## WHY HUMAN NEONATES ARE SO ALTRICIAL

The question of why the human neonate is so altricial is one that has long interested biologists and anthropologists. Certainly, this is so because it is a part of our own existence, yet this fascination also may be because human offspring remain immature longer than those of any other species of comparable size (Montagu 1961). Schultz (1961) argues that differences in altriciality between humans and the great apes are insignificant but this is surely debatable since we probably need at least an additional half year of in utero development to be born as advanced as the great apes (Passingham 1975). Our complex hemochorial placenta permits high fetal growth rates; however, relatively large size is reached at birth without the expected level of maturity. It is this unlikely combination of rapid development with extreme altriciality that distinguishes the human neonate (Campbell 1966).

Gould (1977) discusses that the large bodies and small litters of humans are actually more typical of precocial species. He considers us to be ''secondarily altricial'' as part of a neotenous condition (see also Bolk 1926; Haldane 1949; Montagu 1960, 1961). Our gestation is quickened because of the high neonate weight caused by lengthening of rapid early embryonic development (Olivier and Pineau 1958; Gould 1977). The head of the neonate is especially enlarged by this phenomenon and the neonate must leave the mother earlier than in other primates if it is to pass through the birth canal (Montagu 1961; Washburn and DeVore 1961; Campbell 1966; Passingham 1975; Gould 1977). Indeed, various mechanisms such as maternal pelvic width expansion and narrowing of the newborn's cranium may be necessary for successful birth.

Much has been written on human development and parturition. The most often cited explanation for the extreme immaturity of human neonates involves birth canal-head size arguments. Although we do not offer evidence to refute this explanation, alternative hypotheses are plausible and may be testable. In this paper, we suggest that the developmental state of human offspring at birth is related to mating patterns. In addition, we provide a comprehensive picture of the evolution of human altriciality by combining original and established concepts from a variety of disciplines.

Paternal investment (Trivers 1972) is probably one of the chief advantages of a monogamous mating system (Clutton-Brock and Harvey 1977; Crook 1977; Kleiman 1977; Ralls 1977; Daly and Wilson 1978). Zeveloff and Boyce (1980) suggest that mammalian mating systems may evolve as a function of varying opportunities for paternal investment; an altricial neonate will offer greater potential for male parental care. An increase in male association with the young may result in closer bonds with the mother, as well, since she would also typically be engaged in offspring care. In humans, too, increased possibilities for paternal care may have favored monogamy (Jolly 1972; Benshoof and Thornhill 1979), granted

that there is great variability in human mating patterns (Alexander et al. 1979). We consider humans to be essentially monogamous (Zeveloff and Boyce 1980) especially since even in polygynous societies few males can obtain the wealth or status necessary for multiple marriages (Crook 1980).

An alternative hypothesis to this altriciality-evolving-monogamy scenario is that the neonatal status is a consequence rather than a cause of the mating system. Prolonged immaturity could be a response to group life (Poirier 1977) and trends toward altriciality may be accelerated under monogamy (R. D. Alexander, personal communication). We review how this may occur: (1) females with short gestations may be favored in monogamy since they increase the confidence of paternity and thus the likelihood of male parental investment (R. D. Alexander, personal communication). Paternity confidence has been demonstrated to be a determinant of paternal care in humans (Gaulin and Schlegel 1980). (2) Females that produce altricial young in monogamy will have greater fitness since males will have more opportunities to invest in such offspring and thus enhance their own fitness. (3) Altricial neonates may be particularly effective at performing various attachment behaviors such as grasping, babbling, and crying (see Bowlby 1969) which could solicit male interest. Trivers (1974) suggests that there is a greater sensitivity to offspring cues in species bearing altricial young. Ultimately, monogamy will select for females that conceive immature young since their fitness is increased by a repertoire of tactics allowing the potential paternal investment available in monogamy to be maximized.

This monogamy-evolving-altriciality interpretation and its converse need not be mutually exclusive. Although the mating-rearing system may respond to selection as a unit (Crook 1977), it seems fruitful to examine how the mating system can influence offspring production. Moreover, both the neonatal status and the mating system of humans are important components of a reproductive strategy with profound demographic and evolutionary implications (see Lovejoy 1981).

Loss of estrus, a trait unique to female humans, may also contribute to the evolution of the human mating-rearing strategy. If a male is unable to detect when a potential mate is ovulating, he may be more inclined to guard her continually (Alexander and Noonan 1979; Symons 1979) to ensure higher confidence of paternity. Thus, concealment of ovulation might be another means by which females could increase the likelihood of male parental care (see also Benshoof and Thornhill 1979; Burley 1979).

We also suggest that thermoregulatory considerations may be involved in the evolution of human altriciality. *Homo erectus* probably lost his original hairy coat while hunting diurnally on the hot savanna (Campbell 1966; Morris 1967; Kushlan 1980; but see Schwartz and Rosenblum 1981). As this species increased its range into the temperate zone, clothing and shelter became necessary (Hammel 1969). The first evidence of substantial housing is from the time of *H. erectus* discovered at Terra Amata, France by de Lumley (Campbell 1966). Such shielding from the elements should permit continuance of any trend toward immaturity at birth since a smaller (i.e., altricial) neonate could remain as warm as a larger unprotected one. Case (1978) offers an argument that interconnects energetics with altriciality and monogamy. He notes that since production of an immature off-

spring allows most parental energetic expenses to be shared, it favors monogamy. But this situation may also be interpreted within the framework of monogamy-evolving-altriciality because a female that decreased the energetic burdens of pregnancy in a pair-bond may increase her fitness.

Perhaps the earliest notions about our immaturity at birth center around the resultant extended period for brain development and thus learning (see Schultz 1956; Mayr 1964; Holloway 1972; Passingham 1975). Kuttner (1960) argues that the fetalization or neoteny associated with human altriciality permits more learning for an additional reason. This is that the neural circuitry in such immature young has not yet developed to the point where only rigid, instinctual behaviors can occur. Current theory on the subject implies that there are feedback links between the extension of youth and learning periods, brain development, and cultural evolution (Holloway 1972, 1975; Bonner 1980; Crook 1980). Altriciality is thus favored since skills associated with long development are important components of civilization. Indeed, our culture has become to a large extent the environment of our evolution (Holloway 1972, 1975; Baldwin and Baldwin 1979; Bonner 1980; Crook 1980).

It is logical that the immaturity at birth typical of *H. sapiens* was approximated during the latter part of the tenure of *H. erectus* between 150,000 to 100,000 yr ago. Extreme altriciality was likely in this species since adult head shape, brain size, and pelvic canal size have been quite similar for the past 100,000 yr (Brothwell 1969). Also the greatest increase in cranial capacity occurred with the emergence of *H. erectus* (Tobias 1971). The implication is, of course, that neonate head size was also similar to that of today although this presently remains untested. It is unlikely that australopithecine neonate head size was as large as that of modern hominids given the size and shape of the adult head and the likely lower level of learning.

If altriciality was highly developed in *H. erectus*, we suspect that monogamy was the typical mating system as a result of the connection between these traits elaborated upon earlier. The association between low female investment at birth and monogamy is widespread in mammals (Zeveloff and Boyce 1980). We tested the null hypothesis that no relationship exists between the neonatal status and the mating system in primates by a $2 \times 2$ contingency table analysis. Our results also demonstrate an association between altriciality and monogamy in primates ($\chi^2$ test; $P < .03$) for 18 species examined; altriciality and the multimale hunting band social system are not related. Some (Washburn and DeVore 1961; Washburn and Lancaster 1968) imply that prolonged offspring dependency was permitted during human evolution under this system but it is doubtful that such dependency would be similar to the type favored by monogamy. Etkin (1954) argued that australopithecines were monogamous because of the necessity for cooperation in care of the young in a hunting economy. Cooperative behaviors between the hunting/protecting males and childbearing/gathering females would depend upon long learning periods and hence immaturity at birth (Campbell 1966; Washburn and Lancaster 1968; Baldwin and Baldwin 1979). Thus, a predisposition toward monogamy in later hominids coupled with increasing brain development would continue to select for altricial offspring.

As a final note, we would like to discount the notion that human gestation is determined by delivery through a pelvis constrained by bipedality (Washburn 1960; Jolly 1972). Australopithecines may have been excellent bipedal walkers, yet probably had a smaller pelvic canal and probably did not have neonates nearly as altricial as ours (see Leutenegger 1972; Lovejoy et al. 1973; Lovejoy 1975; Johanson and Edey 1981). In fact, through man's history, the trend has been toward brachypelvia and a widening of the birth canal (Chiarelli 1973; Lovejoy et al. 1973; Preuschoft 1978). Altriciality is not contingent upon bipedality since this form of locomotion does not necessarily favor a smaller birth canal.

To conclude, we suggest that monogamous pair-bonds and concomitant opportunities for paternal investment may contribute to the evolution of human altriciality. Females with short gestation periods, and thus bearing altricial young, offer increased confidence of paternity for their mates and increase the probability of paternal investment in their offspring. This tendency toward increased altriciality may have been reinforced by the thermoregulatory benefits from clothing and shelter and by increased learning periods for juveniles.

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