16. Concealment of Ovulation, Parental Care, and Human Social Evolution

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Alexander et al. (this volume, chapter 15) describe reasons for assuming, from its current attributes, that the human species has been polygynous during much of its recent evolutionary history (i.e., that, generally speaking, fewer males than females have contributed genetically to each generation, although not necessarily that harems have been involved). Considerable evidence already indicates that humans have essentially always lived in bands of close kin, probably containing more than a single adult male (e.g., Lee and DeVore 1968). These two characteristics, however, fit a large number of nonhuman primate species. Alone they tell us nothing about how the human species came to possess its numerous distinctive and social attributes.

Here we approach this question by first listing and discussing a number of distinctive human attributes. Surprisingly, most of these attributes are sexually asymmetrical or involve the interactions of the sexes. They suggest that the human male is not particularly unusual among primate males, except that he is generally more parental than the males of other group-living species. On the other hand, the human female is distinctive in several regards, most dramatically in undergoing menopause and in the concealment of ovulation. Menopause has been associated with parental care by the female (Williams 1957; Alexander 1974; Dawkins 1976), and we shall argue that concealment of ovulation is associated with the unusual amount of parental care by the male. Several other distinctively human attributes, such as length of juvenile life and helplessness of young juveniles, indicate that an increase in the prominence of parental care was one of the most dramatic changes during evolution of the human line.

Concealment of ovulation, as a strategy for obtaining parental care, seems likely to evolve only in certain kinds of social situations. We believe that by considering the nature of these situations, together with circumstances that could lead to the evolution of increased parental care, it is possible to gain insights into the very general question of how humans evolved their distinctive sexual and social attributes.
Distinctively Human Attributes

Most lists of distinctively human attributes include, in some form, the following and little else:

1. Consciousness (self-awareness)
2. Foresight (deliberate planning, hope, purpose, death-awareness)
3. Facility in the development and use of tools (implying consciousness and foresight)
4. Facility in the use of language and symbols in communication (implying consciousness and foresight)
5. Culture (a cumulative body of traditionally transmitted learning—including language and tools, and involving the use of consciousness and foresight)

As suggested by the parenthetical comments, these five attributes are closely related to one another, perhaps inseparable. They are also not strictly comparable to one another: thus, consciousness and foresight are aspects of the human capacity for culture, while language and tools are simultaneously vehicles and aspects of culture. Culture in turn, by its existence and nature, and through its changes, becomes a central aspect of the environment in which the capacities of individuals to acquire and use consciousness, foresight, and facility in the development and use of language and tools have been selected.

Although these five attributes may once have been regarded as uniquely human, it now seems likely that all occur in other primate species, and chimpanzees alone may possess all five, though not in the form or to the degree that they are expressed in humans (Lawick-Goodall 1967; Gallup 1970; Premack 1971; Fouts 1973; Rumbaugh et al. 1973; Gardner and Gardner 1969, 1971; Mason 1976). The problem in understanding this set of related attributes, and why humans possess them, is to determine their relationship to the reproductive success of individuals during human history, when the capacities and tendencies to express them were originating and being elaborated. Despite the attention paid to them, these attributes have not been extensively analyzed as contributors to reproductive success.

Numerous other traits are also distinctive to humans (t), in the list below) or distinctively expressed in humans, as compared to their primate relatives (tc). They may be either cultural (c) or noncultural (nc) in origin, and universal (u) or not universal (nu) among humans. We first list these
additional attributes, then discuss their significance in trying to reconstruct the evolutionary background of human sociality. Our reason for presenting this list, in developing an argument about the relationship of parental care and the concealment of ovulation during human social history, is to emphasize how many distinctive human attributes are somehow sexually asymmetrical (as) rather than symmetrical (s) in their expression (probably all but 6 and 30 in the following list), and how many involve: (1) interactions of the sexes in connection with parental care (especially 9–16) and (2) group-living (especially 17–30). We shall argue that concealment of ovulation could only evolve in a group-living situation in which the importance of parental care in offspring reproductive success was increasing, and that these two circumstances together describe a large part of the uniqueness of the social environment of humans during their divergence from other primates. We make no pretense that the following list is a complete set of attributes unique to humans.

6 Upright locomotion usual (de, nc, u, s)
7 Frontal copulation usual (de, c & nc, u, as)
8 Relative hairlessness (de, nc, u, as)
9 Longer juvenile life (d, nc, u, as)
10 Greater infantile helplessness (de, nc, u, as)
11 Parental care frequently extending into and even across the offspring's adult life (d, c, u?, as)
12 Unusually extensive paternal care for a group-living primate (de, c?, nu?, as)
13 Concealed ovulation in females (sometimes described as continuous sexual receptivity, continuous estrus, “sham” estrus, or lack of estrus (d, nc, u, as)
14 Greater prominence of female orgasm (perhaps—but see Lancaster, in press) (d, nc?, u, as)
15 Unusually copious menstrual discharge (d, nc, u, as)
16 Menopause (d, nc, u, as)
17 Close association of close kin of both sexes, sometimes throughout adulthood (de, c, u?, as)
18 Extensive extrafamilial nepotism (de, c, u?, as)
19 Extensive extrafamilial mating restrictions (de, c, u?, as)
20 Socially imposed monogamy (d, c, nu, as)
21 Extreme flexibility in rates of forming and dissolving coalitions (d, c, u, as)
22 Systems of laws imposed by the many (or powerful) against the few (or weak) (d, c, nu, as)
23 Extensive, organized, intergroup aggression; war (d, c, u², as)
24 Group-against-group competition in play (d, c, u², as)
25 Ancestor worship (d, c, nu, as)
26 Political and other kinds of appointed, elected, or hereditarily succeeding leaders (d, c, nu, as)
27 The concepts of gods and life-after-death (d, c, nu, as)
28 Organized religion (d, c, nu, as)
29 Nationalism; patriotism (d, c, nu, as)
30 Polities of thousands or millions of nuclear families (d, c, nu, s)

What challenges, in the form of differential reproduction, caused the emphasis on (1) consciousness and foresight, (2) social living, and (3) parental activities, revealed in the above list of human attributes (cultural and physiological)? If we assume that the above combination of attributes arose as a result of physical or nonhuman biotic selective forces, such as climate, predators, or food shortages, then an evolutionary sequence diverging humans so far from other species in the particular directions they have taken, with all the intermediate stages becoming extinct, appears difficult to reconstruct (Alexander 1971). In the absence of any clear evidence of a massively unique selective environment in these respects for humans, we would have to postulate that our uniqueness as a primate preadapted us to respond uniquely to some not-so-unique concatenation of environmental conditions, thereby evolving humanness. We regard this hypothesis as unlikely.

The alternative is that something about the evolving human species itself explains the differential reproduction that led to the divergence of the human line, and the extinction of close relatives along the way. This possibility is immediately tantalizing, since it suggests a solution to the problem of human uniqueness. Once set in motion, such a selective force could be self-propelling and, simultaneously, capable of suppressing similar trends in closely related lines. It further implies a reason for the continuing elaboration of cultural patterns, outracing genetic changes so dramatically as to render them trivial in regard to rates of behavioral change.

The attribute that could cause differential reproduction leading to human uniqueness, we believe, is an increasing prominence of direct intergroup competition, leading to an overriding significance in balances of power among competing social groups, in which social cooperativeness and
eventually culture became the chief vehicle of competition. The probable relevance of complex social competition to human intelligence, consciousness, and foresight—and elaborate social tendencies—has been emphasized before (Darwin 1871; Keith 1949; Fisher 1958; Alexander 1969, 1971, 1974, 1975a, 1975b, 1977a, 1978a, in press a; Bigelow 1969; Alexander and Tinkle 1968; Carneiro 1970; Flannery 1972; Wilson 1975). Intergroup competition has not, however, been linked to the human emphasis on parental care or the unusual sexual attributes of humans.

If intergroup competition was a principal guiding force in human evolution and if groups as a result grew in size and in social unity among the individuals comprising them, then parental care would have increased in value in two general ways. First, larger group sizes inevitably meant intensified competition for resources within groups. Juveniles, lacking the strength and sophistication to compete successfully for themselves, would have benefited increasingly from parental protection and assistance in securing resources for growth and future reproduction. Second, the intensification of both within- and between-group competition implies a growing conflict in individual reproductive strategies by pitting the value of direct competition with other group members against potential gain from their cooperation in inter-group competition (or within-group alliances). Individual reproductive success would depend increasingly on making the right decisions in complex social situations involving self, relatives, friends, and enemies. Critical choices would be aided by experience, and an intimate knowledge of the particular social environment. Parents who could impart to their offspring this information and the social skills for using and expanding it, while providing guidance during the vulnerable years of learning, would have realized increasing reproductive advantages over parents who failed to so equip their offspring. Buffered against physical and social disaster by parental protection, the human juvenile may have evolved to abandon efforts at serious direct competition, becoming increasingly helpless over longer periods, while evolving extraordinary abilities to absorb and retain information and develop skills through attachment, identification, imitation, and more formal learning in early years. In other words, because of the existence of groups intensely competitive against one another, and because of the complexity of social competition within groups evolving to be effective in inter-group competition, the human species in some sense became its own most important selective environment, and the pressure of evolutionary change focused increasingly on parental care.

Tendencies to infanticide or enforced desertion of infants would benefit males to the extent that such practices hastened ovulation in females.
and preserved female reproductive effort for the male's own offspring. The increased parental care of human mothers, its greater duration, and the wider spacing of babies associated with more intensive early parental care and infant helplessness would enhance the benefits of infanticide and enforced desertion of children to males acquiring females from other males. Thus, an important aspect of male parental care may have been protection of the child against other group males competing for the female as a reproductive resource. Observations by Bygott (1972) suggest that if a chimpanzee mother with an infant joins a new group, the infant is vulnerable to infanticide by group males. Accounts of men (or women) killing children made fatherless by inter-community warfare and exchange of women, such as among the Yanomamo (Biocca 1969), imply that this may have been an important selective context for paternal care in human history as well, and another indirect consequence of the extension of juvenile dependence.

In ancestral humans, then, an orphan, even at an advanced juvenile stage, was probably doomed to social impotence and reproductive failure, if not pre-reproductive death, unless it was a female old enough to interest a mature male; the extremely derogatory connotation of words for "fatherless" juveniles in non-technological societies supports this inference (see Alexander 1977a). On the other hand, juveniles with powerful parents and other relatives must have been essentially certain of high success. Indeed, the unstratified or egalitarian bands presumed to represent the ancestral kind of human sociality can almost be defined by saying that in them the major resource by which reproductive competition could be maximized is kinspeople (see also Chagnon chapter 14).

To clarify these circumstances we first examine the social situations in which concealment of ovulation might evolve and compare the resulting model with extant nonhuman primates, then consider the situations in which increases in parental care leading to the human condition might be favored.

Why Conceal Ovulation?

The human female has commonly been described as "continually sexually receptive" because she may willingly mate at any time during the menstrual cycle (James 1971). Most other female mammals mate only during a brief estrus period occurring around the ovulatory period. To refer to the human female's sexual behavior simply as "continuous receptivity," however, seems a gross oversimplification. First, this "receptivity" is unlike the rela-
tively uninhibited receptivity of some estrous female mammals, which may accept essentially any male. By comparison, the human female's behavior might best be described as a kind of selective or low-key receptivity, commonly tuned to a single male, or at least to one male at a time. From the point of view of males not bonded to a particular female, it might just as well be termed "continuous nonreceptivity." It is a truly remarkable attribute of human females that their ovulation is often essentially impossible to detect, even, in some cases, through medical technology (Sturgis and Pommerenke 1960; Behrman 1960; Cohen and Hanken 1960).

Conditions in nonhuman primates that seem to approach those of the human female are: (1) sham estrus in langurs (Blaffer Hrdy 1974, 1977), (2) sexual receptivity outside the ovulatory period, especially in rhesus (Loy 1970) and chimpanzees (van Lawick-Goodall, 1971; Lancaster, in press, reviews other primate cases of mating outside the usual estrus period around ovulation), and (3) relatively few external signs of ovulation in gibbons (Carpenter 1941), orangutans (Rijksen 1975), gorillas (Schaller 1963; Hess 1973; Nadler 1975), and possibly bonnet macaques (Simonds 1965; Rahman and Parthasarathy 1969; MacArthur et al. 1972). In the last case we are assuming that advertisement of estrus by pheromones is not unusually exaggerated in species with few visual signs; any efforts to quantify advertisement of estrus among species are necessarily restricted to visual signs because no effort has been made to accomplish this with pheromones.

In nonhuman primates the general period of ovulation always appears to be more or less dramatically signaled to males (even if only by pheromones or other means not obvious to human observers). All of the nonhuman primates in which females are known to show "pseudo-estrus" are group-living species, while the least obvious signs of ovulation seem to occur in monogamous species like gibbons, or polygynous species, like gorillas, which tend to live in single-male bands. Human females are thus unique in that they give little or no evidence of ovulation and may be receptive during any part of the ovulatory cycle. Although some women have discovered ways to determine the time of their own ovulation, it is clear that selection has reduced the obviousness of ovulation during human evolution, apparently to women themselves as well as to others.

Emphasis on the so-called continuous responsiveness of the human female, in trying to model its history, has focused attention on the proximate effect that the male is able to enjoy copulation more or less whenever he desires it. Thus, it has been argued that sexual competition is reduced among human males, allowing larger group sizes and more extensive cooperation (Etkin 1963; Washburn and Lancaster 1968; Pfeiffer 1969), or, that
females keep their males at home by supplying constant sex (Washburn and DeVore 1961b; Campbell 1966; Morris 1967; Crook 1972). Those approaches have not provoked explanations for the male's retaining his interest in frequent copulation with his mate when fertilization of her ovum is unlikely—that is, when she is not ovulating or when she is pregnant. Focusing on concealment of ovulation within the essentially continuous receptivity of the female, on the other hand, raises the question of the value to the female of this concealment. Evidently it deceives all males in the female's vicinity, both those with whom she is copulating and those with whom she is not copulating. Such deceit would be valuable to the female only if recognition of the ovulatory period somehow caused males to gain at her expense. In the absence of parental investment by males, advertisement of ovulation would both assure the female of copulation at times appropriate to fertilization and increase the likelihood of competition among males, thus increasing her likelihood of securing a male of unusual competitive ability (e.g., Cox and Le Boeuf 1977). Concealment of ovulation and more or less continuous receptivity would have little value in this circumstance, although some tolerance of mating may be expected to appear if male insistence was quite deleterious to resisting females (e.g., McKinney 1975, on ducks). Conversely, if males invest parentally, sexual advertisement of ovulation might cost a female her mate's parental care in two ways: (1) by attracting competing males who threaten his confidence of paternity, and (2) by freeing him, after a brief consort period, to seek copulations with other fertile females who would compete later with her for his parental care.

We suggest that concealment of ovulation evolved in humans because it enabled females to force desirable males into consort relationships long enough to reduce their likelihood of success in seeking other matings, and simultaneously raised the male's confidence of paternity by failing to inform other, potentially competing males of the timing of ovulation. If these events occurred in a situation in which paternal care was valuable, but not sufficiently valuable to males to offset philandering (Trivers 1972), and in which desertion was frequent when confidence of paternity was low, they could tip the balance, making increased paternal investment profitable to males. This strategy would be most likely to be successful for females perceived by males to be of unusual value as mates. Thus, its effectiveness would have been magnified during human history first by abilities and tendencies of males to kill or enforce abandonment of fatherless offspring, and, second, by the rise of differences in heritable wealth and status.

To explore the significance of concealed ovulation, we shall now

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consider variations in the advertisement of ovulation among female primates living in different kinds of social groups, which might be considered to parallel certain aspects of the social environment in which human sexuality evolved. We shall begin with the most monogamous forms, such as the white-handed gibbon. The male and female form an isolated, territorial pair and raise their offspring alone. There are indications that adults are hostile to strangers of the same sex, and their territorial tendencies would seem to minimize direct sexual competition (Ellison 1974). Males are virtually certain of their paternity because, usually, no other males are around to compromise it, and females are relatively free of competition from other females for their mate’s parental care. It might be supposed that the human species lived in this fashion during much of its evolutionary history, and that the so-called “continuous receptivity” of the human female evolved because such females tended to keep their husbands home while other husbands went roving, presumably to satisfy persistent sexual cravings. Such an argument, however, does not describe the behavior of modern gibbons, which mate only when the female ovulates, and it is difficult to defend on a logical basis. If males that stayed at home, tending their mates and their offspring, outcompeted faithless males, their doing so would surely not depend on whether or not their mates provided them with constant sex. Indeed, in such circumstances, constant sex would be no more than a useless and potentially dangerous distraction from the business of staying alive and healthy and rearing one’s offspring. Rather than being continuously receptive, females in such families should evolve to be receptive only during a brief period associated with ovulation—just long enough, in other words, to maximize the likelihood of fertilization at the appropriate times. They should not be gaudy or extravagant about their responsiveness, communicating no further than the mate. The male, likewise, should evolve to be interested in sex only during the same period and only with his mate. Gibbons, which appear to behave as these arguments suggest they should, do not provide a suitable model for the history which determined the nature of present human sexuality. Only if continuous sexuality in the male consistently yielded opportunities for philandering should it be maintained by selection and defenses against philandering be evolved by females because of the value of male parental effort; these conditions are likely only when families are either polygynous or in relatively close proximity.

In orangutans one male often controls a territory containing more than one female (Rijksen 1975). It is not clear how effectively such males exclude other males, and males move about, sometimes in groups, and apparently rape females (Rijksen 1975; MacKinnon 1971). Females sometimes
approach males for copulation and are said to prefer "high-ranking" males (Rijksen 1975). Males evidently provide no parental care. From these reports, we might predict that orangutan females advertise ovulation more than gibbon females, and are sexually responsive only at ovulation time. Females may also be receptive when approached by strange males, if such males might benefit from killing an offspring sired by another male or when resistance to rape would be detrimental (infanticide, however, has not been observed in orangutans). To the extent that orangutan females select males, they might profit from concealing ovulation altogether and ovulating reflexively. Males would then gain by copulating with any available female whenever they could. But the orangutan situation, which is still known only very sketchily, appears not to have led to extensive male parental care, nor does it involve extensive group-living, both of which seem essential to a model of human social and sexual history.

Considering single-male primate bands next, such as gorillas," we might again predict a relatively low rate of sexual activity, and a relatively nonobvious estrus period. Although females in a band must compete with one another to some extent for the single dominant male's attention, male competition apparently consists largely in securing and maintaining a harem of females. To the extent that this is true, females would gain little by advertising estrus more than is necessary to secure the male's attention at ovulation time, unless other potentially better males are constantly in range of their signals, and able to use them to usurp ownership of the band. As with gibbons, the male's confidence of paternity is probably high—at least in species in which harem is held for long periods—and some paternal care should thus be evident. Because males are essentially certain of their paternity, females would gain little in terms of a larger share of paternal care by concealing ovulation and prolonging receptivity. Sexual behavior in gorillas is indeed infrequent, estrus is not sharply advertised, and the silverback male's evident willingness to repel potential predators could be interpreted as paternal effort (Schaller 1963; Fossey 1970, 1971).

Although blackback, younger males occur with gorilla bands including but one silverback male, and some bands have two silverback males, we believe gorilla bands are appropriately termed single-male, or at least are different from such species as chimpanzees, cynocephalus baboons, and thence macaques, because of the evident dominance of one male and the fact that one silverback male generally determines band movements (Schaller 1963; Fossey 1970, 1971). Harcourt, Stewart, and Fossey (1976) argue that the dominant silverback gorilla male inhibits other males from mating more effectively than do dominant baboon or chimpanzee males and suggest that some blackbacks are offspring of the silverback male.

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In multi-male bands of nonhuman primates one finds the most dramatic advertisements of sexual receptivity, the most obvious and intense sexual competitiveness, and—aside from single-male harems for which ownership changes frequently (e.g., langurs, Blaffer Hrdy 1974, 1977)—the most striking cases of receptivity outside the ovulation period. In baboons, macaques, chimpanzees, and a few other forms that live in multi-male troops, the females develop bright-colored swollen rumps during estrus. It is difficult to explain these gaudy swellings except on the assumption that females in such groups gain by competing for the attention of the dominant males. Paternal care is evidently minimal in such groups, compared to one-male bands and isolated monogamous pairs, and one apparent correlate is a low confidence of paternity. The gaudy females appear to be competing for the attention of the males most capable of physically monopolizing them at ovulation. There is no necessary correlation between a male’s ability to monopolize a female and his ability to provide paternal care; such a correlation might evolve, for example, if females consistently gained from protection against predators (or other males) during the period of sexual receptivity. If monopoly gives a male high confidence of paternity, his willingness to invest parentally may be raised; in contrast, if a female copulates with a subordinate male, and he is quickly supplanted after copulation, neither male is likely to be willing to provide paternal care.

The trend in the three kinds of social situations just discussed—isolated, territorial pairs, single-male bands, and multi-male bands—seems opposite to that which gave rise to the human condition, at least in regard to advertisement of ovulation by the females and the extent of paternal care. Yet it is commonly accepted that humans evolved in multi-male bands. On the other hand, it is difficult to see how concealment of ovulation could evolve in either isolated monogamous families or single-male harem groups, since there would be no “extramarital” males from which to conceal ovulation. Nor does the evolution of tendencies toward regular and continual sexuality in mated human males and females seem likely in either single-male groups or monogamous families unless takeovers by new males occur frequently enough (Blaffer Hrdy 1974, 1977).

Langurs are probably most appropriately compared to multi-male troops because their rapid changes of ownership by males, and the sham estrus of females by which even pregnant females mate with the new owner of a troop, suggest that rapid shifts of ownership are not a novel or recent phenomenon, as has been argued in criticisms of Blaffer Hrdy’s (1977) conclusions, presaged by Mohnot (1971) and Sugiyama (1967)—see Alexander (1974).
It might be argued that humans were extensively group-living, or multi-male in social structure, when the distinctive attributes of the human female evolved. Perhaps our ancestors lived in isolated monogamous families or in single-male harem-polygynous groups, with initially extensive male parental care followed by expanded group size in response to predator pressure. For two reasons, this alternative seems a less likely route to human sociality than the prevalent view that prehumans lived in relatively large multi-male bands. First, humans are thought to have evolved in open woodland or savannah (e.g., Lee and DeVore 1968; Kolata 1977) where, today, there are no monogamous primates and few single-male, harem-polygynous ones. Moreover, primate species in such habitats today (e.g., langurs, vervets, patas) show anti-predator behavior which seems counter to the trend in human evolution—hiding, secretiveness, and little direct confrontation of predators. Man's most similar relatives, chimpanzees, which inhabit woodland and savannah, have a multi-male, polygynous social structure. Second, the selective pressures generally thought to have been important in human social evolution—cooperative defense, hunting, and inter-group competition—favor group sizes probably greater than one male and his harem. So, even if humans began in small harem groups, they obviously (and probably early) achieved multi-male situations which tend to threaten pair bonds. Cooperation by males against predators occurs both in multi-male bands with harems (hamadryas and gelada baboons) and in so-called "promiscuous" multi-male bands (cynocephalus baboons). In both types of social structure a male's confidence of paternity is threatened to some degree, probably more in the latter case.

In summary, we believe that two coincident circumstances can explain the evolution of concealment of ovulation. The first is a social situation in which females of reproductive age are not completely inaccessible to males other than their mates or consorts (e.g., multi-male groups or defensible multi-female territories). The second is a growing importance of parental care such that the value to a female of a male's prowess in monopolizing her at ovulation time would be overshadowed by the value of male prowess and willingness as a providing or protective parent. Gradual evolution of concealment of ovulation by females behaving so as to maximize their mate's confidence of paternity—hence his likelihood of behaving paternally—would with each step toward concealment improve the female's ability to secure her mate's parental care. Because no male could tell when a female was ovulating, only a male who tended her more or less continuously could be sure of the paternity of her offspring. Occasional forced or
clandestine matings outside the pair bond, in the absence of information about ovulation, would have a very low likelihood of resulting in pregnancy (e.g., Tietze 1960).

According to what sequence of changes might the human female have evolved her current uniqueness in regard to the cycling of sexual receptivity and external signs of ovulation? One might consider three possibilities: either (1) external evidence of estrus diminished first, with receptivity later increasing in duration; (2) receptivity became more or less continuous, with external evidence of ovulation later diminishing; or (3) these two changes occurred together. Since we favor the hypothesis of a human ancestor living in multi-male groups we tend initially to eliminate the first of these three possibilities.

Presumably sham estrus, or receptivity outside the ovulatory period, is effective only if it actually mimics estrus. It can only do this by becoming elaborate like true estrus, or by a reduction in the elaboration of true estrus. One might imagine that females gained directly from dampening signs of ovulation, if pairing and some male parental behavior preceded concealment of ovulation, as they must have. In an extensively group-living species, however, at this stage, opportunities for males to be polygynous must have been numerous, detracting from the value of the pair bond to males, but not to females. It is difficult to see how a female could keep her mate by dampening sexual signals. Rather, a gradual extension of signals beyond the ovulatory period seems a more likely way to lure the male into giving more parental care than he would give if he based his effort on a correct determination of the time of ovulation.

Steep differentials in female quality would enhance the effectiveness of this deception. The highest-quality females (in terms of ability to bear and rear offspring, and, perhaps, to enhance their status or other correlates of reproductive success), would be in demand by the highest-quality males most prone to polygyny; such females could afford to prolong estrus longer than others without risk of desertion by the male. Low-quality females would be at least partially excluded from mating with the highest-quality males by this ploy. Competition for matings by lower-quality males would be reduced (because top-quality males are already committed), making concealment of ovulation advantageous to low-ranking females in securing at least some parental care for their offspring. Once sham estrus became prevalent, reduction of external signs of ovulation seems inevitable if only on the basis of cost reduction. So we postulate that sham estrus evolved for a time to mimic true estrus, and subsequently the elaborateness of both true and sham estrus was reduced.
Bright sexual skins in hamadryas and gelada baboon females at first seem to contradict our hypothesis because these species have harem-polygynous breeding systems. Paternity is more certain here than in the promiscuous polygynous bands of savannah baboons, and one might therefore expect the evolution of paternal care and concealed ovulation in females. However, observations by Kummer (1968) suggest that hamadryas females, too, may be competing for the attention of high-quality males. Although harem-masters do not fight over estrous females or mate extra-maritally they do battle over anestrous females so that females occasionally pass between harems. Females are more “spatially independent” while in estrus, perhaps inviting competition between their harem-masters and extra-marital males, primarily bachelors. Fighting takes place frequently between harem-masters and bachelors, and occasionally between two or more harem-masters. Mating occurs in crowded areas near sleeping cliffs, and adulterous matings with bachelors are common, reducing the confidence of parenthood of harem-masters. Males in this system provide little direct parental care to their offspring, and the willingness of females to stray and mate with other males suggests that securing the best possible mating is more central to their reproductive strategy than maintaining a high confidence of paternity.

Concealed Ovulation and Rape

When females do not reveal their ovulations, unmated males no longer have the opportunity to compete for ovulating females. If our interpretation that human females are better viewed as continuously nonreceptive or continuously selectively receptive is correct, then males not bonded to a female have no way of obtaining reproductively effective matings except by increasing their numbers of matings, more or less randomly with respect to ovulation. Moreover, since female receptivity does not correlate with ovulation, there is no reason, except convenience and lowered risk, for males to seek only receptive females. A forced mating might even be as likely to lead to actual success in reproduction, since unwillingness sometimes would imply a pair bond, hence the possibility of paternal care for the resulting offspring from a cuckolded male. In this sense, then, concealed ovulation and some aspects of rape in humans may be historically related. As females evolved to deny males the opportunity to compete at ovulation time, copulation with unwilling females became a feasible strategy for achieving some reproduction. A raped female, moreover, might sometimes lose too much
by revealing the event to her mate, and this would increase the likelihood of rapists' going unpunished. Compared to other primates, then, a mating with a willing human female is less likely to lead to reproduction (because she is less likely than a willing nonhuman primate female to be ovulating). A mating with an unwilling female is more likely to do so (because she is more likely than an unwilling nonhuman primate female to be ovulating, also more likely to have a male who gives paternal care and whom, on that account, she is unlikely to inform of the rape).

In many societies in which rape occurs rather frequently, women submit to avoid being hurt and usually do not complain later (e.g., New Guinea: Matthiessen 1962; Kenya: LeVine 1977). Such rapes are not necessarily associated with psychological pathology in the males or murder, characteristic of a significant proportion of rapes in the U.S. (but see Amir 1971). The association of rape with murder and psychological pathology in males in the United States may reflect the severe penalties traditionally incurred for violating socially imposed monogamy. Only the most deprived males (in actuality or by delusion) would be inclined to behave as though viewing rape as a viable reproductive strategy in relation to other reproductive alternatives; having committed such a crime, fear of discovery might lead such males to murder their victims—canceling any reproductive gain, but escaping certain death if caught.

Concealed Ovulation and Female Orgasm

Female orgasm was once regarded as unique to humans. Although recent studies suggest that this is untrue (see review by Lancaster, in press) the frequency of orgasm in the human female, and perhaps its intensity or outward signs, may still be unique. To examine the significance of this situation we may note first that orgasms in other primate females have been described in species such as rhesus macaques which live in multi-male groups and rather consistently show sexual receptivity outside the ovulatory period (Lindburg 1971).

Orgasm in the human female, and perhaps other primates as well, may increase the likelihood of fertilization (Fox et al. 1970; but see Masters and Johnson 1966: 122-124). But when should there be external signs of orgasm? We suggest two possibilities: (1) orgasms may sometimes increase the likelihood of abortion, thus decreasing the likelihood of paternity mistakes in some circumstances, and (2) external signs of orgasm may communicate the female's sexual satisfaction to the male. In the latter case the
apparent tendency of female orgasm, in humans at least, to resemble male orgasm, in the apparent absence of a correlation with an event paralleling release of gametes (Masters and Johnson 1966), may suggest (1) that the correlation is to some extent with the pleasure or satisfaction of male orgasm to the male (so that the external signs of a female’s orgasm suggest to the male pleasure on her part similar to his own), and (2) that this aspect of the female orgasm may be a communicative device which tends to raise her male’s confidence that the female is disinclined to seek sexual satisfaction with other males.

To the extent that this interpretation is correct, the obvious outward signs of female orgasms should (1) mimic male orgasms and (2) frequently involve deception, with females pretending to have orgasms when they do not. Moreover, both this function and effects on likelihood of fertilization suggest that orgasms should (1) occur most frequently in (a) deeply satisfying or long-term interactions with males committed to the female and her offspring (Gebhard 1966), and (b) with dominant males or males with obviously superior ability to deliver parental benefits, and (2) occur least frequently in brief or casual encounters, or in copulation with a partner unsatisfactory in the above regards. All of these contingencies seem compatible with what is known about orgasm in human females, while few of them seem to characterize male orgasm. All appear to be consistent with the information reported by Lancaster, except possibly for the suggestion that female macaques in the laboratory achieve orgasms sooner if they have been deprived of sexual activity. According to our speculation, female orgasms would perhaps be more likely in females trying to obtain or keep a “good” male, identified as a male with much parental investment to offer. Thus, we believe that this feature of human female sexuality too may be linked to male parental care and the threat of desertion.

Parental Care and Hairlessness

A possible relationship exists between the relative hairlessness of humans and their emphasis on parental care. In the several published arguments on this question it seems to have been overlooked that the least hairy of all humans are their juveniles. Hairlessness in young mammals otherwise seems to correlate with multiple births and a helpless period in the nest. Humans may be the only mammal giving birth to a naked single offspring. We suggest that the selective value of being a juvenile, or of giving that impression, should be investigated in efforts to explain the gradual evolu-
tion of hairlessness in humans, and its present distribution among humans of different ages and sexes.

Upright Locomotion and Parental Care

Upright locomotion has been associated with the evolution of hunting and tool use (Eimerl and DeVore 1965; Morris 1967). Washburn and DeVore (1961b) suggest that parental care may be implicated in the evolution of bipedalism, as well. They argue that, as the human infant became more and more helpless, and the human mother more hairless, the baby was no longer able to cling unassisted, as nonhuman primate babies do from a few days after birth. Upright posture may, in fact, have tended to evolve first in females in the context of carrying infants. If so, then with the possible exception of frontal copulation (7) and unusually copious menstrual discharge (25), all of the attributes which we have identified as uniquely expressed in humans appear to be related in some rather direct fashion to parental care and other forms of nepotism.

Self-Awareness and Concealed Ovulation

Whether or not the above hypotheses about concealed ovulation are precisely correct, any argument from adaptiveness must take into account that the human female has evolved to conceal her ovulation not only from others in her vicinity but evidently from herself as well. The timing of her own ovulation is not commonly a part of a woman's conscious knowledge. Unless one assumes that other primate females, such as chimpanzees, are also not aware of their extensive behavioral and physiological changes at ovulation, this fact suggests that it has somehow been reproductive for human females actually to lose awareness of their own ovulation.

If disappearance of outward signs of ovulation was favored because they deceived other individuals, suppression of self-awareness of ovulation, unless merely incidental, may appropriately be hypothesized to have furthered the deception. What is implied is that social deception may sometimes be more successful if the deceiver is unaware of it (Alexander 1975b).

Evolutionists can scarcely fail to be puzzled and intrigued that with all the complexity of human consciousness, and its apparent pervasion of all of our social interactions, humans nevertheless express surprise, disbelief, or even outright anger at the suggestion that their behavior has evolved to
maximize their genetic reproduction. Unless one rejects the primacy of differential reproduction this response indicates that it has been advantageous for us to think that we have other goals. Perhaps what has actually been advantageous is for us to be able continually to deceive others in regard to the nature and extents of our likely gains as a result of particular activities with effects on them. That is, except for avowed enemies such as members of alien or competitive groups, it may have been more detrimental, during human history, to us as individuals to have others construe continually that our immediate motivations for each social act were personal gains relative to those with whom we are interacting or for them to know exactly how much we are likely to gain from the interaction. Yet these are the precise criteria of success in differential reproduction.

It is difficult to avoid the conclusion that we are better at convincing others that our acts are truly beneficial to them and theirs, as opposed to ourselves, if we believe it ourselves. Righteousness is a valuable aid and effective deceiver. Deliberate lying is notoriously difficult as a social strategy; we are extraordinarily clever at detecting it, vindictive and grudge-holding in our response to it, and much more likely to be fooled by the selfish person with a sincere belief in his own altruism and integrity.

The ability to deceive, partly by self-deception as to motives, we here suggest to be a central part of human sociality, and of consciousness and self-awareness in the human individual (see also Alexander 1975a). Concealed ovulation we view as a particularly powerful and instructive case of deception of others, linked with self-deception and made more effective by it.*

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* Beverly Strassman has remarked to us that nowhere in this chapter have we emphasized that concealment of ovulation would tend to favor subordinate males, inferior in direct physical competition for estrus females but usually willing and capable in regard to parental effort. We think her point is well taken.