Care and Exploitation of Nonhuman Primate Infants by Conspecifics Other Than the Mother

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I. INTRODUCTION

Maternal care of offspring is both a widespread and relatively unsurprising phenomenon: by investing care the mother is presumably maximizing her

chances of leaving surviving offspring. To the extent that care represents an investment, care by conspecifics other than the parents is more puzzling. In the primate literature, such relations between infants and older animals have been referred to as *aunting* (Rowell *et al.*, 1964), *paternal* (Itani, 1959), or *parental* (Alexander, 1970) behavior. Despite this nomenclature, none of these terms necessarily designate any genetic relationship, although they do not preclude it. As used in this paper, the term "aunt" by definition excludes the mother; a male caretaker, on the other hand, may in fact be the biological father since paternity is rarely known. Recent theoretical suggestions about the role of kinship in the determination of behavior (Hamilton, 1964) and in particular current hypotheses concerning "inclusive fitness"—that is, the sum of an individual's own fitness plus the effects that his behavior has on the fitness of his relatives and vice versa—make it increasingly important to know the extent to which such "aunts" and "uncles" really are related to their charges.

On the basis of Hamilton's theories, one would expect degree of relationship to be a rough predictor of the type of behavior that will be directed toward an infant. Lucid explanations of what Hamilton means by "degree of relationship" and its bearing on behavior are available in his own work (Hamilton, 1964, Part II), in Trivers (1974), and in Wilson (1971, Ch. 17). Very briefly, in diploid organisms such as primates, a parent and offspring, and full siblings share one-half of their genes by common descent; half-siblings are related by one-quarter, cousins by one-sixteenth, and so forth. The likelihood of altruistic behavior will be a reciprocal function of the degree of relationship involved. In order for any given social trait to be favored by natural selection, it should have a positive net effect for the inclusive, as well as the individual, fitness of the carrier. Where benefit differences are attached to different behavior, and where discernment of kinship is possible, as in the case of a sibling or maternal relationship, one would expect discrimination to occur. In the case of paternity, where kinship is less easily determined by an observer, one would expect role differences between those animals in potentially progenitorial positions and those in positions peripheral to the breeding system.

In this paper, instances of care for infants by individuals other than the natural mother, and also instances of abuse of infants by males (Section II) and females (Section IV) of various primate species, are examined, and the advantages and disadvantages of such behavior for the parties concerned enumerated. As an extension of this approach, I explore natural-selection pressures on the infant and on the mother–infant pair to either attract or discourage conspecific attentions (Section V,B). Some differences between male and female treatment of infants are also discussed (Section III).

Throughout this paper, the purpose of enumerating costs and benefits as proposed above is to relate observed behavior to evolutionary theory. Needless to say, the data necessary to test the predictions generated by those theories do not

exist in the primate literature. Long-term (5 years or more) genealogical information gathered under relatively natural conditions is available for only four species: *Pan troglodytes*, in the published and unpublished records of van Lawick-Goodall; *Macaca fuscata*, in the work of Kawai, Kawamura, and others; for *Macaca mulatta* in the work of Koford, Sade, Vessey, and others, and in unpublished records; and for *Presbytis entellus* in the unpublished notes of S.M. Mohnot. In the case of the first three species, where such genealogical data have been used in behavioral analyses (van Lawick-Goodall, 1967, 1971; Itani, 1959; Kawai, 1958; Kawamura, 1958; Koford, 1963a,b; Sade, 1965, 1967; Yamada, 1963; and elsewhere), matrilineal kinship in connection with other life-history parameters has emerged as a crucial determinant of both social status and frequency of association with other animals.

Whether the importance of maternal kin, as seen in chimpanzees and Japanese and rhesus macaques, will hold true for other species remains to be demonstrated as current studies yield more genealogical information and as new techniques are applied to this problem. For obvious reasons, matrilineages have been easier to determine than patrilineages. New possibilities for captive and trapped study populations include biochemical techniques for paternity exclusions and determination of probable paternity. Several analyses of blood proteins carried out for *Macaca nemestrina* (Simons and Crawford, 1969) and *Macaca mulatta* (C. Alper, 1973 personal communication) have already led to paternity exclusions.

For most primate studies, there are no firm data on kinship; the researcher's impression that "there is no particular relationship," or that one monkey is "probably an older sibling" may or may not be reliable. However, the following assumptions can be made with some degree of assurance.

1. In multimale troops, dominant males are most likely to copulate with females at the height of estrus, and females are most likely to be impregnated at this time, e.g., baboons and macaques (DeVore, 1965; Rowell, 1967; Michael and Zumpe, 1970); younger and more subordinate males are less likely either to have consort relationships or to impregnate females.

2. In harems, the length of the leader's reign, and his success in maintaining the breeding integrity of his troop, must be taken into account, e.g., patas monkeys and one-male troops of langurs (Hall, 1968; Yoshiba, 1968), but in general, this male will be the progenitor of that troop's recent offspring.

3. In matrifocal societies in which contact with the mother may continue after birth of the next infant, e.g., Japanese macaques, chimpanzees, Nilgiri langurs (Yamada, 1963, p. 50; van Lawick-Goodall, 1971; Poirier, 1968, p. 49), juveniles or adults that seek recurrent contact with an older multiparous female may be assumed to be her offspring and, thus, her new children their half-siblings.

Using behavioral indices to determine probable degree of relationship becomes

dangerously circular when kinship derived this way is then used as a part of the explanation for observed behavior. Nevertheless, pending the availability of precise genealogical information, these assumptions will allow us to formulate some predictions and to test these tentatively against the data that we do have. It is to be hoped that such an attempt will stimulate research that will allow for a more rigorous consideration of evolutionary theory among the primates.

In the discussion that follows, I hope that it is clear that motivations ascribed to nonhuman primates refer to theoretical interpretations of observed behavior. It is assumed that on average genes of those animals that respond to certain situations in a manner which is reproductively advantageous to them will be disproportionately represented in subsequent generations. On this survival and reproduction level of causation (discussed by Tinbergen, 1963), increased reproductive success is a sufficient explanation for an animal's behavior (Williams, 1972). Proximate mechanisms leading to specific behavior (e.g., endocrinological bases and behavioral conditioning) are not considered in this paper.

II. MALE CARE VS. EXPLOITATION OF INFANTS

From the assumptions listed in Section I, one would expect dominant males (which are probable progenitors, likely to have a greater stake in the well-being of infants born in the troop) and young males closely associated with an infant from its birth (which are likely to be siblings) to engage in behavior that benefits an infant, even at some cost to themselves. Such altruistic behavior is described under Protection and Rescue (Section II,A), Baby-Sitting (Section II,B), and Adoption (Section II,C). Subordinate males, which are unlikely to be progenitors and which have much to gain in terms of "fitness," would be more likely to engage in behavior that benefits them even at the expense of the infant. Whether or not such males discriminate in favor of some infants (such as siblings), should depend on both their precise degree of relationship and how much they stand to gain. Behavior that primarily or exclusively benefits the male is discussed under Agonistic Buffering (Section II,D) and Infanticide (Section II,E).

This chapter is concerned with the potential advantages and disadvantages for the parties involved of each of the five categories of male–infant interactions just listed. Relevant instances are cited from various primate species. No attempt is made to be all-inclusive since patterns of male–infant interactions for all species for which information exists have been recently reviewed (Mitchell and Brandt, 1972). Detailed accounts of what has been termed paternal or parental behavior are available for Japanese macaques and Barbary apes (Itani, 1959; Lahiri and Southwick, 1966; Alexander, 1970). Recent studies that were not included in the review by Mitchell and Brandt will be emphasized here, especially a paper by

Deag and Crook (1971) and one by Ransom and Ransom (1971), which provide the most detailed descriptions to date of males using infants to further their own purposes.

Deag and Crook suggest two major groupings for the behavior exhibited in male-infant interactions: *male care* and *agonistic buffering*. By care they mean maternal-like behavior including holding, grooming, and carrying the infant as well as protecting the infant from other individuals and dangerous situations. By agonistic buffering Deag and Crook refer to situations in which an infant is used by a male as a "passport" (Itani, 1959) or as a buffer to inhibit aggression in some social situation, usually one that involves other males. In other words, two types of behavior are being described: behavior that benefits the .infant and behavior that benefits the male but, if at all, only indirectly benefits the infant. Just how this distinction relates to the likelihood that a male and a given infant will be related is discussed in Section II,F.

At the outset, I need to make clear that I focus here on those cases in which the male approaches the infant. In some primate species, older infants and juveniles do actively solicit male attention. For example, among Hanuman langurs, males generally ignore infants and it is the infants that must initiate contact. Among vervets, juveniles sometimes solicit the aid of one adult male against a third animal (Struhsaker, 1967b). The possibility that younger animals might be using adult males is a subject in itself. This topic will not be discussed here and is dismissed with the following two generalizations: only *older* infants could be expected to take the initiative in this fashion, and, although male exploitation of infants may have serious repercussions for the infant, the converse would rarely be true.

A. PROTECTION AND RESCUE

In those species in which the male remains in the vicinity of the mother-infant pair, protection, which may include threats and actual fighting, is the male's most important contribution to infant survival. The male may protect the infant from external, usually interspecific danger, and defend it in intragroup encounters. It is important to distinguish between generalized troop defense, which indirectly affects the infant, and male reactions aimed specifically at defense of the infant. This distinction is illustrated by the difference between those species in which males show little interest in newborns (*Presbytis entellus, Erthyrocebus patas*) and in which females with infants may even avoid adult males (*Presbytis johnii*), and those species in which males exhibit such solicitude toward infants that mothers of newborns may avoid contact with other group members while staying in close contact with adult males (e.g., *Papio anubis, Papio cynocephalus*). When in trouble a young juvenile baboon may be more likely to seek out an adult male than its own mother (Hall and DeVore, 1965, p. 84).

In those species in which males are least likely to be in close, attentive association with mother—infant pairs (e.g., langurs), the male plays a relatively small role in group defense except to prevent intrusion by alien males. However, the frequently cited indifference of such males toward infants (see Mitchell and Brandt, 1972, p. 175) may be overemphasized. Males of both *Presbytis entellus* (McCann, 1934, p. 620) and *Presbytis cristatus* (Bernstein, 1968, p. 13) have been reported to respond to individual infants in distress.

From observations of squirrel monkeys (*Saimiri sciureus*) in a seminatural Florida environment, Dumond (1968) reports that "on one occasion a subadult male came from ten feet away to retrieve a baby that was alone and which (Dumond) was menacing wildly"; shortly after, the male pushed the baby off but remained nearby. As Dumond continued to stare at the infant the male returned and took the baby onto his back. Such episodes involving male rescue of an externally threatened infant have been reported both for species with multimale defense-oriented troops, e.g., Japanese macaques (Itani, 1959, pp. 66, 84) as well as for those living in one-male groups or groups not normally considered defense oriented, e.g., black and white *Colobus* (Booth, 1962, p. 484; Haddow, 1952), Hanuman langurs (McCann, 1934; and possibly Jay, 1965), perhaps chimpanzees (Rahm, 1967, p. 206), lutongs and squirrel monkeys.

B. BABY-SITTING

Individualized male care of infants may also occur in the absence of any immediate danger. As defined by Ransom and Ransom (1971, p. 183), such *baby-sitting* refers to any association between an infant and an older male, in the temporary absence of its mother, in which the male fosters the infant's well-being. This might involve grooming, reassuring contact, or removal of the infant from harm's way. One anubis baboon mother would leave her son "confidently" with her consort for periods up to 30 minutes, several times a day. Such care may mean important advantages to the infant. In addition to protection from nearby chimpanzees and other predators, benefits may include access to food and increased influence over other animals, especially peers. This influence may mean an improved dominance status, even in the subsequent absence of the male protector. These advantages may or may not extend into adulthood.

There is apparently great variation in the occurrence of care and in its quality. Because so little is known, behavior that may not, in fact, be comparable is lumped into this category. In the case of the macaques, the group about which most is known, the extent of male care varies within the genus (Lahiri and Southwick, 1966; Brandt *et al.*, 1970), and in the case of Japanese and Barbary macaques, between troops of the same species (Itani, 1959; Burton, 1972). Furthermore, the presence or absence of male care may vary according to the situation or the season. Even in the case of rhesus macaques, where male care is

relatively rare, males may be attracted to newborns or to distressed infants. Koford (1963b) reports that 1-year-old rhesus males may be especially attracted to their newborn siblings (though not so much as their sisters are). Spencer-Booth (1968a, p. 546) observed caged rhesus males who were 3 years older cuddling infants whose mother was absent. In some troops of Japanese macaques, males care for yearlings and neonates only during the birth season (Itani, 1959; Alexander, 1970).

In a few species infants at some ages may be more frequently with males than any other animals except mothers. For example, during their fourth and fifth months, young mangabeys (*Cercocebus albigena*) spent nearly 70% of their time with an adult male, the remaining 30% with their mothers. According to the observer, these males displayed a generally helpful attitude toward infants, although in the sample of 2 infants the first contact with males did not occur until the tenth week (Chalmers, 1968, p. 268). In other cases, males as well as females are allowed to hold infants soon after birth, e.g., among caged *Colobus guereza* (Wooldridge, 1969). In the case of wild *Macaca sylvana*, adult females do not normally carry infants other than their own, whereas juvenile, subadult, and adult males (as well as subadult females) carry and care for infants as young as 1 week old (Deag and Crook, 1971; Burton, 1972). In one group of captive Barbary macaques studied by Lahiri and Southwick, dominant males played a particularly active role in infant care; during the first 12 weeks after birth, infants spent an average of 8% of their time being groomed and carried about by them (Lahiri and Southwick, 1966, p. 263). Similar involvement by head males in two troops of Barbary macaques was observed by Burton. In one case the leader held the neonate on four different occasions during its first day of life (Burton, 1972, p. 33).

Individual variation will obviously play a role in the quality of male "sitting," but this is a difficult topic on which to gather information. Van Lawick-Goodall's work with chimpanzees and the Ransom and Ransom study of anubis baboons are of particular interest in this respect, since individual case histories illustrative of different types of male–infant relations are presented; some of these are discussed in Section II,F. These authors raise interesting questions about the effects that adult male–infant encounters could have on the subsequent emotional development of the infants.

C. ADOPTION

Of even greater importance for the infant than such temporary fostering are permanent adoptions of orphans by males. Male adoptions have been reported for the three most studied nonhuman primate groups: baboons, chimpanzees, and macaques. DeVore (1963) reported the adoption of a sick and orphaned baboon infant by a beta male. Itani (1959, p. 66) reports a semiadoption of a

6-month-old Japanese macaque infant by a male of subleader status: although the foster parent never hugged or carried the infant, he groomed it and stayed near it. This relationship lasted for 6 months. In *Papio hamadryas*, a young male on the make may depend on his ability to adopt weaned females and "mother" them to maturity. Motherless infants are invariably adopted by young adult males (Kummer, 1967, p. 70).

In several cases of adoption, the immediate degree of relationship was known; invariably, these cases involved older infants and the foster parent was either the biological father or a brother. Sade (1967) reported that an adolescent male rhesus had his 6-year-old brother as his most frequent companion after he was orphaned at age 4. Van Lawick-Goodall (1968) reported a similar adoption by an older male sibling chimpanzee. Even where a 2-year-old orphan was adopted by an older sister, the adolescent brother "moved around with him and protected him on occasion" (report of Edna Koning in van Lawick-Goodall, 1967, p. 308n). I know of only one instance of a male adopting a very young infant. This occurred under extremely abnormal conditions, in a caged group of rhesus macaques. With the exception of an adult male (the only one in the group) and a 4-month-old infant, each monkey was removed from the cage, operated on, and returned. The male adopted this infant (probably his offspring) subsequent to the mother's operation (Barbara Smuts, personal communication).

The benefits of adoption are obvious: a young primate without a caretaker would be unlikely to survive. The above-mentioned point about weaned infants, however, brings up the great risk involved when adoption means taking an infant away from a lactating female. Furuya (cited in Itani, 1959, p. 66) reports a *Macaca fasicularis* male that took an infant away from its mother by force and retained it until the infant starved to death. A *Callicebus moloch* infant from a caged group died when the male, which in this species normally carries the infant at most times, refused to return the infant to its mother, even for nursing (Lorenz, 1970, p. 79).

D. AGONISTIC BUFFERING

Male–infant interactions do not necessarily benefit the infant. Exploitation of infants by males has been reported for species as different as anubis baboons, Nilgiri langurs, vervets, Barbary macaques, Japanese macaques, and Hamadryas baboons. By *exploitation* I mean behavior from which the male stands to gain but which may or may not benefit the infant, and may actually harm it.

The most typical instances involve some variation of the behavior Deag and Crook label "agonistic buffering." There is good evidence that the presence of an infant, especially a young infant still in its natal coat (Ransom and Ransom, 1971, p. 190) acts as a signal to inhibit aggression in the adults of most species. Van Lawick-Goodall has reported for chimpanzees that "Only on one occasion

was a male seen to attack, very mildly, a female with an infant on her back, whereas twenty-five attacks were recorded on females with infants in the (less visible) ventral position" (van Lawick-Goodall, 1967, p. 311). Whether or not an age difference was involved was not reported. Wooldridge (1969 p. 32) also notes that *Colobus* monkeys carrying infants were less likely to be the object of another monkey's aggressive impulses.

In several baboon and macaque species, this inhibition is used by males to approach other males, usually dominant animals to which they would not normally have access. The following excerpt from a study of *Macaca sylvana* is typical of this procedure: "It was not unusual to see a male running on three legs holding a baby under him with one hand for as much as 30 or 40 m, and taking it straight to another male to which it was then 'presented' " (Deag and Crook, 1971, p. 191). Commonly the baby would be pulled off by one of the other males and placed between them, or else the presenting male might be mounted by the more dominant animal; during the mount, the baby might be mouthed or else simply pulled off by the mounter. Virtually the same pattern of behavior is exhibited by anubis baboon males. According to Ransom and Ransom (1971, p. 187):

> Some of the males tended to establish close proximity to an infant under conditions of stress, proximity which in its most intense form consisted of carrying the infant on belly or back. . . . This kind of relationship appeared to be based on the adult male's ability to increase his effectiveness in interactions with other males, insofar as close contact with an infant seemed to inhibit aggressive behavior from them.

Among Japanese macaques, the center of the troop, with its concentration of troop leaders and dominant females, offers a young male opportunities to enhance his status or to share in resources monopolized by those at the center; one common ploy utilized by males to gain access is close association with infants. One male described by Itani (1959, p. 85) rarely entered the center alone; almost always he took an infant along as a "passport." Subadult Hamadryas baboon males have likewise been reported to use infants to inhibit attacks against them from more dominant animals (Kummer, 1967).

Poirier reports a related phenomenon for *Presbytis johnii* where the key stratagem in an alien male's campaign to join a troop may be associating with infants and juveniles. On one occasion, 3 males approached a troop. During the first 2 weeks of merging, play accounted for 31% of all interactions between this trio and the troop; contact was almost entirely with 1 older infant from the troop. Although the dominant male of the 3 frequently played with this infant during the initial period, once acceptance by the troop was gained, he totally ignored the infant (Poirier, 1969, p. 32). Similarly, peripheral male juvenile vervets may facilitate the entrance of a strange adult male into a troop (Struhsaker, cited in Mitchell, 1969, p. 410).

Other advantages to be gained from contact with an infant may involve the services of a third animal. Ransom and Ransom (1971, p. 189) describe an adult male that repeatedly stole an infant and used it to force its mother to groom him.

Besides these advantages for the male, a number of benefits may accrue to the infant from male attentions. The infant widens his experience of the social, and especially the male, world, and makes influential "contacts." In those species where predators present a frequent danger (i.e., dogs in the case of *Macaca sylvana*; chimps in the case of anubis baboons), nearby males—whether exploiters or caretakers—could carry the infant to safety. Nevertheless, these positive aspects of male care have perhaps been overemphasized in the literature, leaving out the potential dangers for the infants involved. Attention to the details of these interactions from the infant's point of view suggests some of the drawbacks. In making the point that the use of infants as agonistic buffers "may ... keep antagonism between males in the group down to a minimum," Deag and Crook (1971, p. 198) mention "a few observations showing that when actually involved in agonistic encounters males may grab babies and carry them." There is no information concerning occasions when the antagonist failed to notice the infant (as has been reported for chimpanzee females carrying the infant ventrally), but it surely cannot do the infant any good to be caught up in these skirmishes. Several photographs, a series from Deag and Crook (1971, Figs. 5,a-j) and Fig. 5 from Ransom and Ransom (1971), illustrate to what extent the infant's keepers are pursuing their own ends. The *Macaca sylvana* series shows that when not "in use" an infant, which may have been toted some distance from its mother, is simply left sitting alone. Figure 5 in Ransom and Ransom shows an adult male baboon carrying a 3-week-old infant by one leg and upside down!

In the case of a very young infant, a mother may prevent males from taking or even approaching it (van Lawick-Goodall, 1971, pp. 146-147). Hopf (1967, p. 258), describing the attractiveness of a *Saimiri* newborn for its cagemates, writes: "Females sniff, nuzzle and touch it; juveniles tug at its tail or limbs. These manipulations can be dangerous for the newborn. . . . Depending on her rank in the group the mother may prevent large males from touching the infant by threatening or avoiding them."

E. INFANTICIDE

Carried to an extreme, male exploitation could conceivably lead to injury of the infant. In fact, instances of adult males killing infants have been reported for a number of primate species, including several prosimians (Mitchell and Brandt, 1972); free-ranging *Macaca mulatta* (Carpenter, 1942); caged *Macaca fasicularis* (Thompson, 1967); free-ranging *Macaca sylvana* (Burton, 1972); wild *Papio ursinus* (Saayman, 1971); caged *Papio hamadryas* (Zuckerman, 1932); wild *Pan*

troglodytes (Bygott, 1972); and *Presbytis entellus* (Sugiyama, 1967; Mohnot, 1971). In addition, it is suspected that adult males may have killed infants among wild *Alouatta* (Collias and Southwick, 1952), among caged *Saimiri* (Bowden *et al.*, 1967), and among wild *Presbytis senex* (Rudran, 1973).

Both chacma baboon and chimpanzee accounts involved cannibalism. Where the infant was not eaten, however, the suggestion that these incidents represent "male exploitation" of the infants must be accompanied by some demonstration of how infanticide would benefit the male. The circumstances surrounding infanticide are known in only a few instances and are discussed below. In each case where details are known, the male attacked an infant that was almost surely sired by some other male. One possibility is that infanticide here represents a strategy whereby a male increases his own reproductive success while proportionally decreasing that of his competitors (Trivers, 1972). The most detailed evidence in support of this hypothesis comes from studies of hanuman langurs, among which the killing of an infant quickly brings the mother back into estrus.

Infanticide has been frequently reported among langurs (*Presbytis entellus*) under conditions that are both widespread and of long duration (Hughes, 1884). In recent years, infanticide has been reported at Dharwar, in Mysore state, South India (Sugiyama, 1967); at Jodhpur in northwestern Rajasthan (Mohnot, 1971); and at Abu, a hill station in southernmost Rajasthan (Hrdy, 1974). Circumstantial evidence also suggests that infanticide occurs among langurs at Polonnaruwa, Sri Lanka (S. Ripley, 1973 personal communication).

The type case of langur infanticide was reported by Sugiyama (1965b) at Dharwar when a band of 7 males invaded a bisexual troop. The single resident male was wounded while defending his troop and eventually driven out. Subsequently, 1 male from among the invaders usurped troop leadership and drove out his former accomplices. Soon after the takeover, 5 infants in the troop were bitten to death by the new leader.

Of ten takeovers by males from outside the troop, which have been reported at Dharwar, Jodhpur, and Abu, seven were accompanied by infanticide and resulted in the deaths of some 30 infants (Hrdy, 1974, Table VI). To date, assaults by langur males upon infants have only been reported when a male entered the troop from outside it. All females that were under observation after their infants had been killed exhibited estrous behavior within days after the death of the baby and copulated with the new male.

In one troop at Abu, infant mortality over a 3-year period was as high as 80%: 9 of 11 infants present in this troop between July of 1971 and February of 1973 disappeared when males entered the troop from outside it. Local people witnessed the murder of 3 of these infants by an adult male langur; on fourteen occasions, adult males were seen by the observer to attack 3 other infants that subsequently disappeared. The complex events surrounding these attacks and the problems of interpreting them are discussed elsewhere (Hrdy, 1974).

High langur population densities are found at both Dharwar (220-349/square

mile) (Yoshiba, 1968) and Abu (more than 130/square mile). Large numbers of nomadic nontroop males circulate about the bisexual troops, and there is intense competition between males for access to troop females leading to great social instability. Sugiyama (1967) estimates that new males take over troops on average once every 3–5 years. Given these circumstances, a usurping male might make the best of a short reign by eliminating unweaned infants and, hence, short-cutting a 2–3 year birth interval.

Although positive assignments of paternity and, hence, precise measures of reproductive success are nonexistent, it does appear that males are enhancing their reproductive success by killing infants: in three troops for which information on subsequent births is available (Sugiyama, 1965b, 1966; Hrdy, 1974), 70% of the 15 females in these troops whose infants were killed gave birth within 8 months, or just over one langur gestation period later.[1] In the desert area of Jodhpur, however, as many as 27 months elapsed before one infant-deprived female gave birth. The average time between death of their infants and birth of the next live one for 4 Jodhpur females was 17 months (S. M. Mohnot, 1973 personal communication).

In almost every instance in which infanticide may not have been advantageous to the male that killed the infants, his failure to benefit could be attributed either to interference from another male or to noncooperation from females. Confronted with a population of males competing among themselves, often with adverse consequences for females and their offspring, one would expect natural selection to favor those females best able to defend their interests and the interests of their close relatives. At Abu, females formed temporary alliances against attacking males. On at least nine occasions when a male attacked an infant, 2 older females in the troop that did not at that time have infants of their own intervened. These 2 females would engage the male in fierce slapping encounters and would chase him away from the mother–infant pair. The probable relationship between these females and the infant they defended is discussed in Section IV,D. One mother with an infant actually left the troop to travel on her own. A third factor that potentially detracts from the reproductive success of the invading male is that females may thwart his attempts to retain exclusive sexual access to them. At all three locations where infanticide occurred, a few females were also observed sexually soliciting males other than those that had killed their infants.

Even though competing males and troop females may limit the advantages of infanticide for the invading male, on average infanticide appears to benefit males that practice it by rendering females reproductively available. A similar sexual selection interpretation has been offered by Thompson (1967) to explain the

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[1]Langur gestation periods of 200±10 days have been reported at the National Center for Primate Biology at Davis (L. J. Neurater, 1971 personal communication) and are close to those of 6–7 months reported by Sugiyama in the wild.

incident he observed among crab-eating macaques. This infanticide was the unexpected outcome of an experimental study of the effects of familiarity or the lack of it on opposite sex pairs. When paired with his usual companion and her infant, the adult male displayed typical behavior: he mounted the female briefly and then set about exploring his surroundings; he entirely ignored the infant. Paired with an unfamiliar mother–infant pair, the male responded quite differently. After a brief attempt at mounting, he attacked the infant as it lay clutched to its mother's ventral surface. When the mother tried to escape, he pinned her to the ground and gnawed the infant, making three different punctures in its brain case with his canines. As Thompson points out, the intensity of the male's attack, and his selectivity were remarkable; only the infant and only a strange infant was harmed.

If, indeed, males profit from killing infants sired by their competitors, this interpretation might explain events that occurred during the first year at the Cayo Santiago colony before the groups had stabilized: "more infants were killed usually by adult males but also sometimes by females . . . than died of all other causes" (Carpenter, 1942). Similarly, it may be significant that in the case of chimpanzee infanticide and cannibalism (Bygott, 1972) the infant eaten was the offspring of a strange female who had not been seen before in the area. Obviously though, acceptance of this male–male competition hypothesis must await more precise information on the efficiency of infanticide in increasing the reproductive success of those males that practice it.

F. CARE VS. EXPLOITATION AND DEGREE OF RELATIONSHIP

For several species the examples cited appear to fit predictions generated by kin-selection theory. Males most likely to be fathers are apparently those males that also protect and care for infants. Males caring for infants would be expected to discriminate in choices of charges: familiarity with the mother may play a crucial role in such discrimination. On the other hand, males peripheral to the breeding system may be those most likely to exploit infants indiscriminately. Unfortunately, no conclusions can be drawn from this apparent fit, as the data relevant to the problem are too skimpy. Furthermore, multiple biases were implicit in their collection and a new bias has been added here, that is, examples were selected for their "pertinence" to the theory. The presentation of these examples here was based on three assumptions (see Section I) which, although reasonable, are far from proven.

With these qualifications understood, the following is a synopsis of present knowledge of male care vs. exploitation of infants and how such behavior might be a function of genetic relationship.

For those rare occasions when a male was observed defending a particular infant at some risk to himself, the expectation raised by Hamilton's theory is that these two individuals would be closely related. In fact, for three of the

rescue instances encountered (for *Colobus*, langurs, and lutongs; see Section II,A), the male involved was a dominant male of the harem and very likely the father. In the case of the *Saimiri* rescue by a subadult male, there was no clue to probable relationship. Multiple copulations which may include younger animals are common in this species; the subadult could have been a father, a sibling, an unrelated individual, or anything in between.

For those cases of male adoption in which information on relationship was available (for free-ranging rhesus, caged rhesus, and for chimps), the foster parent was either the probable father or else an older brother. In the case of macaques, young and relatively subordinate males are rarely involved in infant care; brothers, however, are reported sometimes to groom and protect younger siblings (Kaufmann, 1967; Sade, 1965, 1967).

Although Hamadryas males are known to adopt (or kidnap) unrelated or distantly related females, this fostering can best be considered as an installment toward a future harem. A future consort relationship may also be an issue in some cases of male care reported for anubis baboons (Ransom and Ransom, 1971). The Japanese macaque records provide suggestive data on this point: whereas there was little sex difference (28 males versus 34 females) among 62 yearlings cared for by males, there were 20 females in a group of 25 2-year olds cared for by males (Itani, 1959). Are these females more likely to breed with their former caretakers when they mature? It is possible that the information to answer this question already exists in the records of the Japanese Monkey Center, although it has not yet appeared in English.

Most interesting in terms of kin-selection theory is the possibility of differential treatment of closely related vs. more distantly related infants. Since so few data have been collected with this problem in mind, a statistical analysis of which infants are cared for and exploited most frequently by which males is not possible. To phrase this as a question deserving further research: Are there detectable trends in the age and status of the males involved in infant care, and what difference, if any, does previous association with the mother make?

In a recent study, Ransom and Ransom (1971) were the first to collect relatively long-term data (over an 18-month period) relevant to this problem. Their findings suggest that in the case of at least one baboon species, a male's status dictates the type of relationship that he has with fertile females and that this relationship affects his behavior toward her offspring. Among anubis baboons, fully mature males are more likely than younger animals to be engaged in consort relationships, and these males participate more frequently in "paternalistic" care including baby-sitting and active protection. The attentions of males that were involved in sustained consort or pairing relationships or that were potentially involved in such relationships were aimed at a specific infant or at the offspring of a specific female over either a sustained or a temporary time-span. Six such relationships were observed by the authors; five of these involved

mature males, whereas the sixth involved a male that was "barely mature" and still somewhat peripheral (T. Ransom, personal communication). The type example of such "paternalistic" care might be the old male Harry (actually past his prime at the time of the study) that was bonded with the multiparous female Myrna. This bond was expanded to include the infant Moley and its juvenile sister Loy; both associated with him freely and were extended contact, comfort, and protection preferentially; that is, Harry did not extend these privileges to other youngsters (Ransom and Ransom, 1971, pp. 184-185).

Although usually high-ranking anubis males do not form pair bonds with females that have not had more than one offspring (Ransom and Ransom, 1971, p. 193), such a male may occasionally focus his attentions on a first infant in response to certain special conditions. For example, in the case of one primiparous and casual mother which was slow to react to her infant's distress signals and which was not sufficiently heedful of her infant's proximity to potential predators such as chimpanzees, a high-ranking male took over the role of protector; he stayed close to the infant and carried it for extended periods. His attentions were confined to that infant, and he was never seen to generalize such behavior to include another infant; when the infant died of unknown causes his relationship with the mother ended (Ransom and Ransom, 1971, p. 185).

In contrast to males that appear to be "choosing" infants, a number of anubis males that had no previous consort relationships were less discriminating and more opportunistic in their relations with infants: other criteria such as availability and usefulness proved more important than familiarity with the mother. Young males (approximately 4-10 years old) often took an interest in the infants of young low-ranking females. Due either to inexperience or to lack of other bonds, these young mothers were more willing than higher-ranking females to allow males to take their infants (Ransom and Ransom, 1971, p. 186). One male using infants to enhance his social effectiveness was observed to switch from an older to younger babies (the most effective agonistic buffers) as they were born into the group (Ransom and Ransom, 1971, p. 190).

If agonistic buffering is a maneuver allowing a subordinate animal to approach a dominant male, one would expect younger males to depend on infant contact more than older males do for social effectiveness. No quantitative data are known to support this point, and a number of apparent exceptions are known. Deag and Crook (1971, p. 191) write that *Macaca sylvana* "of all ages" are involved in agonistic buffering. Furthermore, Crook reports that "the wild Barbary macaque does not seem, on present evidence, to limit his interest to a particular infant" (Crook, 1971, p. 244), suggesting that no discrimination is going on, regardless of age or the probability of being in a progenitorial position.

In the case of anubis baboons, where mature male consorts seem to discriminate in favor of their probable offspring, high-ranking males are reported to use infants as buffers when confronted with the presence of a potentially powerful

and relatively untested animal (a young male or a newcomer to the group). Of 8 adult and subadult males that sought contact with 9 infants for this purpose, the 3 engaging most frequently in agonistic buffering were high-ranking animals (Ransom and Ransom, 1971, pp. 187-188). However, this particular set of examples does not necessarily contradict the above prediction, for the importance of predominating over a new male (potentially a threat to all future reproductive success) may overrule any risk entailed in using an offspring.

There is no information on discrimination in other species comparable to that for anubis baboons. The two reports available for *Macaca fuscata* suggest that, within the leader and subleader class, interactions with infants are not dependent on individual ranking. Itani (1959, p. 62) writes that there exists "no great difference between (the males') behavior towards their infants and the behavior of a mother towards her infant." Alexander (1970) classifies all contacts between males and infants as "affiliative" (defined as gross body contact, co-feeding, or grooming); no distinction is made between "care" and behavior that might not benefit the infant. Nevertheless, several features of Itani's description suggest that (*1*) males likely to be fathers are behaving differently from those that are not, and (*2*) male care is in some instances inferior to maternal care and that agonistic buffering is going on.

Care of infants during the birth season has been reported in four separate Japanese macaque troops: at Takasakiyama and Takasakiyama B (Itani, 1959), at Takahasi (Furuya, cited in Itani, 1959), and in the enclosed troop at the Oregon Regional Primate Center (Alexander, 1970). Among the free-ranging troops, only males of the leader (ca. 20 years or more) and subleader (15 years or more) class were commonly involved. In the Takasakiyama troop most intensively studied by Itani, thirty-five instances of paternal care were observed for 6 males of leader status; sixty instances for 10 males of subleader status; and four instances for 10 young adult peripheral males. There were virtually no occasions involving the 2-3 year old males that live on the periphery of the troop and exhibit little interest in babies. It is not known to what extent these interactions with infants reflect opportunities of access. Itani determined that interest in infants was most characteristic of males in the middle rank of each of the two top classes and of animals that exhibited an interest in the central part of the troop. In the enclosed Oregon troop, subordinate males were seen to interact with older infants, but only dominant males participated in "nursery groups" containing the very young; of thirty-two "play" and "affiliative" interactions between adult males and neonates, 88% involved dominant animals (Alexander, 1970, p. 281). It is important to note that the motivation for subordinate animals to use infants as "passports" may have been reduced in this troop; among the enclosed animals the central-peripheral troop structure with young males on the outside had largely disappeared (Alexander, 1970, p. 277).

If infants are being used as passports, it is not surprising that the males that engage most frequently in infant care are those ranking in the middle of their class and those termed by Itani as most "interested" in the center of the troop; that is, these are the less well-established, middle-ranking animals that have an ambitious interest in being near dominant animals and that could profitably use infants to achieve this end. Itani (1959, p. 72) mentions that closely ranked subleader males sometimes vie with one another to care for the first infants born each season. Incidents in which males drop the infant that they are carrying or else pull them about by force were reported (Itani, 1959, p. 62). This apparent nonchalance and self-absorption in the young macaque males in caring for infants is reminiscent of the agonistic buffering reported for anubis baboons (see Section II,D). A further comparison of macaques and baboons must await quantitative data on the breeding success of leader and subleader males, and information on the quality of care dispensed by members of each class.

If the kin-selection interpretation offered for the anubis situation is valid and if it applies to the Japanese macaques as well, one would expect that a male would direct solicitude toward the infants of females that were familiar to him either by virtue of common sibship or because the females were former consorts and that the ambitious middle-ranking leaders that appeared to be using infants would not be in progenitorial roles. This possibility is supported by the work of Imanishi (1957a,b) and Nishida (1966) indicating that among Japanese macaques increased frequency of consortship with estrous females is correlated with higher status, just as it probably is for baboons. However, progenitors or not, such middle-ranking males could be siblings or uncles. Yamada (1963, pp. 46–47) points out that the frequency of *Macaca fuscata* infants cofeeding with their brothers and sisters was second only to their frequency of doing so with their mothers. The basis for a familiarity that could potentially influence choice of infants to care for is there, although, for a number of Japanese macaques, such sibling–nephew–niece preferences would be ruled out by the departure of young males from their natal troops (Smuts, 1972, p. 72; Koyama, 1970).

In this section, degree of relationship and how it affects interindividual behavior has been discussed only in terms of a limited span of genealogical time. A totally unexplored level of inquiry involves the interplay between population genetics and behavior. Breeding integrity of the troop and stability of troop composition over a period of time will greatly influence the inbreeding coefficient and the degrees of relationship between individuals in the group. For example, in geographically isolated troops or troops with little immigration and social turnover, individuals will be more closely related than will those individuals living in population belts (that is a number of interbreeding populations over a large area) or where there is social change resulting in new leaders (i.e., the langurs of Dharwar and Mt. Abu). One would expect behavioral differences

between those groups in which most animals share a number of genes and have done so for some time and those groups in which animals are closely related to only a few individuals.

III. NURTURE VS. ABUSE–MALE AND FEMALE ROLES

The preceding section reviewed instances of male care and male exploitation of infants. From the published examples, it appears that infants are more frequently injured by males than they are by females. Without exception those incidents of maternal abuse in which the infant was killed (reported for *Macaca mulatta,* Harlow *et al.,* 1966; for *Saimiri sciureus,* Bowden *et al.,* 1967; *Gorilla gorilla,* Schaller, 1963) occurred among captive animals and could be attributed to conditions of stress and severe social deprivation. Excluding a special phenomenon termed "aunting to death" (discussed in Section IV,B), only 1 case of serious injury has been reported for females living under natural conditions. In this instance, an infant langur was mortally wounded by a female from another troop (S. Ripley, personal communication). Minor mistreatments due to incompetence are discussed in Section IV,A.

If valid, this observation regarding male infanticide would hardly be surprising. Whereas males of most species may greatly improve their reproductive success by aggressive behavior, females usually cannot. With a physiological ceiling on her fertility, a female's best strategy will be adequate care of the infants she does produce; the fitness of any female insensitive to an infant's needs would be drastically reduced. [Without any direct comparison intended, it is perhaps of interest that American males are far more frequently involved in damaging abuse of children than females. Although children were abused by their mothers or a mother substitute in 47.6% of a recent sample (N = 1380), 29.5% of these instances occurred in fatherless homes. Where males were present in the home, fathers or substitutes were involved in two-thirds of the incidents. One-third of the males involved were stepfathers rather than biological fathers (Gil, 1970, pp. 116-117).]

These differences between male and female roles are not the same in all primate species. In tamarins (*Saguinus species*) for example, the female is reportedly more aggressive than the male (Hampton, 1964; Hampton *et al.,* 1966). A theoretical paper by Trivers (1972) provides a neat explanation for such phalarope-like role reversals as are found in tamarins. In these monogamous New World monkeys, the male investment in offspring may be almost as great as that of the female with the result that females are no longer the resource limiting male reproductive success. According to Trivers's model, males in such a species would not be involved in intraspecies competition for females and, hence, would not be subject to sexual selection for increased aggressiveness.

A basic role distinction can only be part of the answer for the greater part played by males in infant abuse. Although quantitative cross-species information on this point is not available, one would expect that the likelihood of male abuse would vary from species to species and would be correlated with the optimum strategy for maximizing reproductive success in that species; this strategy, however, might vary with conditions such as population density. Furthermore, since females can and do discriminate between their own and other infants, and in some cases between infants of close relatives, one would expect a high degree of selectivity in genetic relationships connected with nurturing activities. As yet, there is no conclusive evidence for this assumption.

In most primate species for which there is information, individual mothers vary greatly in permissiveness and nurturing activities. For example, Jay observed differences among langur females as to whether they would allow infants other than their own to nurse once the alien infant had found the nipple. Of all those females observed holding an alien infant, however, less than one-quarter deliberately helped the infant find the nipples. Childless, nonlactating females were less discriminating. Similarly, Hinde (1965, p. 71) noticed that females with an infant of their own were more aggressive toward alien infants than were childless females.

From their work with pigtail and other macaques, Jensen and Bobbitt (1968, p. 43) write that "most monkey mothers are quite punitive towards a strange infant." Rosenblum's (1968, p. 228) work with caged *Macaca nemestrina* confirms this impression; pigtail infants separated from their mothers were generally ignored or actually rejected by other group members. Rosenblum found bonnet macaques more solicitous toward separated infants; however, as with langurs there was great variation. One *Macaca radiata* "supermother" named Brunie nursed 2 infants in addition to her own (3 in all), 2 at a time. Almost certainly, however, Brunie's generosity was influenced by her experimenter's methods; the first alien infant was introduced to Brunie after her own had been removed, and the third infant was introduced in the absence of the first 2. The bonnet mothers observed in the field were more discriminating: "The female resents another's baby trying to cling to her and drastically removes it" (Rahaman and Parthasarathy, 1962, p. 157).

In general, nonhuman primate mothers nurse only their own infants, although individuals may vary in their tolerance toward other infants. Two exceptions to this rule have been reported among the Colobinae. Wooldridge (1969) reports that an infant *Colobus guereza* born at the National Primate Research Center suckles regularly from another lactating female in addition to its mother. In his study of wild Nilgiri langurs, Poirier (1968) noted that "When a female had two infants at her chest, there was often a struggle as to which infant would nurse. Even if one of the infants was her own offspring, a mother did not help it obtain the nipple. It seems possible that any lactating female might nurse another's

offspring." It would be of interest here to have further information on the genetic relationship, if any, between nurse and nurslings.

Experimental studies with rhesus macaques reveal temperamental differences between the sexes which are apparent early in development (Harlow and Zimmerman, 1959; Jensen et al., 1968; Mitchell, 1968). Male infants, for example, were generally rougher in their play (Hansen, 1966), whereas preadolescent females directed significantly more positive social behavior and less hostility toward an infant than did young males (Chamove et al., 1967; Spencer-Booth, 1968a). Captivity studies with chacma baboons and field studies with other savannah baboons (Bolwig, 1959; Ransom and Rowell, 1972, p. 130; DeVore, 1965; also cited in Hamburg, 1969) revealed a greater interest in newborns by immature and postpubertal females than by young males. The sexes differed in similar respects among free-ranging vervets (Lancaster, 1971, p. 174).

These studies, undertaken for only a limited number of primate species, do not mean that differences between the sexes will exist to the same extent or even in the same direction for all primates. Not counting motherhood, rhesus macaque females still have more intimate contact with infants than males do at all stages of their lives, and the same is true to a lesser degree for chacma baboons (Bolwig study). This is not, however, universally the case in macaque and baboon species, namely in *Macaca fuscata, Macaca sylvana, Papio anubis*, and *Papio hamadryas* (see Section II,B). There is great variation both within (see Itani, 1959) and between species in the amount of time males spend with infants. In some species (e.g., marmosets) males possess maternal qualities commonly associated with females.

Although females rarely nurse another female's infant, other forms of nurturing—cuddling, grooming, protection, and reassuring contact—are common. Such aunting behavior is discussed in the next section.

IV.   THE PROS AND CONS OF AUNTING

The relationship between infants and other group members has been a topic of particular interest in some, and of at least peripheral interest in most, primate field studies. Universally, primate neonates are objects of attention, and females may be especially attracted. Within and between species, however, individual mothers vary as to the freedom that they will allow such females with their infants.

From current information, four species are remarkable for their permissiveness: among *Presbytis entellus* (Jay, 1962), *Colobus guereza* (Wooldridge, 1969), *Presbytis obscurus* (Badham, 1967), and *Pygathrix nemaeus* (Hill, 1972), infants may be held by other group members and carried to some distance from the mother within hours after birth. For other species in which aunting is common,

first transfer is substantially later, that is, around 8 days for *Cercopithecus aethiops* (Lancaster, 1971), although exceptional transfers have been recorded at 14 hours (Struhsaker, 1967a, p. 37) and at 2 days (Gartlan, 1969); around 10 days for *Presbytis johnii* (although the first week of life was not observed—Poirier, 1968, p. 52) and *Cercopithecus cambelli lowei* (Bourlière *et al.*, 1970); and as late as 2-3 weeks in *Saimiri sciureus* (Dumond, 1968, p. 125) and in caged *Macaca mulatta* (Rowell *et al.*, 1964).

In some species, mother–infant contact is more intense and relatively uninterrupted throughout the early weeks, lasting until mother and infant of their own accord begin to spend time apart. *Macaca radiata.*[2] (Simonds, 1965, p. 192; Rahaman and Parthasarathy, 1962, p. 157), *Macaca nemestrina* (Rosenblum, 1968, p. 227), and *Macaca fuscata* (Sugiyama, 1965a) appear to fit this description, although with great individual and contextual variation. Itani describes such variation among Japanese macaques: "There are fond mothers who hate to let their infants go for a long time after birth, while there are also such cold mothers as Elk ... who left her infant two days old on the ground and busied herself in feeding" (1959, p. 68). There are conflicting reports as to whether caged monkeys are more or less possessive (obviously conditions will vary). It may be that free-ranging macaques (Southwick *et al.*, 1965; Jay, 1965, p. 577; Itoigawa, cited in Wolfheim *et al.*, 1970) are less permissive than the caged animals studied by Rowell *et al.* (1964). Similarly, in one group of captive *Erythrocebus patas*, a mother allowed her 14-day-old infant to be taken from her by another female even though such permissiveness has never been observed under natural conditions (Hall and Mayer, 1967, p. 232). With the exception of the "greeting" behavior allowed by baboon mothers, the savannah baboons (DeVore, 1963) and *Erythrocebus patas* (Hall, 1968, pp. 105–107) epitomize possessive mothers. As described by Hall (1963), *greeters* are animals permitted to pick up the infant, usually by the hind legs, touch its rump with their mouth, embrace it, and so forth; these greeters are most often adult females, but may also be males and younger animals.

Aunt-infant relationships were first observed in caged rhesus at Madingley, Cambridge (Rowell *et al.,* 1964; Hinde, 1965; Spencer-Booth, 1968a). More recently, mother–infant relationships have been studied in caged squirrel monkeys (Rosenblum, 1968, 1971). To date, the most detailed field report and functional analysis of aunting is based on a study of vervets (Lancaster, 1971). Except for a general review of the relationships between infants and conspecifics other than mother or peers for all mammals (Spencer-Booth, 1970), the primate literature on aunting behavior is scattered and as yet unreviewed. Only special

[2]Rosenblum (1968, p. 221) has characterized captive bonnet macaque mothers as "permissive," but he means permissive relative to pigtail macaques, the animals with which they were being compared.

aspects of aunt–infant interactions, related to the potential advantages and disadvantages of aunting behavior for the parties involved, is discussed here.

A. LEARNING TO MOTHER

In her article on "play-mothering" among juvenile vervets, Lancaster emphasizes the relatively small number of offspring that monkey and ape mothers have during their lifetimes. "Most do not mate until their third year of life or even later and the long gestation combined with the annual breeding patterns and single births, make the loss of an infant through neglect or inexperience very costly" (Lancaster, 1971, p. 162). The position taken by Lancaster, Gartlan, and others (Jay, 1962; Struhsaker, 1967a; van Lawick-Goodall, 1967, p. 293) is that "maternal behaviour is a highly skilled performance, and there is ample evidence, that although the basic patterns may be innate, the behaviour is subject to the normal rules of learning. It is clearly more efficient for an adult female to be capable of dealing with an infant by the time her infant is born than to lose it through clumsiness" (Gartlan, 1969, p. 148). In the opinion of Gartlan and Lancaster, aunting behavior is practice for motherhood.

The learning to mother argument rests on three points: (1) the existence of a disparity in maternal competence between primiparous and multiparous mothers which may be lessened by aunting experiences prior to motherhood; (2) predominance of nulliparous females participating in aunting behavior; and (3) some demonstration that maternal competence is correlated with reproductive success.

1. Primiparous vs. Multiparous Mothers

The literature on primiparous chimpanzee and monkey mothers has been reviewed by Lehrman (1961) who concluded that the primiparous mothers tended to provide their offspring less adequate care than multiparous ones. In a reconsideration of the same observations, however, Seay (1966, p. 163ff.) finds them "inconclusive." Seay's (1966, p. 162) results from an experimental comparison of primiparous and multiparous wild-raised rhesus mothers demonstrated striking similarities in maternal categories such as cradling, restraining, retrieving, embracing, and nipple contact. The only significant difference involved maternal confidence as reflected by the higher anxiety of the primipara, and the higher percentage of physical rejections as well as the increased firmness with which rejection was accomplished among multiparous mothers. Seay (1966, p. 163) concluded that "primiparous rhesus mothers normally give adequate care to their infants."

Field observations of vervets (Gartlan, 1969) and rhesus macaques (Kaufmann, 1966) lead to a similar conclusion. Within species, individual variation and life history appear to be far more important than parity. Whereas some primi-

parous mothers are extremely nonchalant about such things as separation from their infants (e.g., Gartlan, 1969, p. 147; Itani, 1959, p. 68; van Lawick-Goodall, 1971) or are otherwise incompetent (e.g., a study of caged rhesus reported in Rowell, 1963a, pp. 48–49), other primiparous mothers in these same studies were perfectly adequate.

In the wild, the case for incompetent female care rests almost entirely on observations of juvenile or subadult nulliparae. By the time of motherhood, most females are practiced. Of the seven occasions when Jay (1962, 1963) observed langur females carrying infants so awkwardly that they dropped them, all were very young females and 4 were known to be subadults or nulliparous. Similarly, vervet females seen carrying infants upside down or otherwise awkwardly were subadults (Gartlan, 1969).

The important point for the learning to mother argument is that those animals (including Seay's subjects) for which parity was relatively unimportant had all been raised in the wild. The strongest case for multiparity making a difference derives from caged and socially deprived animals. Harlow *et al*. (1966) found that mothers that were themselves "motherless" made abusive and even murderous mothers themselves. These same mothers that were abusive with their first infant, might care for their second and third offspring: of 6 rhesus mothers that were indifferent or abusive toward their first offspring, 5 had second infants that received "adequate" treatment. This familiarization process may also apply to apes. A caged female gorilla that had killed her first infant, cared for a second 2 years later (Schaller, 1963, p. 287). Inexperienced captive chimpanzee mothers likewise are often afraid of their firstborns, refusing to touch them or to allow them to cling (van Lawick-Goodall, 1967, p. 292). These reports do not distinguish primiparous from multiparous mothers, but rather mothers that have had *prior experience with infants*, whether with their own or with another female's, from those that have not.

2. Primiparous Participation in Aunting

As both Hamburg (1969) and Lancaster have pointed out, in virtually all species, females raised in the wild will have had some contact with infants prior to motherhood. Differences exist, however, in the extent of this contact and the age of the infant at first access. In some species, other females are not allowed access to very young infants (see beginning of Section IV); in others only older females are allowed to hold infants. Poirier (1968, pp. 54-55) reports for Nilgiri langurs that juveniles and subadults never tried to take an infant from its mother and that transfer of infants occurred only among adult females. Among *Lemur catta* only other mothers are allowed access to very young infants (Jolly, 1966, p. 115).

Given that the mother often determines who holds her infant (see Section IV,G), one would expect that in those cases in which the mother allows only other mothers (i.e., experienced females) to approach, the benefits of having a

young aunt do not outweigh the potential disadvantages, such as harm to the neonate due to inexperience. Such discrimination might occur in species in which infants are relatively undeveloped at birth or in which the mothering of a newborn infant entails delicate skills, e.g., *Colobus verus* (see Section IV,B). Because Poirier also mentions the "strong desire" of nulliparous females to participate in transfer sequences, the preference for older nulliparous Nilgiri langurs may be a compromise between (a) young females that are dangerously inexperienced and (b) no aunts at all; this kind of trade-off is discussed in later sections.

In species in which only older females are involved in infant transfer, learning to mother does not appear to be a sufficient explanation for the existence of aunting behavior. However, for most species in which aunting frequently occurs, and for some species in which it rarely occurs, juvenile and subadult females play the prominent role. In squirrel monkeys, aunts are often nulliparous females that are either pregnant for the first time or that were too young to become pregnant during the previous mating season (Dumond, 1968, p. 123). Similarly, Itani (1959, p. 69) reports that among Japanese macaques, nulliparous females are strongly interested in infants and make them their "playthings."

Quantitative information regarding which females exhibit the greatest interest in infants is available for three species: caged rhesus macaques (Spencer-Booth, 1968a), vervets (Lancaster, 1971), and Hanuman langurs (unpublished data from February and March of 1973). In each case, a disproportionate number of nulliparous females participated in aunting behavior. Of 347 "affectionate contacts" between vervet infants and females other than their mothers, 295 involved females between 1 and 3 years old that had never had an infant. Nulliparous females composed 38% of the females, yet were responsible for 85% of the aunting. Furthermore, contacts between infants and juveniles tended to be more sustained. Gartlan (1969, p. 149) reported that even vervet females that were too small to carry the infant for long distances would attempt to carry one and would play with infants. Similarly, in a study of langurs at Abu, Rajasthan, nulliparous females constituted 15% of the available caretakers (including juvenile males that also occasionally held infants), yet were responsible for 140 of 196 observed episodes in which a troop member other than the infant's mother held or carried an infant.

Among species such as bonnet macaques (Rahaman and Parthasarathy, 1962, p. 157) in which first transfer occurs relatively late, juvenile and subadult females are among the first aunts. Spencer-Booth (1968a, pp. 556-557) reported that female rhesus macaques around 2 years old are the most likely to participate in aunting behavior.[3] She also noticed that whereas nulliparous females were more hesitant in approaching, they exhibited a greater proportion of

[3]In their early report, Rowell *et al.* (1964) defined an *aunt* as a female around 2 years old.

touching and cuddling behavior than did multiparous females (Spencer-Booth, 1968a, p. 546). DeVore also has emphasized that older juvenile and subadult baboon females appear highly motivated toward a new infant, much more so than young males (DeVore, 1965; also cited in Hamburg, 1969, p. 10).

3. Reproductive Success and Previous Experience

The observations of Seay and others suggest that primiparous mothers are more anxious, more affectionate, and more hesitant at weaning than multiparous females. From an evolutionary point of view, however, maternal "inadequacy" is measured only in terms of surviving, reproducing offspring, and evidence from field studies on child-rearing casualties is too slim to derive measures of primiparous versus multiparous efficiency.

Although there is virtually no primate species in which wild females have not been exposed to infants prior to childbirth, great variation exists in the age at first access to these "practice" infants. Whether or not differences in the survivorship of first infants exist between species such as langurs and vervets, in which aunts have early access, and species such as patas and baboons, in which first access is relatively late, remains to be determined. The possibility of disparate developmental rates must also be considered; that is, neonates of some species may be more or less vulnerable to maternal inexperience.

No conclusions are possible without data on the reproductive success of large samples of mothers. Very recently, Drickamer (1974) published "A ten-year summary of reproductive data for free-ranging *Macaca mulatta*" showing that in this La Parquera population between 40–50% of infants born first or second to a female did not survive. Drickamer also found that infants born to high-ranking females had a higher rate of survival and that daughters of such females themselves gave birth at an earlier age. (This well-demonstrated correlation between female rank and reproductive success is highly relevant to comments in Section IV,F). Thus, the available evidence does support rather than contradict the importance of learning to be a competent mother. Lancaster's (1971) hypothesis that juvenile aunting or "play-mothering" is practice for motherhood almost surely is correct as it applies to vervets and langurs, and perhaps as it applies to all species where aunting is common.

B. INCOMPETENCE, KIDNAPPING, AND "AUNTING TO DEATH"

Assuming that aunting is practice for the aunt and assuming that it increases the aunt's reproductive success by making her a better mother, the question remains: Does aunting benefit the mother-infant pair? If the mother controls access to her infant, one would not expect her to allow another female to take her infant, running the risk of losing it unless (*1*) the aunt was a close relative of hers, or (*2*) certain benefits for the mother–infant pair accrue to aunting which

offset the potential disadvantages. Since instances are known where aunting harmed, or could have harmed the infant, and since in some species mothers do permit unrelated females to take their newborn or slightly older infants, such benefits must exist. These potential advantages will be discussed in Sections IV,C and D; here, only the potentially disadvantageous consequences of aunting for the mother-infant pair will be considered.

A number of differences observed between young females and multiparous animals entail techniques of holding and carrying the infant and related motor skills. Incompetence could result in dropping an infant, holding it in an awkward position (i.e., upside down, where it cannot reach the nipple, where the infant cannot orient itself, etc.), holding the infant too tightly, and so forth. The female holding an infant in such an awkward position could belong to the small percentage of "clumsy" mothers. More frequently, however, she is a young aunt at practice. Except for distress vocalizations, no signs of damage to the infant from such treatment have been reported, but it seems inevitable that occasionally injuries do occur. Another potential source of damage is altercations between aunts or between the aunt and the mother as to which should hold the infant. Gartlan, for example, mentions how vervet infants are squeezed and pulled about in such disputes (Gartlan, 1969, pp. 148-149). Other potential drawbacks to aunting involve the naïveté of aunts concerning environmental hazards (e.g., Dumond, 1968, pp. 125-126).

In most species where aunting has been reported, so has maternal supervision of the aunts (e.g., Dumond, 1968, pp. 125-126; Bourliére et al., 1970, p. 316; Lancaster, 1971). At the first symptoms of distress, usually the vocalizing of her infant, the mother retrieves it. Lancaster has suggested that such watchfulness on the part of the mother enhances the process of learning to mother by conditioning the aunt to keep the infant contented and quiet: "Instances of carelessness, clumsiness, or real abuse will, in effect, be punished. ... Normally, if anything should make an infant cry out, its mother will come and retrieve it. If the infant is being abused, she may even bite the juvenile female (Lancaster, 1971, pp. 175-176).

The vulnerability of an infant monkey decreases rapidly with age as its grip strengthens and it grows more robust. This necessary period of development provides a reasonable explanation for the postponement of aunting behavior in most species, although it certainly does not explain all of the time differences (see beginning of Section IV). The possibility that rates of development could be speeded up through selection in proportion to the advantageousness of aunting must be kept in mind. Other species-specific traits could also be involved. For example, it has been reported that newborn olive *Colobus* monkeys are carried in their mothers' mouth, perhaps as an adaptation to the extremely thick forest through which these arboreal monkeys move or perhaps because the adult pelage is too short for a four-fingered infant to cling to (Booth, 1957, p. 427; Wool-

dridge, 1971, p. 483). Whatever the reason, the risks of early aunting in such a species might be considerably greater than for monkeys that cling from birth.

The great attractiveness of the newborn infant for other members of the group has been mentioned; this appeal may be at the root of both inter- and intraspecific kidnappings. Chimpanzees are notorious for stealing baby monkeys (Kortlandt, 1967), although this behavior might also be classified as predation (Ransom and Ransom, 1971; van Lawick-Goodall, 1971; Teleki, 1973). Other interspecific examples include a female spider monkey that carried a howler infant until it died of starvation and interspecific adoptions among caged animals. Intraspecific kidnappings also occur between troops. At Dharwar (Sugiyama, 1966; Yoshiba, 1968) Jodhpur (S. M. Mohnot, personal communication), and Abu (personal observations) langur females occasionally steal infants from a neighboring troop. Other females from the kidnapping troop then prevent the mother from retrieving her offspring.

A number of intraspecific kidnappings appear to be direct outgrowths from aunting behavior. Gartlan (1969, p. 149) describes an extremely tenacious vervet aunt that took a 3-weeks-old infant, retaining it for over an hour. Whenever the mother approached, she ran away. Temporary stealing has also been reported for captive *Colobus guereza* (Wooldridge, 1969, p. 81) and macaques (Schultz, 1969, p. 331; Hinde and Spencer-Booth, 1967a, p. 268).

In relating how "the importance of the aunts was first brought to our attention," Hinde and Spencer-Booth (1967a, pp. 344–345) suggest a surprising side effect of aunting–kidnap behavior. They describe an adolescent female whose attempts to take an infant were so persistent that she made the mother ill: "During the period of illness such particularly acute deteriorations in the mother's condition were noted nine times and in at least seven of them, the baby was known to have been stolen within the previous twenty-four hours. It seems clear, therefore, that these were effects of the aunt's behavior." (Hinde and Spencer-Booth, 1967a, p. 345).

More serious results of kidnapping have occurred when nonlactating aunts took an unweaned infant and did not return it and, subsequently, it starved to death. Such occasions of "aunting to death" have been reported for wild *Cercopithecus cambelli lowei* (Bourlière *et al.*, 1970, p. 317) and caged *Saimiri sciureus* (Rosenblum, 1971, p. 105). The kidnapping of the Lowe's guenon is of particular interest. Soon after parturition, the mother became ill, and her infant was taken by another female. On the second day, other aunts (including a 23-month-old female sibling of the infant) that had been following the real mother transferred their attentions to the "new" mother. The sick female was ignored except when she attempted to approach; on these occasions she was threatened away by the two oldest females involved. The infant died at 4 days old, apparently of starvation, and the mother subsequently recovered.

This incident illustrates two extremes, the worst possible and most positive

consequences of aunting. As it turned out, aunting in this case was lethally inopportune. However, had one of the females been lactating, or had the mother recovered sooner and retrieved her infant, aunting could have meant survival for both mother and infant.

In Japanese macaques, and other species, kidnapping may occur when a mother has lost her own infant and she attempts to steal another, often from a female of lower rank (Itani, 1959, p. 64). Not all infant-stealing females, however, are childless themselves. One curious outcome of a neonate's attractiveness is that monkeys have been known to neglect their own, slightly older, infants in their eagerness to hold a newborn belonging to another female; so far as I know, this phenomenon has been reported only among caged animals, for example, *Macaca radiata* (Bullerman, 1950) and *Cerocebus albigena* (personal observation).

C. ADOPTION

If a kidnapper is lactating, the consequences for the mother–infant pair are less severe, and in terms of reproductive success may even be advantageous. The mother is free to resume cycling while the foster-mother bears the cost of raising her offspring. If, as in *Macaca fuscata* and *Macaca nemestrina* examples, the foster-mother ranks higher than the real mother, the infant as well stands to gain in fitness, to the extent that its foster-mother's rank entitles it to differential access to food and protection, and to higher status in dealings with other group members (see especially Bernstein, 1969b, p. 456). Such kidnappings by lactating females may occur when a mother has lost her own infant and aggressively sets about obtaining a substitute (Itani, 1959, p. 64; Rowell, 1963a, p. 43).

Although clearly starvation does sometimes occur, several factors operate in favor of the infant. In those species in which infants are born in the space of a limited birth season (e.g., Japanese macaques, some baboons, and some langurs), the likelihood that an orphan will be adopted by another lactating female is increased. Also, the odds are in the orphan's favor in that a mother loses her infant more commonly than an infant loses its mother. Even in cases where the foster-mother was not lactating, adoption has been known to induce lactation. Production of apparently normal milk by nonpregnant, initially nonlactating females has been observed in caged rhesus macaque foster-mothers (Harlow *et al.*, 1963; Hansen, 1966; also cited in Spencer-Booth, 1970, p. 45). A further possibility is that a female that was already lactating might be hormonally "geared" for motherhood and, hence, more motivated to adopt an orphan. The *Macaca radiata* "supermother" Brunie (see Section III) may be such an exmaple.

Orphans are uncommon in the wild, but when observed they have almost invariably been adopted by another female in the group. Usually, the foundations for adoption have been laid before the actual transfer became necessary,

through aunting behavior. This priming has been best documented for caged rhesus (Rowell *et al.*, 1964) and for *Cercopithecus sabaeus* (Marsden and Vessey, 1968). This last, caged green monkey example, is abnormal in that (*1*) the infant adopted was a hybrid (the son of a *Cercopithecus sabaeus* female and a *Cercopithecus aethiops* male) and (*2*) the true mother continued to live in the same cage after the adoption took place without making any effort to regain it. When the hybrid infant was 2 weeks old, the second female lost her own infant; transfer occurred soon after. Prior to this adoption, however, during the second week of the hybrid's life, it spent 65% of its time (down from 100% during the first week) on the nipple of its own mother, 18% on the nipple of its future foster-mother, and 20% on nipples at large. Prior to adoption the infant was actually groomed more frequently by his future foster-mother than by his own mother (Marsden and Vessey, 1968, Table 2.). It is true for several species that mothers may not groom their infants as frequently as less closely related females. For example, *Presbytis johnii* mothers are seldom observed to groom their own infants, and even under normal conditions do so only about 7% of the total time that the infant is groomed (Poirier, 1968, p. 55), about the same as this green monkey mother. Among *Lemur catta* as well, aunts groom the infant more than its own mother does (Jolly, 1966, pp. 115-116).

When the adoptive animal is a close relative, such previous familiarity can be assumed, especially in species such as macaques and chimpanzees where matrilineal relatives have preferential access to the infant. Van Lawick-Goodall (1967, 308n, 1968) has reported three instances of adoptions among chimpanzees, in two cases by older juvenile sisters, and in a third by an older brother; Sade (1965) reports similar adoptions by older sisters for rhesus macaques. Adoption (between generations) within matrilines may also occur. When a female Japanese macaque of the Takasakiyama troop gave birth to a pair of twins, one of these was cared for by the mother's presumed mother. However, the grandmother had not bred that year and was unable to nurse her twin; it died about a week later, apparently of starvation (Itani, 1959).

Twins should be somewhat more common than orphans. Schultz suggests that twinning probably occurs at roughly the same rate in most primates, including man, i.e., at around 1 pair/100 births. Nonhuman primate twinning rates have rarely been calculated using large samples but from numbers of twins known for chimpanzees and langurs, there is no reason to question Schultz's approximation. [His estimate does seem high, however, for rhesus macaques; Koford *et al.* (1966; also cited in Spencer-Booth, 1968b) found 4 pairs of twins in 1748 births.] One would expect aunting behavior, whether from juvenile females, siblings, or older relatives to be particularly advantageous in the case of twins. According to Schultz (1969, p. 184), marmosets and tamarins are the only members of the entire suborder of Anthropoidea that regularly produce more than one offspring at a time (single births are the exception). It is of some interest

that it is in this species group that paternal care is most pronounced. The possibility that twinning and paternal care are related raises a question about maternal capacity to care for twins unassisted.

Three cases of twins being reared successfully in the wild are known for Hanuman langurs: one pair to 2 years, one pair to 1 year, and the third to 4 months when the twins died from external causes (personal observations of Mohnot and Blaffer). Such mother-twin trios have never been studied intensively in the wild, and it is not known whether survivorship was influenced by aunting. The successful nursing of 2 infants younger than 2 months by 1 female (1 her own and 1 a presumed orphan) has been reported for bonnet macaques (Jay, 1965, p. 577), a species in which aunting may be much less common than in langurs. Both infants appeared in "excellent physical condition." Cage studies of *Macaca radiata* (Rosenblum, 1968) and *Macaca mulatta* (Spencer-Booth, 1968b) corroborate the finding that some females, under some conditions, are capable of rearing multiple young.

In terms of aunting, it is important to note that nursing might be the most important limiting factor on twin survivorship (probably dependent on the individual mother and on environmental circumstances) and that aunts do not normally nurse their charges. In other words, the main advantage of aunts for the mother-twins would be in case of danger when the aunt could carry 1 twin. Under normal conditions, monkeys can and do carry 2-3 offspring at a time, for instance, the bonnet macaque and Hanuman langur examples and also Nilgiri langurs (Poirier, 1966, cited in Bernstein, 1967, p. 12). Poirier (1968, p. 49) has reported, however, that overall movement in Nilgiri langurs decreases as soon as any female in the group gives birth and that the group may be slowed down for as long as there is an infant under 3 months. Terrestrial primates that need to cover long distances during the day might find an extra infant an even greater burden than it is for more sedentary arboreal monkeys.

D.   OTHER BENEFITS FOR THE MOTHER-INFANT PAIR

Aunting to death and successful adoption of orphans represent extreme and relatively rare outcomes of other than maternal care of infants. The effects of day to day aunt-infant interactions, which might include grooming, play, infant-tending, or minor rescues, are cumulative and inconspicuous. Some of these benefits from aunting include (*1*) foraging freedom for the mother, (*2*) socialization of the infant, and (*3*) potential help for the infant in case of contingencies.

The benefits of such routine aunting may be quite subtle, as in the case of foraging freedom. One of the common patterns of aunting among Nilgiri langurs (Poirier, 1968), vervets (Lancaster, 1971), caged patas (Hall and Mayer, 1967, and personal observation), as well as among caged rhesus (Rowell, 1963a), is for a mother to deposit her infant near another female and proceed to feed some distance away. Among Nilgiri langurs, for example, approximately one-half of observed infant transfers were followed by the mother going off to feed, al-

though the frequency of this sequence varied somewhat with the age of the infant (see Poirier, 1968, Chart V).

In such cases the mother gains unencumbered moments for foraging in the shrub level where she is relatively more vulnerable to predators (i.e., dogs). She can afford these excursions because her infant is safe above her.

On these occasions when the mother seeks freedom to forage, the baby sitter does not necessarily take the initiative. This pattern has been described as follows for Nilgiri langurs:

> A female need not have indicated a desire to mind the infants left in her care; rather she was often the last individual remaining in a rest or sleeping area. The "baby-sitter" role alternated frequently as the original "sitter" left and another female took its place with as many as three females assuming the role in a short period of time [Poirier, 1968, p. 55]

Such sequential baby-sitting has also been noticed among patas monkeys living in partitioned but connected cages (see Section IV,E). It often appeared that the mother's "decision" to move into the next cage to feed was correlated with another female's proximity to her infant. Once the mother had moved away (although never out of sight since she could see through the partitions) the first sitter might herself leave if there was a second sitter nearby. Only infrequently was the infant left alone in a cage.

One benefit of baby-sitting for the mother-infant pair is that, without much risk to her infant, the mother is better fed, and hence more "fit" to be a mother. Why the sitter should cooperate is more complex. If she is a subadult or nulliparous female, the experience may of course be mutually beneficial. If, however, the aunt is not related, nor learning to mother, and if her status does not improve from holding an infant, she has little to gain, and I believe that this is reflected in the apparent nonchalance reported for some sitters. For example, Poirier writes that "The 'baby-sitter' did not protect a youngster(s) left in her care and the youngster was frequently unattended when she left" (Poirier, 1968, p. 55). Even such a "neglected" Nilgiri may be better off than an infant in a similar situation which is not left at all. For example, in wild bonnet macaques, the mother may temporarily abandon her infant, leaving it alone in the trees or bushes while she goes into the fields to feed (Simonds, 1965, p. 191).

Other benefits of aunting behavior affect the mother only indirectly by enhancing the fitness of her offspring. The infant, however, may be directly affected insofar as aunting contributes to its development of skills, socialization, and survival. The "general helpfulness" of aunts has been widely documented. This solicitude is perhaps best described in the following excerpt from Rowell *et al.*:

> As the infants grew, aunts sometimes watched them when they tried new physical feats and hovered anxiously nearby, going to the rescue if necessary. They seemed to be aware of dangers to young infants—for instance showing care when using the heavy swing door connecting the two parts of the pen if babies were near, and occasionally holding it open for an infant to scramble through.

> When a baby approached the observer an aunt would sometimes threaten, with the result that the baby went away, and on a few occasions an aunt punished another female who had been aggressive to a baby. Occasionally a baby rejected by its mother would go to an aunt and be cuddled. [Rowell et al., 1964, pp. 221-222]

Bourlière et al. (1970) report that a Lowe's guenon aunt may carry an infant in difficulty, for example, when the infant is climbing on wet tree trunks after rain. A langur aunt has been observed to push a timorous infant off of a limb into the waiting arms of its mother in the next tree (personal observation).

Less subtle and also less common than this general solicitude are the benefits that infants derive when the aunt protects them in sudden danger when the mother is out of reach, or in case of orphanage. A curious practice reported for black and white *Colobus* monkeys underscores the rescue potential provided by caretakers. A mortally wounded mother pushed her infant away from her before she fell (Booth, 1962, p. 484). If another animal then takes the infant, this practice would be adaptive. As in the case of common langurs, *Colobus guereza* infants are passed around soon after birth. Moreover, the snow-white newborn is a striking object eliciting group-wide attention. These two characteristics, infant-sharing and dimorphic natal coats, may be instrumental in the success of the *Colobus guereza* mother's strategy. It is interesting that her behavior is exactly opposite to that of the related *Colobus verus* mother, which when wounded does not release her infant (which is carried in her mouth) and, if anything, grips it more tightly. Although it is not known whether aunting is as frequent among olive *Colobus* as among black and white *Colobus*, care of the very young by other-than-maternal females seems unlikely (see Section IV,B).

A number of cases illustrate that prior contact with an aunt increases the likelihood that an infant will be rescued by that female. Dumond, for instance, reports:

> A (*Saimiri*) mother and an aunt that was carring the infant were travelling as a pair. . . . As the pair approached a grey squirrel in their route, the mother violently shook the branch causing the squirrel to move away. A few moments later the baby was off the aunt's back alone, and both the mother and aunt had gone about fifteen feet ahead. As the grey squirrel was returning to where the infant had been left, the aunt ran to the baby and presented her shoulder to it, making a purr call as the infant climbed on. [Dumond, 1968, pp. 126-127]

Such examples, however, do not answer the question of why the mother-aunt bond formed in the first place.

Even when no special relationship between the aunt and the mother-infant pair was previously apparent, the aunt may defend the infant. The langur case where 2 childless females persistently and audaciously interposed themselves between an infant and the adult male attacking it was mentioned in the discussion of infanticide. Several features of langur life may contribute to the occurrence of this protective behavior. Whereas males frequently leave their natal

group to join male bands, the composition of females in a langur troop remains more or less stable over time, increasing the likelihood that any 2 females will be related. To the degree that they are related, altruistic behavior will be adaptive (Trivers, 1971). In addition, infant-sharing soon after birth may serve to familiarize a number of older females with the infant.

Outside of "general helpfulness" and care in case of contingencies, little is known about how experiences with other-than-maternal females of various ages influence infant development. It is possible, however that by offering an alternative source of solicitude, the presence of one or more aunts increases the infant's confidence in his surroundings which may promote separation from the mother and lead to earlier independence. Conflicting information on this matter will be presented in the next section.

E. AUNTS AND INFANT INDEPENDENCE

Universally, mammalian infants spend more time away from their mothers as they develop. In rhesus macaques, baboons, and probably most primate species, the responsibility for this independence[4] lies with both the infant that wanders more and the mother that rejects it more frequently (Hinde and Spencer-Booth, 1967a) and otherwise encourages its departure (e.g., Ransom and Rowell, 1972, p. 119). Some evidence suggests that insecure mothers are less likely to facilitate the departure of their infants. For example, caged primiparous macaque females, which are presumably less experienced and less confident, hesitate more in initiating the separation process that normally begins around 3 months. Similarly, Harlow's "motherless mothers" exhibit a much lower rate of rejection after the 3-month period than normal mothers do (Harlow et al., 1965). (Before this period, however, motherless mothers are much more rejecting than normal mothers.) Chalmers (1972) has shown that caged Cercopithecus mitis mothers stayed closer to their infants and restrained them more when the adult male had been temporarily removed, presumably because they felt less secure in his absence.

As this example suggests, external factors may greatly influence the amount of mother-infant separation. A totally safe but stimuli-poor environment in which mother-infant pairs are isolated from other monkeys (Jensen et al., 1967, p. 49; Hinde and Spencer-Booth, 1967a, p. 363) may be as unconducive to infant independence as an overly stimulating one which is perceived by the mother as dangerous. Hinde and Spencer-Booth (1967b) found that isolated mother-infant pairs initially spent more time apart than group-living monkeys did, presumably because the mother was less restrictive. Later, however, in the second 6 months of development, these infants spent more time with their

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[4]*Independence* means physical separation from the mother; other implications of the term are not considered here.

mothers. In both types of situation, isolated and overstimulating, the mother and infant may maintain intense contact long after the normal onset of separation.

In two studies, the presence of aunts worked counter to infant independence (Hinde and Spencer-Booth, 1967b; Wolfheim et al., 1970). For example, rhesus mothers were more permissive in the absence of aunts; in the presence of aunts, infants spent a smaller proportion of their time away from their mothers. Hinde and Spencer-Booth suggest that the presence of aunts that might take infants irretrievably was perceived as a threat by their mothers. Wolfheim et al. compare their results with those of a Japanese observer who noticed that Macaca fuscata mothers restrained their infants more frequently in the wild than in the laboratory. According to them, this parallel illustrates an adaptive mechanism whereby the mother becomes more protective in potentially dangerous situations.

According to Rowell et al. (1964), just how "threatening" an aunt is to the mother may depend on the rank of the females involved. Females that were allowed to cuddle and carry the first 5 of 7 infants born into the group were all subordinate to the mother. Whereas high-ranking females were able to control other females' interactions with their infants, low-ranking females were unable to do so. To avoid giving up their infants, these low-ranking mothers would have to pick them up and move away. If the mother's status in relation to the aunt affects her chances of retrieving the infant, this could provide an explanation as to why rhesus mothers should show this preference for subordinate females. To me, this preference is curious. From one point of view it would make sense for the mother to prefer the most prestigious aunt available since among rhesus macaques, as in other macaques, the status of the mother or caretaker affects the status and privileges of the infant. Also, it may be that such discrimination is shaped by the circumstances of captivity.

The finding that rhesus infants old enough to spend time away from their mothers do so less in the presence of aunts is somewhat surprising. Assuming that the amount of time spent away from the mother is determined by (1) differences between mothers, (2) the mother's confidence in her environment and especially her ability to retrieve her infant, and (3) the infant's "motivations" to wander deriving from both physical maturation and the availability of attractive alternatives, one would expect aunts to increase infant independence insofar as they increased mother–infant confidence in their surroundings (e.g., the deposit-and-forage pattern in Nilgiri langurs and patas; Section IV,D) and insofar as they presented alternative sources of solicitude.

Part of the problem here is my definition of aunt—any female, older than the infant, that associates with it; as with Lancaster's (1971) definition, this one overlaps with "playmates." In their 1964 work, Rowell et al. were referring to females over 2 years old. Even among caged rhesus, one would expect that the presence of very young aunts (especially juveniles whose mothers were either less

dominant or absent) might encourage mother-infant separation. A great deal of the problem must also have to do with peculiar features of rhesus macaque female dominance hierarchies. At any rate, it is not clear that the presence of aunts decreases mother-infant separation in other species. Unfortunately, the evidence to support this point among other species is less adequate than that from the rhesus studies; it is either qualitative or else based on samples that are too small to indicate anything except that further research is needed. In addition, age differences and differences in maturation rates, which cannot at this time be controlled, raise questions as to the comparability of cross-species information.

Baldwin and Baldwin (1971) have suggested that the availability of infant and juvenile peer play experience is important in determining the degree to which squirrel monkeys accommodate to and engage in social and nonsocial activities. They point out that in small *Saimiri* troops, infant and peer socialization groups are small; because a youngster in such a group had fewer animals in the same sex and age class to play with, it therefore might play less. Another possible effect would be that infants played with whatever other young animals were available, regardless of age and sex. This was the case in a caged group of 6 patas monkeys at the Tigoni Primate Center in Kenya: the single infant (6 weeks old) in the group spent most of the time that it was away from its mother with an older juvenile female named Anxious as well as time with an undersized subadult female, Huiha.

In an experimental study of the effects of other group members on mother-infant contact (see Chalmers, 1972), various animals were removed and replaced at 2-day intervals over a period of 14 days. This particular experiment with a patas group was part of a series of experiments under the direction of Dr. Neil Chalmers; the procedure and results are described in an unpublished manuscript (Blaffer, 1970). Briefly, in 35 hours of monitoring, the infant spent 20% fewer 0.5-second intervals away from its mother during the 2 days when his "favorite" aunt Anxious was removed than it did during either of the adjacent controls; significant differences were not observed during the absence of other animals.

The presence of the juvenile female Anxious appeared to influence (*1*) the likelihood that the infant would leave its mother, (*2*) the distance that would separate them, and (*3*) the length of time the separation would last. If the distance separating mother and infant is taken as a measure of their confidence in their surroundings, the proximity of the aunt apparently increased this confidence. An analysis of the proportion of times that the infant approached the mother minus the proportion that he left her ($\% Ap_1 - \%L_1$) during the interval when Anxious was absent, indicates that the increased proximity to the mother during this time was largely due to the infant (Chalmers, 1972).

Until more information is available, it is not possible to say conclusively that aunts contribute to mother-infant separation, although it is likely that this will

turn out to be the case for some groups. Because of great variaton in habitat use and social organization both between and within species, and because of differences in maternal responses to aunts, the effects of aunting on infant independence will differ from case to case. Nor is it clear that early independence is necessarily advantageous. Whereas Hinde (1965, p. 71) reports that maternal restrictiveness among rhesus mothers in the presence of aunts retarded motor achievements of the restrained infants, the relatively late independence of some arboreal monkeys (Chalmers, 1972) may be important for infant survival. More subtle effects could be reflected in the infant's dealings with other animals.

F. STATUS BENEFITS FOR MOTHERS, AUNTS, AND INFANTS

In a number of species, mothers with infants are treated differentially and their role in group life may be changed after parturition, and in some cases even in pregnancy (e.g., baboons, Japanese macaques, black and white Colobus, chimpanzees, and langurs). As has been mentioned, animals carrying an infant are less subject to attack from conspecifics (e.g., chimpanzees and Colobus monkeys; see Section II,D). After the birth of their infants, baboon mothers stay closer to the center of the troop, protected by the dominant males (Hall and DeVore, 1965). Although Hanuman langur females do participate along with males in intertroop encounters, pregnant females and mothers carrying infants are rarely involved (Ripley, 1967, p. 247).

Assuming that the special status accorded to mothers is advantageous, the question arises: Does an aunt holding an infant share in maternal prerogatives? If so, how equivalent is aunting in these instances to "agonistic buffering"? Wooldridge has reported for Colobus guereza that whichever female was holding an infant, whether she was the mother or not, was immune to attack from the adult male. Once she had given up the infant, however, she was again vulnerable (Wooldridge, 1969, p. 32). It is unlikely that such aunting is ever as exploitive as its masculine counterpart, but, in fact, this possibility has never been investigated.

Another possible status benefit to an aunt from aunting might be the contact she makes with other females. Ploog (1967), for example, reports that among squirrel monkeys a relationship was occasionally formed de novo between 2 females several weeks after 1 of them had given birth—apparently due to the aunt's interest in the infant. Rosenblum (1972, personal communication) has suggested that in squirrel monkeys aunting may be reciprocal; that is, the mother whose infant is aunted may repay the compliment when the aunt herself gives birth. Obviously though, such reciprocity could only apply in those species in which multiparous females participate in aunting.

An infant too might be deriving status benefits from association with a high-ranking aunt or foster-mother. If this is so, one would expect that, in those

species with a pronounced female dominance hierarchy, mothers would invite aunting and in doing so prefer dominant patrons. However, there is no evidence that a mother ever discriminates in this way, and in the case of caged rhesus macaques, the opposite appears to be true. Apparently, the drawbacks to permissiveness among rhesus macaques outweigh the advantages; for example, a subordinate mother could risk losing her infant, whereas a dominant one might be wasting the privileges of her position if she were to loan her infant to another animal. It may be that only in species with less pronounced hierarchies could the benefits of early aunting outweigh the disadvantages.

Observations of postnatal infant-sharing in the wild are limited to *Presbytis entellus* of India (Jay, 1963; Sugiyama, 1965a) and to *Colobus guereza* of East Africa (P. Marler, personal communication, cited in Wooldridge, 1969). Bernstein (1968) has also reported infant-sharing in *Presbytis cristatus* of Malaysia, but the timing of the first transfer was not mentioned. Instances of transfer within the first 24 hours after birth have also been reported for caged colobids, including two Southeast Asian langurs, *Presbytis obscurus* (Badham, 1967) and *Pygathrix nemaeus* (Hill, 1972). The occurrence of infant-sharing in geographically disparate species belonging to the same subfamily (Colobinae), strongly suggests phylogenetic determination of the trait.

Such a phylogenetic interpretation, however, does little to explain why postnatal sharing should have been adaptive in the first place. Any explanation for such a complex behavioral trait must take into account the social context in which it evolved. For example, if it turns out that female dominance hierarchies are as "relatively unstable and poorly defined" among other Colobinae as Jay (1965, p. 233) found them to be among the langurs she studied, then several of the disadvantages of early sharing suggested in the case of rhesus macaques cease to apply, possibly predisposing members of this subfamily to the evolution of early aunting. Needless to say, this suggestion, if true, would lead to a host of questions.

G. PREFERRED AND AVAILABLE AUNTS AND INFANTS

Observations from a number of species indicate that to a large extent the mother controls access to her infant. Even in cases of relatively low-ranking females, a mother may either fight off or avoid more dominant animals attempting to take her infant (for baboon and rhesus macaque examples, see Ransom and Ransom, 1971, p. 191; Rowell *et al.*, 1964). Mothers have been observed to push away, threaten, bite, or otherwise thwart any animals, including adult males, on behalf of their infants, for instance, sifakas (Jolly, 1966, pp. 67-68), Hanuman langurs (Jay, 1965), and vervets (Lancaster, 1971).

Assuming that the mother controls access to her offspring, does a mother discriminate in the matter of aunts? Clearly, in some species she does. As men-

tioned, Nilgiri langurs only permit adult females (Poirier, 1968), and *Lemur catta* (Jolly, 1966) only other mothers, to approach their infants; caged rhesus favor subordinate females and "best friends." Although among wild patas other females have never been seen to take very young infants away from their mothers, on one occasion Hall (1963; also cited in Hall, 1968) saw an adult female briefly hold an infant while remaining next to the mother; in order to do so, this female had glanced up at the mother in the manner typical of a subordinate animal anticipating attack. These cases suggest that, in animals with pronounced female hierarchies (i.e., rhesus and patas), subordination may be a prerequisite for infant access.

In other species maternal preferences are not apparent; the eagerness of the other female to take the infant may determine aunthood. Occasionally aunts may resort to subterfuge. Instances of a prospective aunt grooming the mother in order to gain access to the infant have been reported for chimpanzees (van Lawick-Goodall, 1971), for vervets (Lancaster, 1971, p. 173; Gartlan, 1969, pp. 148-149), and for caged patas (personal observation). However, it is unlikely that such stratagems would succeed if the mother were determined to hold her infant.

Since the "cost" of permitting aunting may vary according to the age and status of the aunt involved, in those cases in which the mother discriminates, one would expect her to do so on the basis of which female provides the advantages of aunting (in terms of foraging freedom for the mother, socialization and protection for the infant, adoption when the mother is sick or if she dies, etc.) with the minimum of its disadvantages (i.e., incompetence, kidnapping, etc.). Thus, among caged rhesus the mother prefers subordinate females that are least likely to succeed in kidnapping her infant (see Section IV,E); among ring-tailed lemurs or Nilgiri langurs, only older animals, which are least likely to damage the infant through inexperience, are permitted access.

When such an "optimum" aunt is not available, the possibility of a "dangerous" aunt has to be weighed against the potential disadvantages of no aunt at all. If aunting behavior does not occur to the same extent in all primates, it must be because this trade-off varies both between and within species. Although many patterns of primate social behavior are phylogenetically determined, variations may also be induced by historical and environmental factors. Just as species differences in the maturity of infants at birth will affect the amount of aunting behavior, so will predation pressure, a particularly vulnerable habitat, troop composition as it affects numbers of available aunts, individual differences such as maternal status (i.e., a dominant rhesus female will have more aunts to choose from than a low-ranking mother), and so forth.

Where aunting, even from an inexperienced animal, is more advantageous than no aunt at all, mothers may allow any female, including juveniles and subadults, to take their infants. The willingness of the aunt to take the infant or else her

availability (i.e., "the last female in the sleeping tree," see Poirier, 1968, p. 55, discussed in Section IV,D) will be the deciding factor. In some cases, for example, in caged squirrel monkeys (Rosenblum, 1968, p. 227), no previous association between aunts and the mother is apparent. Where the mother is related to the aunt, the odds as to when aunting is favored and when it is not are complicated by the mother's double stake in the acquisition of maternal competence by her older daughters and her nieces, as well as in the well-being of her own infant.

Among chimpanzees, rhesus macaques, Japanese macaques, perhaps Nilgiri langurs, possibly squirrel monkeys, and undoubtedly others, the strongest and most persistent bond is between mother and infant (see Southwick et al., 1965, p. 155; Yamada, 1963). For many species the reports on the duration of mother-infant contact are ambiguous. For example, Jay (1963, 1965) reported for Northern langurs that mother–child relations were totally severed at weaning prior to the birth of the next offspring. Yoshiba (1968) reported, however, that weaning among Southern langurs could take place as long as a year later. In contrast to DeVore (1963), Ransom and Ransom (1971, p. 81) reported that at Gombe the bond between mother and infant is not severed at the birth of the next infant and may even be intensified, inducing renewed proximity and grooming and nursing. In most cases, female–juvenile relationships have not been traced because of the short duration of study, although they have sometimes been inferred (e.g., Poirier, 1968, p. 49). In the absence of concrete information, however, it has been tacitly assumed that female infants in some species maintain contact with their mothers throughout life whereas in others they do not. This presumed distinction makes a term such as *matrifocal* worthwhile temporarily. The fact that the only species for which long-term information is available are all matrifocal (or at least females maintain contact with their mothers) suggests that more research is needed to validate the distinction if it is to be really useful.

In such matrifocal species, infants and juveniles maintain close contact with their mother after weaning, and often, after the birth of a new offspring, these siblings may have preferential access to the infant. For example, chimpanzee babies less than 5 months old are usually protected from contact with other animals except their own siblings (van Lawick-Goodall, 1967, p. 148). Such access affiliates older siblings into the new mother–infant bond, and may be extended to include more distant matrilineal relatives (e.g., maternal grandmothers; see Section IV, C). The effects of this early association may be longlasting. Yamada (1963, p. 50) reported that among Japanese macaques the frequency with which an infant cofeeds with its siblings is second only to the amount of time spent feeding in the company of its mother; by the time the infant is a juvenile, however, it may feed more often with siblings than with its mother.

A corollary of this close association and preferential access is the special attitude of siblings toward the new infant. The Madingley caged rhesus work has demonstrated that siblings show more attention toward an infant than do less closely related animals of the same age and sex in the group (Spencer-Booth, 1968a, p. 557). Field reports have confirmed this among wild chimpanzees (van Lawick-Goodall, 1967). In these species in which there is early sibling-infant association, the foundation for care and potential adoption by older siblings is laid almost from the infant's birth. At the same time the mother's female off-spring have priority in learning to mother with her new infant. One interesting question here is, Which animals if any are preferred by primiparous mothers?

Macaques and chimpanzees may be at the extreme end of the matrifocal continuum; this remains to be determined. From current evidence, it appears that among other species allocation of training is less nepotic. Although a black vervet infant spends much of its first few months in the company of its mother and siblings, it may also be in contact with adolescent females from other genealogies (Lancaster, 1971, p. 166). From Lancaster's impression and from what data there are, it appears that availability of the infant (in this case due to maternal permissiveness) was more important than genetic relationship in choice by the aunt of an infant, and that maternal permissiveness was not influenced by degree of relationship (Lancaster, 1971, p. 172).[5]

Eagerness to take the infant seems to vary with the age and status of the female, and one would suspect that this variation reflects the differential benefits derived from being an aunt. A female nursing an infant of her own may be more punitive toward alien infants than a childless one, presumably because nursing another infant could detract from her own reproductive success. In a group of wild sifakas, 2 mothers with infants of their own were the only group members not to show interest in other newborns (Jolly, 1966, p. 66). In a number of species (e.g., vervets, savannah baboons, squirrel monkeys, Lowe's guenons, langurs), nulliparous females show the greatest interest in holding infants. Among caged squirrel monkeys, pregnant females are the most likely to retrieve an infant separated from its mother (Rosenblum, 1972, Fig. 2); generally, such aunting is nonexclusive. According to Rosenblum (1968, p. 227), females may act as aunts to several infants.

This undiscriminating eagerness to hold infants on the part of pregnant or nulliparous females implies that they have something to gain; almost surely they are "learning to mother" (see Section IV,A). Unfortunately (for mothers and

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[5]In Table III, Lancaster (1971) presents frequency of contacts between infants and juvenile or adolescent females; also where known, individuals belonging to the same genealogy are designated. A Mann-Whitney nonparametric ranking test for contacts of infants on the basis of kinship and nonkinship showed that there was no significant relationship between contact and genetic relationship. The obvious limitation of the data here, however, is that the fact that no genetic relationship was known to exist does not mean that one could not have existed.

infants), the willingness of aunts to aunt may be inversely correlated with their competence in handling infants (see Section IV, B). More experienced multiparous females have less to gain. Unless they either have a preexisting bond with the mother (including genetic relationship), or they are forming such a bond, these females would be less likely to initiate aunting behavior. When females who have not initiated aunting are forced into the role by "infant deposit," such aunts would be expected to make nonchalant caretakers (see Section IV,D).

The infant, too, may exercise choice in its response to an aunt or uncle, especially as it matures. Rosenblum (1968, p. 214) reports that an older infant squirrel monkey may temporarily prefer an aunt to its mother. This was true of the young patas infant described in Section IV,E, which would actively seek his "favorite" aunt. One of the infant baboons at Gombe would avoid all contact with a particular adult male that treated it roughly, while seeking out the more solicitous male Harry (Ransom and Ransom, 1971, pp. 189–190). Very young infants have less choice and cling to the female currently holding them. In 19 of 49 infant transfers witnessed among *Presbytis cristatus*, the infant vigorously resisted (Bernstein, cited in Poirier, 1968). Similarly among *Presbytis entellus*, females wishing to hold an infant often had to obtain it by force (Sugiyama, 1965a, p. 228). Although an infant may recognize its mother within days of birth (Jay, 1963, p. 443), before this point infants occasionally resist returning to their own mothers; after an infant learns to recognize its mother, he may resist being taken by another female (Wooldridge, 1969, p. 81, 1971, p. 483). This tendency to cling has an obvious adaptive value: presumably the infant is safest with its mother, but once any other female has taken it, survival depends on not becoming separated.

The apparent fit between the evidence on aunting behavior in this section and kin-selection theory is subject to the same qualifications as were mentioned for male care (see Section II,D); in particular, the data were selected for relevance to the theory. By way of a summary, some predictions concerning which females should attempt to aunt and which should be preferred as aunts will be presented. Until these are tested, a proper conclusion is pointless.

Maternal permissiveness should depend on a tally of the pros and cons of aunting for the mother and her infant under the circumstances in which they find themselves. If the available aunts are related to her, the mother's behavior should reflect both this tally, and her stake in the acquisition of maternal competence by her female relatives. In those species in which the period of contact between a mother and her female offspring overlap with the birth of subsequent offspring, these daughters will be the preferred aunts. Daughters as aunts means that the "cost" of aunting is deductible in that a close relative profits; the cost may even be reduced. For example, the status of the mother in relation to her offspring should be clearly defined; disputes over who holds the infant and kidnapping will be less likely. The cost from incompetence remains the same for related as for unrelated females. Due to the proximity of siblings to the mother

and newborn, and to preferential access, related infants might also be the most available candidates for an older sibling's aunting attentions. One would expect that such females would be discriminating and prefer infant siblings to unrelated infants (whether aunts are choosing siblings because they are more attracted to *them* or because they are more available due to familiarity with the mother needs to be investigated).

Aunts unrelated or distantly related to the infants tended may include: (*1*) nulliparous females eager to hold infants; (*2*) adult females in the process of establishing a relationship with the mother; and (*3*) more or less uninterested females that have been conned into aunting. Whereas the first two will be solicitous in order to prevent retrieval of the infant or even termination of the relationship by the mother, the third need not be. Only the female interested in a bond with a particular mother could be expected to discriminate; availability of the infant would be the most important single factor, and this availability will depend on the mother's assessment of the situation.

These predictions represent a combination of what one would expect to be true if kin-selection theory applies to aunting and of what does seem to be true. In other words, current evidence does not contradict these predictions, but more research is needed to confirm them.

V. SELECTIVE PRESSURES ON THE INFANT

A. NATAL COATS AND OTHER TRAITS OF ATTRACTION

Generally, primate neonates are attractive to some and occasionally, as in the case of *Colobus guereza*, to all, nearby conspecifics. There is great variation in the strength of this attraction; its onset and duration;. the age, sex, and status of the animals attracted; and the likelihood that perception of the infant will elicit solicitude. Features that may contribute to the infant's attractiveness include: size at birth, peculiar sounds (e.g., the "purring" noises made by howler and rhesus babies), infantile facial expressions and motor patterns, skin color (often white or pink), relative hairlessness, distinguishing morphological features such as big ears or tail tufts, and distinctive coat color.

Of the natal features, coat color is often the most variable and most striking. A number of observers have noted the apparent correlation between the natal coat stage and the concern for the infant exhibited by adult females and other conspecifics among Colobinae and African cercopithecines; as the natal coat changes to a color characteristic of older animals, interest in the infant declines (Booth, 1962, p. 485; Gartlan, 1969; Jay, 1965; Lancaster, 1971, p. 177; Poirier, 1968, p. 50). Other observers have speculated on the effectiveness of natal coats and other distinguishing features (e.g., the chimpanzee white tail

tuft) in inhibiting aggression (Ransom and Ransom, 1971) and in eliciting protection and rescue. According to Booth (1962, pp. 484–485), among vervets and black and white *Colobus*, "the sight of an infant in natal coat in human possession resulted in marked agitation on the part of adult wild monkeys of both sexes."

A similar episode, when wild adults approached a human observer holding an infant, has been reported for *Presbytis cristatus* (Bernstein, 1968, pp. 12–13). Yoshiba (1968, p. 242) reported that the leader of a *Presbytis entellus* troop attacked an observer who "showed him a newborn infant from another troop." Yoshiba suggests that the male attacked because the man held a strange infant; another possibility could be that the male was attacking the human who had captured a dark infant.

The only experimental work on this subject seems to be that mentioned in Booth (1962, p. 485). According to her, a stuffed natal coat skin will agitate adult *Cercopithecus* monkeys if it is being moved. Their agitation dies down if the skin lies still. Booth (1962, pp. 483–484) also states that *Cercopithecus* mothers do not show much interest in dead babies. This observation is in marked contrast to reports for other species. Among savannah baboons (DeVore, 1963), bonnet macaques (Rahaman and Parthasarathy, 1962, p. 157), Hanuman langurs (personal observation), and squirrel monkeys (Clewe, 1969), mothers carry and protect dead infants for days after their death, suggesting that factors other than movement are involved. Clewe has suggested that the presence of hair may be the crucial stimulus, since squirrel monkeys born without hair are dropped to the cage floor, whereas those born with it are held (Clewe, 1969, p. 154). However, without controlling for length of pregnancy and the mother's hormonal state, it would be impossible to attribute confidently the mother's response to the state of the vellus.

The remainder of this section and the next one focus on natal coat colors; for the purpose of this discussion, species will be divided into three classes: species born with "flamboyant" natal coats, species with coats that are distinctive but discreet, and those with coats that are scarcely distinguishable from the adult pelage.

1. "Flamboyant" Natal Coats

Here *flamboyant* refers to striking differences from adult coloration perceptible at a distance to members of other species (including predators) as well as to conspecifics. In this category are included at least five species in the Colobinae subfamily. Newborn infants in *Presbytis rubicundus* and *Colobus guereza* are pure white at birth. *Presbytis geei* newborns are almost white, but this coloring does not differ greatly from the golden pelage of adults. Among *Presbytis aygula* and *Presbytis melalophus* the newborn is white with a dark stripe from head to tailtip which is crossed by a stripe between the shoulders in

what has been called a "cruciger" pattern. *Presbytis cristatus* are born with white skin, white faces, hands and feet, and bright orange body hair; skin and coat color begin to darken within days of birth (Bernstein, 1968, p. 3). *Presbytis obscurus* newborns are whitish yellow all over (Furuya, 1961-1962, p. 42). *Presbytis johnii* have little pigmentation and are sparsely covered with reddish brown hair; skin and fur begin to turn black like adults at around 10 weeks (Poirier, 1968, p. 49).

Outside of the Colobinae, striking natal coats are less common. The young of *Macaca arctoides* are much paler than the adults. The same is true for *Hylobates lar* and *Hylobates hoolock*, although in the case of the hoolock gibbon the situation is complicated by the occurrence of a similar color dimorphism between adult males and females. Both males and females are a pale grayish white at birth, turning dark with age. At puberty, females turn a pale yellowish brown whereas males remain black (McCann, 1933). The color similarity between infants and females of child-bearing age suggests that camouflage (i.e., the infant would not be visible on its mother) as well as distinctiveness may be involved.

Whereas the flamboyant neonates mentioned above would be hard to camouflage unless they were covered by the body of another animal, in several species flamboyant natal features are localized and more discreet. If natal features are indeed a message, the broadcast in these cases could be limited to conspecifics. For example, among *Nasalis larvatus*, newborns have a small up-tilted nose and vivid blue facial skin which is quite distinct from the flesh-colored faces of adults (Pournelle, 1966, p. 4). *Pan troglodytes* infants have coats that are approximately the same color as those of adults, but they have white tail tufts (van Lawick-Goodall, 1965). Similarly, newborn orangutans are distinguished by white circles around their eyes.

2. "Discrete but Discreet" Coats

Newborns in this category are characterized by distinctive coats that are not strikingly different from those of adults; usually, these are a darker or else a paler version of the adult pelage. Dark natal coats, pink faces, and large ears are typical of the savannah cercopithecines, i.e., the baboon species, *Cercopithecus aethiops* and *Erythrocebus patas*. Some forest-dwelling New World monkeys also have black newborns (e.g., *Ateles*). By contrast, the majority of the forest-dwelling *Cercopithecus* species in West Africa have natal coats that are "not significantly different" from those of adults (Gartlan, 1969, p. 149).

Although the majority of the *Presbytis* and *Colobus* genera for which information is available have flamboyant natal coats, some species in the Colobinae subfamily, such as *Presbytis entellus*, have dark natal coats. Newborns in the *Presbytis senex* group are gray with white cheeks (adults are gray or black), although a tendency for "partial albinism" has been reported (Napier and Napier, 1967). In *Presbytis entellus*, as in some other species, there is an inter-

mediate, juvenile coat color. At about 5 months of age, the black coat is replaced by cream-colored fur which persists until the young langur turns gray around 2 years of age.

Several of the Colobinae, *Procolobus verus* and *Colobus badius*, have natal coats resembling those of adults (Booth, 1957, p. 422; Dekeyser, 1955, cited in Booth, 1957), and these probably belong in the third category.

3. Adultlike Pelage

This represents a somewhat arbitrary category simply because all newborns are distinguishable from older animals. Regardless of coat color, newborns are invariably small, relatively hairless, etc. Nevertheless, in some species, such as marmosets, *Saimiri*, possibly orangutans and rhesus macaques, newborns appear to resemble adults more than newborns do in other species.

B. PHYLOGENY, ENVIRONMENT, OR AN INDUCEMENT TO CARETAKERS

In this section various explanations for the presence or absence of striking natal costs will be considered. The main argument here is based on two assumptions which, although they seem reasonable, remain to be proven. First, it is taken for granted that color dimorphisms are not accidental and that they serve, or once served, some purpose—in this case, to single out neonates as objects of special attention. Second, it is assumed that flamboyant natal coats increase vulnerability to predation. To phrase this as a testable query, one might ask: Does a raptorial bird or other predator respond more readily to a white or golden colored infant, and will predators choose such an infant more often than a discreetly colored one when presented with both choices? Actually, except for predation by other primates, predation upon primates has rarely been witnessed, possibly because the human observer was a deterrent. Only a few incidents, such as Cynthia Booth's account of a monkey eagle carrying off a *Colobus* infant, are known (cited in Jolly, 1972).

The predominance of Colobinae among the species with flamboyant natal coats suggests the importance of phylogeny for this trait. However, flamboyant natal coats are not universally found in this subfamily (exceptions include *Presbytis entellus, Procolobus verus*, and *Colobus badius*), and several non-Colobinae exhibit the trait to some degree (e.g., *Macaca arctoides* and *Hylobates lar*). Furthermore, such a phylogenetic explanation only leads to further questions. The first of these might be: Why, when in a number of species neonates manage without flamboyance, should this potentially disadvantageous trait evolve at all?

Any answer to the question of why flamboyance occurs must take into account the selective pressures on both the infant and on the infant's potential

caretakers. To the extent that infants benefit from caretakers, and to the extent that aunts and uncles benefit from temporary possession of the infant, their interests coincide; but they do not necessarily do so. Selective pressures may work on either party to behave in a way counter to the interests of the other, as shown by male exploitation of infants (see Section II,E) and cases of infants resisting transfer (Sugiyama, 1965a; Bernstein, 1968). When it is to the advantage of an uncle to take an infant, he attempts to do so regardless of whether the infant possesses a natal coat or not—although very young infants may be preferred in such cases simply because their natal coats are effective in forestalling aggression. Typically, the natal coat lasts for the first 3-5 months, but, after this period, in several species the most intense interest in holding the infant is displayed by nulliparous females, e.g., in vervets (Lancaster, 1971) and by subadult to adult males, e.g., among baboons (Ransom and Ransom, 1971) and Japanese macaques (Itani, 1959). In these species, the dark coat color does not coincide with the period when caretakers are apparently benefiting the most from caring, but rather it is the time when the infant is most helpless and in need of benefits, such as rescue and adoption, from conspecific attention.

One would expect that the presence or absence of an extravagant natal coat reflects the needs of an infant within a given socioecological setting; degree of flamboyance should be related to its advantages and disadvantages in each species. Factors that affect the balance might include: degree of terrestriality, or, in the case of completely arboreal species, canopy preference; mode of infant transport (i.e., ventral or oral carriage among arboreal species as opposed to the jockey style adopted by terrestrial species); other factors affecting the visibility of the infant; maturation rates and the period of infant dependency (very few comparative data are available on maturation rates; to date, the most informative study is that of Chalmers, 1972); and especially the competence and availability (i.e., the motivation and proximity) of caretakers. One would expect that in those species with bright coats at birth, either special advantages accrued to attracting conspecific attention or else that the risk of attracting predators was diminished.

The fact that no terrestrial nor partially terrestrial species are reported to have flamboyant natal coats suggests that bright coloring may be related to being found among the leaves or else to not being found on the ground, or both. For example, in a species such as *Erythrocebus patas*, which depends for survival on concealment from predators, the disadvantages of a striking natal coat would outweigh all possible advantages. The vivid blue faces of newborn *Nasalis larvatus* (a colobid species with a markedly "terrestrial tendency," Kawabe and Mano, 1972), on the other hand, represents one possible solution to the problem of how to attract caretakers without inviting predators as well. Not all arboreal monkeys have flamboyant natal coats, but many arboreal monkeys with bright natal coats have predators. Living in the trees may make bright colors more

feasible, but habitat alone does not provide an explanation as to why natal coats are advantageous.

Gartlan (1969, p. 149) and Lancaster (1971, p. 179) have suggested that natal coats in vervets are related to the greater vulnerability of savannah dwellers to predation. According to them, the evolution of distinctive natal coats in conjunction with the intense interest in newborns would ensure that infants were always watched out for. However, it is just as possible that in the context of all primates, the dark natal coats of ground-dwelling species such as baboons and vervets represents a compromise between flamboyance and no distinction at all.

Lancaster (1971, p. 177) has also suggested that among species with no contrasting natal coats, infants may be kept in close contact with their mothers for a longer period of time; in this case, attracting the attention of other group members as a means of protection would be less important. Examples of such undistinguished neonates in close contact with their mothers might include chimpanzees, rhesus macaques, and orangutans. The fact that in these species infants do not need to attract attention may also be a function of "automatic" aunts in a matrifocal system where siblings or true aunts are at hand.

Several of the species that practice infant-sharing soon after birth (*Presbytis obscurus* and *Colobus guereza*) have striking natal coats; the fact that a third species, *Presbytis entellus* has dark rather than flamboyant newborns, is almost surely related to habitat use; common langurs are the most terrestrial members of the Colobinae subfamily. In some areas these animals may spend over 50% of their day on the ground. Infant-sharing also occurs in other Colobinae with flamboyant natal coats (e.g., *Presbytis johnii* and *Presbytis cristatus*), but first transfer of the infant may be substantially later than in the foregoing examples. If maternal permissiveness is equated here with an invitation to aunts, the apparent correlation between flamboyant neonates and infant-sharing lends back-handed support to the following hypothesis: in species without flamboyant natal coats, individuals do not benefit (overall) from encouraging other than maternal caretakers in the first months of life, and in species with extravagant natal coats, infants may benefit by attracting other group members. For instance, *Procolobus verus* neonates resemble adults at birth. If the suggestion offered in this paper (Section IV,B) is valid, namely that early aunting would be dangerous for an infant in this species, then that finding would support the hypothesis.

In summary, three distinct strategies have been suggested here.

1. As in *Colobus guereza* and *Presbytis obscurus*, infants may be strikingly colored and passed around soon after birth; *Presbytis entellus* represents a ground-adapted modification of this system: there is postpartum infant-sharing, but a more discreet natal coat.

2. As in vervets and baboons, infant coloration may be discrete but discreet, and mothers may be more possessive. Handling of infants by aunts and uncles

occurs much later and care in these instances may be initiated by these animals for purposes of their own.

3. As in rhesus macaques, infants may be virtually undistinguished from adults in their coloration. In such matrifocal systems, matrilineal relatives will be at hand, and mothers may be more possessive of their infants in the presence of less familiar animals.

It is suggested here that elements of the first strategy would not work or would not be advantageous in the social context of species such as the rhesus macaque. The rhesus social system with its pronounced female dominance hierarchy (see Section IV,E) would preclude widespread infant-sharing as a solution to the need for caretakers; mothers could not afford to lend their infants to dominant females, and infants might lose in terms of status benefits by being under the charge of subordinate females. Just as the rhesus social system precludes sharing, their terrestriality precludes the possibility of striking natal coats; instead, infant-care is assured in other ways, by the availability of siblings, true aunts, and grandmothers.

VI. SUMMARY

Field and laboratory instances of infant care and abuse by conspecifics other than the infant's mother have been reviewed and an attempt made to analyze these in terms of the individual and "inclusive" fitnesses of the participants. Partial summaries of this synthesis are provided at the end of Sections II and IV. The possibility that flamboyant natal coats and postnatal infant-sharing reflect past selective pressures on the mother–infant pair to invite conspecific care was also considered; this argument is summarized at the end of Section V.

It was stressed in the first section and throughout the paper that the data necessary to test Hamilton's (1964) theories among the primates simply do not exist and that all statements made can only be regarded as hypotheses and predictions in need of testing. In particular, almost no quantitative information is available on the reproductive success of animals involved in various infant-care and exploitation strategies. For this reason it is not yet possible to assign realistic weights to the costs and benefits that such behavior has for those involved. Nevertheless, it is assumed that the animal's behavior does reflect a preponderance of advantages over disadvantages and that this balance sheet of effects must be calculated within the individual's ecological and social context. This tally would be expected to change as the individual adopted different roles in the course of a lifetime.

In the case of male care, several expectations are raised by evolutionary theory. To the extent that dominant males sire a disproportionate number of offspring, one would expect high-ranking males to exhibit greater solicitude

toward infants than subordinate males do. Instances where troop leaders take risks to rescue infants were cited, and evidence presented from enclosed troops of Japanese macaques and from Barbary macaques in which dominant males participate actively in infant care. An adequate testing of the prediction awaits fine-grained studies of male–infant interactions which take into account the effects that contact with males of different ranks have upon the infant. Subordinate males would be expected to care for infants to whom they were closely related as siblings or true uncles. Cases of sibling adoptions among rhesus and chimps were cited; the possibility that older male siblings would not be available due to migration was also discussed in the case of macaques.

Whereas males caring for infants would be expected to discriminate in regards to the infants that they adopt, protect, or otherwise benefit, males abusing infants would be less likely to do so. Case studies of anubis baboons (Ransom and Ransom, 1971) suggest that males either actually or potentially involved in consort relationships are more likely to baby-sit and to protect infants, and that these males often direct their attentions toward a specific infant. Researchers on other species have not focused on this problem, and only slim evidence is available; what data there are for Barbary apes do not support the above prediction. There is some evidence for baboons, macaques, and langurs that the males most likely to exploit infants are those in positions peripheral to the breeding system or that are just entering it; these are subordinate and "outsider" males that would have the most to gain and the least to lose from behavior (such as agonistic buffering) which benefits them at potential risk to the infant involved. It has been suggested that cases of infanticide reported for langurs and crab-eating macaques represent an extreme example of such exploitation; the case for this cannot be settled, however, until some quantitative measures become available for infanticide's efficiency in increasing reproductive success.

In the case of aunting, it was suggested that maternal permissiveness and the willingness of aunts to aunt reflect a balance between potential benefits and risks. From the mother's point of view, the possible advantages of aunting for her infant (e.g., rescue, adoption, status, and socialization benefits) and for herself (e.g., foraging freedom) must be weighed against the likelihood that her infant will be adopted or kidnapped by a nonlactating or incompetent female who either injures it or exposes it to danger. Factors involved here include not only age, experience, and parity of the aunt, but the vulnerability of the infant at birth, its rate of maturation, and the availability of desirable caretakers. With the exceptions of studies of aunting by Rowell, Hinde and Spencer-Booth and research by Chalmers on comparative maturation of Old World monkeys, evidence on these points is derived largely from chance observations and from peripheral data included in general reports of social behavior.

The eagerness of the aunt to take the infant may reflect quite different interests from those of the mother and conceivably could conflict with those of

the infant. For example, the advantages to the aunt of holding the infant may be inversely proportional to her competence in infant care, as an inexperienced female has the most to gain from learning to mother. Similarly, the younger and more vulnerable the infant, the more potentially relevant holding it might be for the unpracticed nulliparae. The infant's mother and the aunt then would not necessarily agree on the optimum time for first transfer. Among squirrel monkeys, baboons, and bonnet, Japanese and rhesus macaques, young females appear highly motivated toward infants. A predominance of nulliparous females participating in aunting has been quantitatively demonstrated for vervets, langurs and caged rhesus macaques. An aunt may also be influenced by the desirability of an alliance with the mother or status benefits attached to holding an infant. There are no data on this point. To the extent that aunting would detract from care of her own infant, mothers are not expected to care for or nurse unrelated infants unless the probability of reciprocation is high. Where an aunt is closely related to the infant, the balance will be complicated both by the mother's stake in the aunt's competence and the aunt's stake in the infant's well-being. No research to date has addressed itself specifically to these problems.

Acknowledgments

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