout the cycle (Savage-Rumbaugh and Wilkerson 1978), but a more recent study by Furuchi (1987) reports that 82% of copulations took place when swellings were maximal. This finding was reinforced by a study of two additional groups of bonobos in which 77% and 67% of copulations occurred during maximal swelling (Takahata, Ihobe, and Idani 1996). In humans there is no such pronounced increase in copulation around the time of ovulation. Summarizing the literature, Hill (1988) concluded that 10 of 12 studies found a postmenstrual increase in the probability of copulation, 8 of 12 showed a luteal decrease, 4 of 12 showed a premenstrual increase, and 6 of 12 showed a midcycle peak (though not an exclusive one). The hypothesis that humans display a chimpanzee-like preference for copulation around the time of ovulation was not supported. Prior to the 20th century, many gynecologists believed that ovulation coincided with menstruation (reviewed in Strassmann 1996a), and reproductive biologists (e.g., Marshall 1910) confounded menstrual bleeding in women with pre-estrus bleeding in dogs. Among the Dogon of Mali, people use the same term for menstruation in women as for estrus in domestic animals. They recognize that dogs and cows are most fertile just after bleeding has stopped and assume that the same is true for women; husbands therefore often insist on copulation immediately after a woman returns home from the menstrual hut (Strassmann 1996a). Rather than being an isolated example, the Dogon view appears to have been cross-culturally widespread. In the Standard Sample of 186 societies, the prevailing belief was that conception occurred immediately after menstruation (Strassmann 1996a; see also Paige and Paige 1981). Thus, Pawłowski’s view that ovulation in women is not truly concealed is hard to reconcile with both (1) the ob-

served distribution of coitus across the menstrual cycle and (2) the widespread misidentification of the timing of the fertile period.

Although Pawłowski is skeptical of the evidence for concealed ovulation in humans, he nonetheless suggests that estrus is absent in many other primate species. Phylogenetic analyses suggest that sexual swellings were independently lost in primates about 6 times (Strassmann 1996b, c) or 8–11 times (Sillén-Tullberg and Møller 1993). However, the absence of swellings does not constitute the absence of estrus unless the behavioral and olfactory cues that signal ovulation are also absent. To the best of my knowledge, in all nonhuman primate species the highest frequency of copulations occurs around the time of ovulation—implying that in nonhuman primates estrus signals remain present.

Although the 18th-century French philosopher Montesquieu was not technically correct when he wrote, “Man is the only animal who eats when he is not hungry, drinks when he is not thirsty, and makes love in all seasons,” his emphasis was in the right direction. Some primates copulate throughout the calendar year, but the loss of estrus is apparently unique to humans and requires explanation. Because estrus conveys such reproductively significant information, it is hard to see how it could be lost as a mere side effect of ecological and cultural factors. A trait that enables males (and other females) to detect the fertile period does not seem like one to which selection would have been indifferent. Instead it seems more plausible that changes emerged in the costs and benefits of signaling ovulation. Two decades have elapsed since debate began on the evolution of concealed ovulation (e.g., Alexander and Noonan 1979). Data to resolve this debate will be difficult or impossible to obtain, but I venture the prediction that hypotheses based on sexual selection will remain at the core of future discussions.

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The sphere of human sexual behaviour, guarded in our culture by numerous taboos, is rather readily stereotyped even in anthropology. The life of the stereotypes formed in this field is very long, especially when they are supported by the conviction of the unique position and role of our species in nature. Pawłowski rightly questions one of these—the significance of change in sexual behaviour and sexual signaling for hominisation. Because of the vastness of the problem he analyses only one of its aspects, one particularly deeply rooted in anthropogenetic interpretations—the notion of the constant sexual receptivity of females (including so-called concealed ovulation). Far from limiting himself to questioning the stereotype, he advances his own proposal for the interpretation of evolutionary changes resulting in

the present condition of human beings with regard to the above-mentioned traits.

Exposition of the case on the constant receptivity of females related to the lack of oestrus and symptomless ovulation is in fact a relatively easy task. Pawłowski has been able to draw abundantly upon the argumentation presented by the authors of numerous contradictory conceptions. In particular, he has tried to demonstrate the falsity of the belief in the uniqueness of constant receptivity in women, this phenomenon, like the loss of the symptoms of ovulation, being observed in at least a few other primates. He has also attempted to show that it is impossible to find a straightforward dependency between this feature of the sexual cycle and the increase in informational complexity (socialisation) within a group. Finally, he has sought to show that in fact women's receptivity cannot be regarded as absolutely constant and their ovulation is not entirely symptomless.

His work is, however, based on the published literature, and I assume that he has not dealt with the sociobiological or ethological issues on the experimental level. It is worth remembering that, even though no hypotheses are tested, this does not affect the reliability of the account. The numerical weight of the materials, one of the parameters of the reliability of experimental research, is represented in literature-based work by the number of the publications referred to, and this number is undoubtedly sufficient. At the same time, whereas the number of measurements taken in an experiment (usually) indicates high reliability (repetitiveness), the situation with a set of published sources may be entirely different—especially when the works come from the methodological fringe as in my opinion do many works in the field of human ethology. In this context, the persuasiveness of table 1 is very limited. Pawłowski implies that it is difficult to interpret the results of research conducted on contemporary American or European women because of the great many cultural factors that can only be partly controlled. However, he readily accepts the results of research on “hunter-gatherer peoples,” which in my view are not lacking in cultural factors (beyond control in the research) that affect the rhythm of sexual behaviour of their members. What is more important, he does not comment on the fact that, although the symptoms of ovulation in women (and in several other primates) are concealed, *Homo* is the only species with a clearly marked point of the cycle opposite to ovulation, namely, menorrhoea. In speaking about constant receptivity we usually do not mean receptivity during menstruation.

Despite these objections, I am inclined to agree with Pawłowski that the (relative) symptomlessness of ovulation and the specific character of sexual behaviour are a consequence rather than a cause of significant changes giving direction to the process of hominisation. He offers a taxonomic proposal that could be the subject of a separate study in itself. His stand on the taxonomy of the Hominidae is absolutely right, in my opinion, expressing the view supported by the majority of an-

thropologists though practised by few. He points to the incorrect division of the families Pongidae and Hominidae and appropriately recommends a separate Homininae taxon (subfamily) for the australopithecines and humans.

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There is much positive to be said about this article. Pawłowski argues that modern humans share many characteristics of their reproductive biology and sexual behavior with the other anthropoid primates. He supports his argument by pointing out that for humans and the anthropoid primates lacking a sexual swelling (that is, those with concealed ovulation) the act of mating may or may not be timed to ovulation. Moreover, he argues convincingly that the extreme sexual swellings of chimpanzees and bonobos arose after the Paninae/Homininae split. Likewise, his review of the literature suggests that human sexual behavior is not completely independent of the hormonal fluctuations of the menstrual cycle and follows a pattern similar to that found in other anthropoids—in other words, that the overall pattern of human sexual behavior is not unique among the anthropoid primates.

Taking into account the similar behaviors of human and other anthropoids, Pawłowski reasons that human reproductive biology and sexual behavior are not the product of recent sexual selection or a new reproductive strategy. I concur. Alternatively, he argues that climatic and nutritional stresses were the significant forces in the hominization process. He does not, however, address the question of the causal factors involved in the changes from the basic mammalian reproductive pattern to the sexual behavior of the anthropoid primates. This pattern of continuous sexual receptivity with fluctuations in proceptivity and attractiveness over the course of the menstrual cycle is typical of the anthropoid primates including humans. Because this pattern of sexual behavior is widespread among the anthropoid primates, it probably evolved early in their evolutionary history, perhaps as early as the Oligocene. Compulsive sociality, intense social relationships, increased brain size, and greater behavioral flexibility are among the factors that may have helped to alter the basic mammalian reproductive pattern.

The question of the evolution of the sexual behavior of the anthropoid primates is, of course, one of the more interesting problems of primate evolution. An understanding of the evolution of human sexual behavior will come only as we expand our knowledge of the relationship between receptivity, proceptivity, attractiveness, and sexual activity in humans and the other anthropoid primates. The endeavor to understand primate sexual behavior requires interdisciplinary research, and Pawłowski is to be commended for bringing together the lit-

erature of several different disciplines. Future attempts to understand human and nonhuman primate sexual behavior will require a similar interdisciplinary approach.

Reply

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I thank the commentators for their responses and insightful comments on some points of my paper. There is little consistency among them, and some of their opinions are contradictory to those of others (e.g., the recognition of the signs of ovulation in women by Møller and Sillén-Tullberg and the denial of any such signs by Strassmann). I am pleased with the general agreement on my main points of Strzałko and Wolfe and glad to have the opportunity to take up the challenges by Møller and Sillén-Tullberg and by Strassmann.

Møller and Sillén-Tullberg agree that "chimpanzee-like anogenital swellings are unlikely to have occurred in ancestral Hominidae or Homininae" and recognize that ovulation in humans is signaled nonvisually. Both of these points undermine their critiques based on phylogenetic analyses of visually concealed ovulation (not to mention that there is no consensus on analyses of this trait and that there are primates that do not fit them). I doubt that this argument is good enough to allow conclusions about the operation of sexual selection on the traits in question in our ancestors. There is still considerable debate about "sexual behaviour and social mating systems in hominids," and therefore I do not know either what other evidence or what scenario these models are supposed to fit. Møller and Sillén-Tullberg also take for granted that *Homo sapiens* is monogamous. I am afraid that in the light of morphological (sexual dimorphism in body size), ethnographic (the majority of societies are polygynous), and psychological (men desire to have more partners and adultery is frequent in both sexes) evidence even this assumption does not seem so obvious.

The variability of human reproductive strategies in contemporary human populations (monogamous, polygynous, polyandrous, and polygynandrous [see Daly and Wilson 1983]) indicates great flexibility. This may mean that, contrary to the opinions of some writers, selection on reproductive behaviour could not have been very strong or rigid in human evolution. There is also an increasing tendency among the primate taxa towards less rigid ovarian hormonal control over sexual receptivity (Dixson 1998:331). This general tendency in primates to lose oestrus without any corresponding reduction in the variety of mating systems represents a problem for Møller and Sillén-Tullberg's idea of specific sexual selection pressure in human evolution. In addition,

these tendencies confound Strassmann's claim that humans are unique in lacking oestrus.

I agree with Møller and Sillén-Tullberg that intraspecific variation in copulation frequency is common in the animal kingdom. I wanted to show how some cultural factors can influence this variation as well. The main variation is of course biological, and this is why I emphasized the fact that reproductive behaviour due to sexual selection may become more important in terms of general fitness when other (natural) selective pressures on individuals' fitness are relaxed. Becoming successful in avoiding predators, acquiring adaptations to variable climatic conditions, or being very effective in food extraction in harsh (i.e., resource-poor) environments leaves more room for the discriminative role of sexuality (e.g., in the stages of mental evolution in hominines when some relaxation of natural selection probably occurred). Møller and Sillén-Tullberg are right that copulation rate increases in social contexts where extrapair copulations are frequent. This explains why sexual activity is not as frequent in single-male (e.g., gorilla) or monogamous (e.g., gibbon) social structures, where sperm competition is negligible, as in chimpanzees or macaques. Nevertheless, the copulation rate in Western societies is determined not only by the altered conditions for extrapair copulations, as Møller and Sillén-Tullberg suggest, but also by hormone levels due to various factors (e.g., the ecological and economic conditions I mentioned).

Møller and Sillén-Tullberg seem to have overlooked my suggestion that bipedality, olfactory communication (in hot, open environments), a prolonged period of development, and other biological (N.B.: not cultural) traits may have been important in the evolution of human sexual behaviour. I have used cultural data to show instead why (1) in some cases the results of research on sexual behaviour across the female cycle do not fit the expected fluctuation rates and (2) we should be careful about drawing conclusions and suggesting evolutionary mechanisms for hominines or early *Homo* on the basis of data from one or two particular cultures.

Contrary to their suggestion, I do not assume that "current variations in sexual behavior, mate preferences, and reproductive success are cultural artifacts." I did not deny the existence of sexual selection on such features as body symmetry or general physical attractiveness (for example, waist-to-hip ratio) and certain psychological traits influenced by sex. Rather, my aim was to undermine the position of writers such as Parker (1987), who, in postulating mechanisms of human evolution, have overestimated the role of sexual selection—particularly when their main arguments are based on the assumption that the loss of oestrus and concealed ovulation are uniquely human.

I agree with Møller and Sillén-Tullberg about the importance of unconscious olfactory communication, which influences the frequency of sexual behaviour and thus increases the probability of fertilization. Olfaction still performs a reproductive function, though I doubt that it is in the "intense [my emphasis] sexual selection

... associated with particular body odors" as Møller and Sillén-Tullberg (citing Gangsted and Thornhill 1998) write. My claim does not depend entirely on the masking of natural odours and reduced conditioning to such odours in the very early stages of life in our culture, both of which lessen the functionality of the information they convey. Apart from information about the fertile period of the menstrual cycle and some clues about genetic distance (e.g., Wedekind et al. 1995), odours do not convey much information about the partner's value that would serve as a measure of potential reproductive success. The physical attractiveness (appearance) or age of a woman and the wealth, status, or intelligence of the man seem more important and valuable information for the opposite sex in long-term mate-choice strategies. In addition, we should not forget that sexual preferences have evolutionary value only when positively correlated with reproductive success.

Møller and Sillén-Tullberg emphasize the "current role of sexual selection in shaping female reproductive strategies," but when we speculate about the past we must keep in mind that many other traits that have emerged in human evolution may have influenced human reproduction—perhaps even more than one could expect solely by means of sexual selection. In many primates that lack visual signals of ovulation there are some vestiges of a swelling either in pregnancy (e.g., in orang-utans) or in adolescence (e.g., in patas monkeys, gorillas, rhesus monkeys, and stump-tailed or Japanese macaques) (Anderson and Bielert 1994). The lack of obvious vestiges in the human female may mean either that our ancestors never had this swelling or that the disappearance of the swelling may have an important physiomorphological basis specific to this line (e.g., bipedality, fur loss, and/or subcutaneous fat tissue increase).

I concur with Møller and Sillén-Tullberg that it is unlikely that human evolution was devoid of sexual selection pressures. The problem is on which traits it worked, whether this selection was in some way unique or different from the sexual selection in other primates and calls for special explanation, and whether this selection was responsible for the hominization process. Even if the loss of oestrus and the way in which ovulation is (or is not) signaled were really unique for humans (and they do not seem to be), we cannot rule out the possibility that the lack of continuity of these traits among the anthropoids is just a side effect of other novel and/or unusual (for primates) traits that emerged in the evolution of the hominines.

Strassmann questions that primates other than humans have lost oestrus. According to some writers (e.g., Chalmers 1979; Dixson 1998; Martin 1990, 1992; Wolfe 1991) and in line with the original definition of oestrus by Heape (1900, cited in Dixson 1998), the existence of oestrus in anthropoids is rather dubious. Indeed, Martin (1990) has proposed calling oestrus and the menstrual cycle "the female cycle." Therefore there is nothing contradictory in my statement about the lack of human-specificity of this trait despite the fact that the

highest rate of copulation is observed at midcycle in the majority of anthropoids.

Strassmann cites copulation percentages during the period of maximal swelling for chimpanzees and bonobos from Takahata, Ihobe, and Idani (1996). Copulation rate during tumescence ranges from only 62–65% (Wallis 1982, Coe et al. 1979) in chimpanzees to 82% (Furuichi 1987) in bonobos. Wallis (1986, cited in Wallis and Englander-Golden 1992) found that chimpanzee female receptivity did not vary with cycle phase. The results may vary with ecological conditions (e.g., the different results for wild and captive chimpanzees may, as I have suggested, be the effect of the relaxation of natural selective pressures in captivity).

We should remember that the period of maximum swelling can constitute as much as 40% of the cycle for chimpanzees and 47% for bonobos (Takahata, Ihobe, and Idani 1996), and it is much longer than the periovulatory period, approximating the entire length of the proliferative and ovulatory phases in humans. From the data we have on sexual activity in humans—for example, in addition to the earlier-cited results of research by Harvey (1987) and Matteo and Rissman (1984), Bancroft et al.'s (1983) report of mid-proliferative-phase weekly frequencies of ca. 2.8 compared with ca. 1.9 in the later phases and 1.3 in the early proliferative phase—allow us to estimate that probably an average of more than 50% (or even 60%) of sexual activity takes place in these two phases (therefore in about 40% of the cycle). All of these results were obtained despite the many disturbing and novel factors in Western society which can influence sexual behaviour. Unfortunately, we have no detailed data that might allow the calculation of percentages of sexual activity across the cycle in !Kung San women, but I think it is justifiable to assume wider fluctuations in all the human ancestors. For the bonobos in group E2, 67% of copulations took place during 39% of the cycle (Takahata, Ihobe, and Idani 1996); it seems that this species does not have a true oestrus, as this distribution is not dissimilar to that of sexual activity in some humans.

The major problem posed by the data from Mahale—where 94% of copulations took place during the period of maximal swelling—is that the adult sex ratio was highly biased towards females (10:39). Given that, according to Takahata, Ihobe, and Idani (1996), there was no ovulatory synchrony, one would expect males to have preferred the most attractive females (i.e., those with maximal swellings). This skewed sex ratio also explains why (1) 80% of conceptions at Mahale occurred in opportunistic matings (and not at all in consortships, as at Gombe [Tutin 1979]) and (2), contrary to the results of other studies, at Mahale adult females often took the initiative in copulation.

High female proceptivity was linked with intense female-female competition over access to males. The adult sex ratio was also skewed in the case of two groups of bonobos in Takahata, Ihobe, and Idani's data (ranging in different years from 7:9 to 9:13). In all groups, then, males were in a relatively good position

and were more prone to copulate only with females with maximal swellings. Very high percentages of sexual activity in the period of maximal swelling in chimpanzees may also be due to the fact that in this species the increase in the copulation rate in this phase is much greater than in humans (50 copulations per day for a chimpanzee female [Wrangham 1993]). This may mean that there are no great differences between chimpanzees and humans in terms of copulation rate in other phases of the female cycle and only much more pronounced sexual activity (e.g., due to the intense sperm competition between males) in the period of maximal swelling in chimpanzees. Bonobos mate at lower intensity than chimpanzees and have less than 70% of copulations in the period of maximal swelling.

The other problem with the chimpanzee data is the age structure of the group. Including the sexual activity of adults, subadults, or even juveniles may produce different degrees of fluctuation across the female cycle. The more indiscriminate (more equally distributed) sexual activity across the female cycle in many subadult primates prompted me to suggest that human sexuality may be the result of the prolonged period of the development in ontogeny and/or "behavioural neoteny." Prolonged development is linked to increase in brain size, which may mean that some differences in sexual behaviour between humans and alloprimates are at least to some extent side effects of the encephalization process in the course of human evolution.

Strassmann is unhappy with the chimpanzee as a reference for humans. Perhaps some macaques (*M. fascicularis* or *M. arctoides*) or vervet monkeys (*Cercopithecus aethiops*), which do not have so pronounced an increase in copulation rate in midcycle, would be a better model for the distribution of sexual activity across the female cycle in humans. My comparison of humans with chimpanzees or macaques is based on the general pattern of fluctuation of sexual activity across the female cycle rather than its degree. As I have said, the human distribution of sexual activity may be flatter than in other anthropoids, but this may not be a qualitative difference. The question is whether one can speculate about unusual sexual selection pressure on humans during their evolution on the basis of quantitative differences alone. Similar differences can be found between some species of macaque, and it does not seem to alter their social structure very much. The general question would be what degree of quantitative difference would call for explanation in terms of specific, direct selection pressure in the course of human evolution. A more fruitful approach, as Wolfe suggests, would be to seek to identify the mechanisms underlying the anthropoids' tendency to lose oestrus.

Strassmann's comment on my scepticism about concealed ovulation in humans and my claim that oestrus is absent in many primates shows that she does not appreciate the fact that lost oestrus need not be accompanied by concealed ovulation. She supports her claim that there are no signs of ovulation in the human female by citing cultural misidentification of the time of ovulation. Humans do not need to have conscious knowledge

of ovulation, however, because the fluctuation in sexual indicators and spontaneous sexual activity are sufficient to signal the fertile phase of the cycle. There are other signs as well (see, beyond those cited in my paper, the comment by Møller and Sillén-Tullberg), and one can add to these the pain at the time of ovulation in some women). In all of human evolution, as in that of other animals, it is not knowledge that facilitates the reproductive efficacy of sexual behaviour but the steroid hormones. Apart from refraining from sex during menstruation, one possible ultimate reason for the preference for women in the early rather than the later proliferative phase in some societies and in harems (Betzig 1992, Einon 1998) could be selection for women with shorter cycles (and thereby those who ovulate frequently and are in better health) and thus an increase in reproductive success for men who choose to fertilize such women. I think that Strassmann would agree that copulation in the early proliferative phase offers more opportunity for conception to occur than copulation in the relatively long postovulatory phases. Research on the moment of conception across the cycle confirms the possibility of conception for at least two-thirds of the cycle, with the peak between the 8th and the 14th day (Martin 1992). Perhaps we concentrate too much on the evolutionary meaning of concealed ovulation rather than, as Burt (1992) suggests, on why conspicuous advertisements of ovulation have developed in some primates.

I agree with Strzałko that there are cultural factors influencing sexual behaviour even in hunter-gatherer societies, but they are still better living societies to model our ancestors' sexual behaviour on than Western society. Menstruation and its evolution were not the subject of my paper, but Strzałko wrongly assumes that the menstruation is uniquely human. It is covert in prosimians and platyrrhines but is very marked (i.e., with copious vaginal bleeding that is highly visible) in many catarrhines. Does the human female bleed more during menstruation than Old World nonhuman primates? Here again we have a problem with quantitative difference. Studies show (Dixson 1998:273) that after multiple nonconception cycles many female primates have heavier menstruations. Frequent and copious menstruation in women may simply be a reflection of abnormal physiology (adult females are pregnant or lactating most of the time), and, as Dixson states, this does not seem to be relevant to evolutionary questions.

Wolfe rightly points out that we need to think more about the general trend of receptivity in anthropoid primates, but first we need to admit that humans follow the general primate trend and are not the exception. It is not going to be an easy task, but the research direction that Wolfe indicates could be very promising for the understanding of the evolution of human and non-human primate sexuality. On the basis of the greater variability of gestation time in the anthropoids, Martin (1992) suggests that the loss of oestrus and the distribution of sexual activity throughout the female cycle in many Old World primates could be explained by more vital spermatozoa, longer ovulation, or more frequent

multiple ovulation. Another possible explanation might be some new element in addition to the many ecological factors that determine sexual behaviour. One possible candidate for such an element is the relative increase in size of the brain or some part of it (e.g., the neocortex) and more complex control over the hormones involved in sexual behaviour. In primates living in multimale groups with higher neocortex ratios, the correlation between male rank and mating success is lower (Pawłowski, Lowen, and Dunbar 1998). Perhaps lower-ranking males achieve the relatively frequent mating that increases their reproductive success by exhibiting more flexible sexual behaviour (e.g., forming consortships, as in chimpanzees, and more indiscriminate sexuality across the female cycle). Somewhat bigger brains (or rather parts of brains) might have made possible multifunctional (not just reproductive) sexual behaviour. To allow this variance, sexual activity cannot be restricted just to the short period when fertilization is most probable. Constant female receptivity is the first step towards fulfilling these aims; in addition, it can be promoted by an increase in intrasex competition and a strategy of constant receptivity on the part of lower-ranking females. Referring to Strassmann's comment, I am afraid that Montesquieu was wrong at least as far as lovemaking is concerned. Some nonhuman primates make love in all seasons; for instance, the proportion of mating on days on which the female is infertile (including sexual activity in adolescence, pregnancy, postpartum, and on infertile days of the ovulatory cycle) is around 88% for chimpanzees and as much as 98% for bonobos (Wrangham 1993).

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Institutions

At a meeting of the Permanent Council of the International Association for the Study of Human Paleontology in Sun City, South Africa, on July 3, 1998, concern was expressed about a proposal to send certain original African hominid fossils to an American museum for display. The matter was discussed and the following resolution was adopted:

1. Recognising that hominid fossils are an irreplaceable component of world heritage, we, the members of the Permanent Council of the International Association for the Study of Human Paleontology, strongly support

the use of replicas of hominid fossils, rather than the original hominid fossils, for public display to promote public awareness and understanding of human evolution.

2. We strongly recommend that original hominid fossils should not be transported beyond the country of origin unless there are compelling scientific reasons which must include the demonstration that the proposed investigations cannot proceed in the foreseeable future in the country of origin.