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Implications of Monogamy for Infant Social Development in Mammals

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INTRODUCTION

Monogamy is a relatively rare mating system among the mammals, probably because of the ability of the mammalian female to rear offspring in the absence of any parental investment by a male. Females both gestate and lactate, and they can typically ensure their offsprings' survivorship to the point of weaning and independence (Kleiman, 1977). Monogamy has evolved in diverse mammals, and the basis for its evolution appears to have differed in different groups. Some of the selective forces that may have influenced the evolution of monogamy in mammals include high rates of intrasexual aggression among females, limited polygyny potential in males, and nonshareable indispensable male parental care (Kleiman, 1977; Wittenberger & Tilson, 1980).

Monogamous mammals vary in the degree of sociality they exhibit (Kleiman, 1977, 1981). Among some species, there is a dispersed social system whereby the bonded pair are rarely seen together or with their offspring, a condition I have previously referred to as *facultative monogamy* (Kleiman, 1977, 1981). Other species exist as bonded pairs in close contact but are seen only seasonally with their young. In the more social

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monogamous species, one sees nuclear families in which several generations of offspring cohabit with the mated pair, or with extended families, which include the mated pair, the offspring, other genetically related adults, and even unrelated individuals (Kleiman, 1981).

The selective forces influencing the evolution of the mating system, whether monogamy or polygamy, are independent of those factors selecting for the degree of sociality within a species, although they may act in concert during evolution. Thus, an analysis of the potential influence of monogamy on infant development must take into account the variability in sociality among species and, as a result, the variability in the numbers, ages, and sexes of conspecifics with which an infant might interact. For example, in the rufous elephant shrew (*Elephantulus rufescens*) (Rathbun, 1979) and the agouti (*Dasyprocta punctata*) (Smythe, 1978), the precocial young are hidden during early development and interact rarely with either parent. Because these species usually bear only singletons or twins, the potential for an infant to interact with more than one littermate is limited, as is the frequency of social interactions with the parents.

The extreme opposite condition prevails in some of the pack-hunting canid species (Frame, Malcolm, Frame, & Van Lawick, 1979; Malcolm, 1979) and in the marmosets and tamarins (Epple, 1975), whose young develop not only in close contact with the parental pair but with adult relatives, siblings of various ages, and littermates. Here, there is a rich opportunity for socialization, which occasionally extends beyond puberty.

Those selective factors promoting or retarding the evolution of sociality have been discussed by several authors (e.g., Alexander, 1974; Eisenberg, 1966; Wilson, 1975). For example, sociality may be negatively influenced by the adoption of an antipredator strategy involving crypsis, as in the small forest-dwelling elephant shrews, which rely on immobility and camouflage as protection from aerial and ground predators (Rathbun, 1979). By contrast, other species use sociality and group vigilance as an antipredator mechanism, as in the diurnal plains-dwelling African mongooses (Rood, 1983). In some species, sociality is promoted through the improved foraging potential of a larger social group; for example, canids (wild dogs and wolves) that hunt in packs may be able to kill larger prey through a group effort than with a solo hunting strategy (Kleiman & Eisenberg, 1973).

Regardless of the degree of sociality, there is a major difference between polygynous and monogamous mammals in infant development because the male, or father, almost always contributes to infant development, even if his investment is indirect (Kleiman & Malcolm, 1981). Among most polygynous species, the mother–young unit is the primary

unit for infant socialization; highly social species usually incorporate a number of mother–young units without significant involvement by adult males. Yet, even in monogamous mammals that are asocial, the mother–father–young unit is the primary context in which infants are reared.

MONOGAMY, SOCIALITY, AND LIFE HISTORY CHARACTERISTICS

How certain life history characteristics are correlated in monogamous mammals depends on the degree of sociality exhibited, including the quality of the pair bond, the quality and quantity of parental care, the age of juvenile dispersal, and sex-role differences (Kleiman, 1981). These characteristics are summarized in Table 1. In asocial monogamous forms, the pair bond is weak, as expressed by a relative lack of affiliative interactions between the mated male and female. Although an elephant-shrew mated pair jointly occupies a single territory, the male and female rarely interact, do not synchronize their activity, and are rarely in the same location at the same time. Except at mating, a female is often

TABLE 1.   Correlations among Life History Characteristics of Extremely Asocial (Facultative) and Extremely Social (Obligate) Monogamous Mammals[a]

	Asocial	Social
A. Pair bond	Weak	Strong
1. Interactions	a. Infrequent	Frequent
	b. Asynchronous	Synchronous
	c. Agonistic > affiliative	Affiliative > agonistic
B. Territorial behavior		
1. Long calls	—	♀ ≥ ♂
2. Scent marking	♂ > ♀	♀ ≥ ♂
3. Aggression to conspecific intruders	♂ > ♀ (Intrasex)	♀ ≥ ♂ (Intrasex)
C. Parental care		
1. Father	Indirect	Indirect and direct
2. Siblings and other "helpers"	—	Indirect and direct
D. Sexual dimorphism	Rare	Rare
E. Juvenile development		
1. Neonatal condition	Often precocial	Often altricial
2. Maturation rate	Rapid	Slow
3. Reproductive suppression	Rare	Typical

[a] From Kleiman (1981).

aggressive to the mate. However, territorial boundaries are rigid, and the territorial defense activity of each member of the pair provides little opportunity for mating outside the pair bond (Rathbun, 1979). At one level, monogamy is forced on elephant shrews (low polygyny potential) because of evolutionary and ecological restraints, such as a cryptic antipredator strategy, small size and mobility, the need for a familiar home range, and the disadvantages of social foraging.

The relatively weak pair bond is correlated with an absentee parental care system in elephant shrews. The precocial young are hidden, and the parents visit them singly, with the female nursing only infrequently. The young mature rapidly, and although they may remain on the parental home range after weaning, they eventually disperse to seek a territory and a mate. Because elephant shrews are small and not very long-lived, the turnover in pair mates is probably high, which may contribute to the weakness of the pair bond. This system is distinguished from an asocial polygynous condition by (1) the restriction of one pair to a single territory, implying an inability by the male to successfully encompass the territories of more than one female, and (2) an active role by the male and the female in eliminating intruders of their own sex, which serves to prevent adulterous matings.

Among the more social species, pair bonds are stronger and are characterized by pairs synchronizing activity, jointly exhibiting territorial behavior (mainly toward animals of the same sex), and exhibiting frequent affiliative social interactions. Sex roles with respect to maintaining the pair relationship are less dimorphic, with the female contributing equally (Kleiman, 1977, 1981). The close bonding of the male and the female permits the expression of direct parental care by the male from soon after the birth of the young.

Among monogamous species that are highly social (obligate monogamy), one rarely, if ever, sees an absentee parental care system with highly precocial young. Also, developmental time appears to be somewhat retarded, in that older juveniles and subadults may not become socially weaned from the parental family group until after the age of puberty. The degree to which the young disperse at sexual maturity (with the parents reverting to a pair condition), as opposed to the young becoming incorporated into the family, depends on the evolutionary forces selecting for a greater degree of sociality. As already mentioned, improved foraging efficiency and a group antipredator strategy may be two causes of the evolution of sociality among monogamous species. Without such selective forces, the young are likely to disperse at the earliest ages possible.

The retention of older juvenile offspring requires mechanisms for preventing postpubertal animals from independently reproducing within

the family group. Kleiman (1980) discussed some of the inhibitory mechanisms that have evolved among different mammals exhibiting obligate monogamy, ranging from the physiological suppression of estrus and/or pregnancy in subdominant females in some marmosets and tamarins (Hearn, 1977; Lunn, 1978) to behavioral solutions, such as the killing of the offspring of subdominants or the inhibition of their lactation and nursing behavior in some canids (Altmann, 1974; van Lawick, 1973). Among males, physiological suppression seems to be rare; in most cases, it appears that subdominant males are simply prevented from breeding with the reproductively active female (tamarins—Epple, 1972; Kleiman, 1978, 1980) and/or breed with her during the least optimum period (dwarf mongooses, *Helogale parvula*—Rood, 1980). The different mechanisms used for the suppression of reproduction in subdominant individuals suggest that it is more important to inhibit female than male reproduction under conditions of obligate monogamy. Indeed, not only are the female suppressive mechanisms more highly evolved (e.g., physiological), but one also sees significantly more aggression among females, which may result in female emigration (Greenwood, 1980) and/or death (Kleiman, 1979; Frame *et al.*, 1979).

MALE PARENTAL CARE

An Overview

The influence of monogamy on infant social development can be evaluated only through an understanding of the quantity, the quality, and the timing of male parental care. Kleiman and Malcolm (1981) have separated indirect forms of male parental care from direct forms of investment. Among asocial monogamous species that exhibit facultative monogamy, it is more typical for males to provide care to their offspring in an indirect manner, by maintaining the integrity of the territory, providing safe refuges secure from predators, and ensuring, through the choice of the territory, that resources sufficient for the development of the offspring will be available. Such behaviors contribute not only to the survivorship of the offspring but to the survivorship of the father himself. Thus, the male's own survival and the survival of any offspring are both contingent on the same set of male behaviors. There is some slight evidence to indicate that the male's indirect investment increases with the appearance of young, which would clearly differentiate between the occurrence of the behavior in a parental versus an individual survivorship context. Classically, parental care by males of the indirect type has rarely been considered a form of parental investment. More attention

has always been paid to the direct interactions of males with young that one sees only in the more social species. The differences in these behaviors have been described in Kleiman and Malcolm (1981).

There are several important points that should be considered with respect to the quality and the quantity of male direct parental care. First, other than nursing the young, the males and the females of the species tend to exhibit a high correlation in their parental care behaviors, in terms of both quantity and quality (Hartung & Dewsbury, 1979; Kleiman & Malcolm, 1981). Second, within any species, the form of parental care depends strongly on the life history strategy of the species. Because of morphological or ecological constraints, neither a male nor a female exhibits behaviors that are of high cost to them and of low benefit to the young. For example, neither an ungulate male nor an ungulate female carries food to its young because it would be impossible for a parent to provide sufficient food for survival without incurring a great cost. The parental feeding of weanlings occurs mainly in species where large food packets of high nutritional value can be provided to the offspring at a single time. Huddling with young, which may reduce thermoregulatory costs for the offspring, is a low-cost behavior that male and female parents can provide and that may have very positive benefits for the growth and development of the offspring (Dudley, 1974a).

Another aspect of parental care (which has great potential influence on the differential development of offspring) is the degree to which any behavior performed by the mother or the father can be shared among all the offspring (nondepreciable) or must be partitioned among several (depreciable) (Altmann, Wagner, & Lenington, 1977). A depreciable behavior is one that is reduced in availability to one individual once it has been expended on or used by another individual. Species differ in the degree to which even the same behavior pattern may be considered depreciable or nondepreciable. For example, if littermates typically rest separately from each other, any parent that slept with a single young would be said to be sharing a depreciable investment with that young, in contrast to a species whose parents can sleep together with an entire litter and thus not discriminate among the littermates. The importance of differentiating between depreciable and nondepreciable investment is that depreciable investment requires that the donor discriminate among the benefactors. In the case of parent–offspring interaction, the parent must thus make a choice among the available offspring of different ages and sexes when it performs parental care behaviors. For example, in a species that provides food to offspring at the time of weaning, the parents must make a choice with respect to which individual offspring will receive food at any given time if the food items are very small in relation to the size of each offspring and cannot be shared, as in marmosets and

TABLE 2.   Categories of Indirect and Direct
Parental Investment

Indirect	Direct
Resource acquisition	Carry or transport young
Resource maintenance	Huddle with young
Resource defense	Groom and clean young
Shelter construction and	Retrieve young
maintenance	Babysit
Sentinel and antipredator	Play with or socialize young
behavior	Active defense of young
Care of female	Provide food to young

tamarins (Hoage, 1982). In direct contrast, in species like the pack-hunt-
ing canids, large quantities of food may be stored in the stomach and
regurgitated to the young in such a way that littermates may jointly
share the food (Malcolm, 1979).

The six main categories of indirect investment and the eight main
categories of direct investment by parents are detailed in Table 2 (see
Kleiman & Malcolm, 1981). Variations in the correlation of the behavior
of males and females (except for lactation) with respect to parental care
often relate to the timing of the male's involvement and the retrictions
imposed on the females, which promote different parental roles. For
example, whereas females may retrieve infants that have been displaced
from the nest at an early age, the male may not exhibit such behavior
if he does not become involved in parental care activities until the young
are sufficiently well developed so that retrieval is no longer important.
Crab-eating fox *(Cerdocyon thous)* males do not appear to interact with
their offspring until after the young emerge from the den (Brady, 1978).

Indirect Care

Indirect care by males is seen in almost all monogamous mammals,
through their activities in territorial maintenance and defense. Indeed,
it is rarely emphasized because it is so much less dramatic than direct
care and more difficult to quantify. Koontz (1981, personal communi-
cation) has data indicating an increase in trail-cleaning behavior by cap-
tive male elephant shrews after the birth of young. The trails run
throughout the territory and are maintained by the animal's sweeping
debris (with the forefeet) off the substrate in selected locations (Rathbun,
1979). The trails are used for orientation and for escape from predators
within the territory. A well-maintained trail system presumably benefits

the young as they begin to explore within the parental home range. I. Porton (personal communication, 1982) has noted greater aggression toward keepers by male maned wolves *(Chrysocyon brachyurus)* after the mate has given birth—even when the pair are housed separately in adjacent cages.

Providing food to the mate may improve a female's condition during pregnancy and lactation. Anecdotal accounts of such behaviors abound, although quantitative documentation is weak (but see Brown & Mack, 1978, for the golden lion tamarin). In general, documentation showing changes in indirect care with the appearance of offspring is lacking.

Direct Care

The distribution of the categories of male parental care among selected mammalian species is shown in Table 3. The carrying of young is generally restricted to the primates (and bats that are little known). Among marmosets and tamarins, male carrying is initiated at any time between Day 1 and Day 30 (Christen, 1974; Epple, 1975; Hoage, 1977; Ingram, 1977). Among the gibbons (Hylobatidae), male carrying may or may not occur; it is common in the siamang *(Symphalangus syndactylus)* beginning when the infant is approximately 6 months old (Chivers, 1972, 1975). Carrying young is an energetically expensive behavior, which may explain its relative rarity among male primates.

Methods of providing food for young differ. Among canids that feed on relatively large prey items, food may be regurgitated to the young, beginning at weaning. Smaller prey items may be carried whole, or the young may be led to a kill. Prior to weaning, regurgitated food may be available to the female if the demands of lactation preclude her actively being involved in hunting (see Malcolm, 1979, for the African wild dog, *Lycaon pictus*).

In species feeding on smaller prey items, or high-energy foods that occur in small packets (e.g., fruits and insects), food items are usually carried directly to the young—again beginning at weaning (e.g., Hoage, 1982 for lion tamarins; Rasa, 1977, for dwarf mongooses). For species in which food provisioning is an important parental care activity, male involvement usually does not begin until the time of weaning, although the male may carry out other parental activities prior to that period.

Babysitting and huddling with the young are universal to most species in which male parental care is shown. Dudley (1974a,b) has shown how this behavior contributes to the growth and the survival of young, through improved temperature maintenance, in infant California mice *(Peromyscus californicus)*, which thermoregulate poorly. Even in species in which the infants have good thermoregulatory abilities, the heat conservation provided by the male may promote growth and develop-

TABLE 3. Categories of Direct Male Parental Care Seen in Selected Monogamous mammals[a]

	Huddle	Carry	Retrieve	Groom	Feed	Babysit	Defend	Play
Rodents								
(1) *Peromyscus californicus* (mouse)	X		X	X		X	?	?
(2) *Microtus ochrogaster* (prairie vole)	X		X	X		X	?	X
(3) *Castor fiber* (beaver)	X		X	X	X	X	X	X
Carnivores								
(4) *Helogale parvula* (dwarf mongoose)	X		X	X	X	X	X	X
(5) *Lycaon pictus* (hunting dog)	?		X	?	X	X	X	X
(6) *Speothos venaticus* (bush dog)	X		X	X	X	X	X	X
Primates								
(7) *Leontopithecus rosalia* (lion tamarin)	X	X	X	X	X	X	X	X
(8) *Symphalangus syndactylus* (siamang)	X	X	?	X	?	X	X	X

[a] From: (1) Dudley, 1974a,b; (2) Hartung and Dewsbury, 1979; Wilson, 1982b; Thomas and Birney, 1979; (3) Wilsson, 1971; Svendsen, 1980; (4) Rood, 1978; (5) Frame et al., 1979; van Lawick, 1973; Malcolm, 1979; (6) Jantschke, 1973; C.A. Brady, personal communication; I. Porton, personal communication; (7) Hoage, 1977, 1982; (8) Chivers, 1972, 1975.

ment by reducing the energy expended by the young on maintaining high body temperatures.

One of the thorniest contributions by the male is in the area of play and socialization. Wilson (1982a) has shown for the degu (*Octodon degus*, a nonmonogamous rodent) that certain forms of social interactions are reduced among siblings when the father is present (e.g., nosing of the body). This difference is significant because Wilson believes that nosing (or sniffing) interactions are of major consequence in the development of sibling relationships. Thus, the male's presence may have an inhibitory effect on his offspring.

The greater male social involvement with the offspring may inhibit the young, but in so doing, it may reduce parent–offspring conflict and permit the maintenance of longer term bonds among parents and young. Biben (in press) has examined infant development in three South American canid species (bush dogs, *Speothos venaticus*; crab-eating foxes; and maned wolves). Two findings relevant to this discussion are that (1) the young interact socially with the father more than with the mother in the two species with the stronger pair bonds and (2) the young "roll over" onto their backs in a submissive posture more toward the father than toward the mother or their littermates. This finding suggests a major role of the father in maintaining subordination behavior among offspring. It also indicates some degree of role differentiation in fathers and mothers during rearing, a finding that is also true for other monogamous mammals, both social and asocial.

To a large extent, the influence of paternal care on social and behavioral development in mammals may only be inferred because it requires the rarely tested assumption that the behavior of a father toward his young always has positive effects. Indeed, tests of the effects of "helpers" on the survivorship of young birds and mammals are only just appearing (jackals, *Canis aureus* and *C. mesomelas*—Moehlman, 1979, 1983), and in some cases, clear-cut benefits improving the survivorship of the young have not been obtained (Malcolm, 1979). Attempts to prove the necessity of paternal care are confounded by the fact that those species in which paternal care is most highly developed are also the species in which helpers are most common. There are few social monogamous mammals in which the pair alone care for their offspring and juveniles disperse prior to the subsequent litter's birth.

THE EFFECTS OF HELPERS

In most species of monogamous mammals in which the young are retained and act as "helpers," the influence of both the mother and the father is reduced because a greater percentage of parental care and social

interactions directed toward the infants is performed by the helper class. In large groups of dwarf mongooses, Rood (1978) has found that both parents contribute less than the expected frequency of babysitting with and feeding the young. Similarly, Wolters (1978) has found that parental carrying frequencies are much lower in larger groups of cotton-top tamarins *(Saguinus oedipus)*. When more animals are available for interactions, the relationship between parents and offspring suffers some dilution, which may reduce the degree of parental control, to some extent, or result in the parents' having to assert themselves more dramatically when conflict arises.

COMPARISON OF NUCLEAR VERSUS EXTENDED FAMILIES

Definitions

As already discussd, the degree of sociality varies among monogamous species. As a result, some species live in permanent extended families with a single breeding pair and nonreproductives, including offspring of several ages, mature siblings of the breeding pair, and, occasionally, nonrelatives (e.g., dwarf mongoose—Rood, 1978, 1983). This form of extended family contrasts with that of species in which the breeding pair coexists only with their immature offspring. If reproduction occurs annually and each set of young disperses before the next breeding season, the pair may spend significant parts of the year alone (e.g., red foxes, *Vulpes vulpes;* crab-eating foxes). In other cases, there may always be some young together with the parents (e.g., most gibbon species). Obviously, if immature young provide assistance to the parents in parental care duties, then there is some overlap in the functioning of the two family systems. Yet, there are major differences in the evolutionary costs and benefits to infants and juveniles of developing in these two conditions. Table 4 details some of these advantages and disadvantages; however, it should be recalled that each family system is assumed to be an evolved strategy that is adaptive for any species in which it occurs.

Growth, Development, and Survivorship

In larger families, food acquisition for weanlings may be greater, in that larger families may collect more food, either as hunters or in locating rich food sources. The better foraging abilities of extended families may provide more—and more variable—foods for young animals as well as the opportunity to learn about appropriate and inappropriate food items. Food sharing by parents and helpers may reduce food competition among

TABLE 4. The Costs (C) and Benefits (B) to an
Infant of Developing in a Nuclear (Parents
Only) or Extended Family (Parents and
Helpers)[a]

Nuclear family		Extended family
	Growth and development and survivorship	
C	Thermoregulation	B
C	Food acquisition	B
C	Food sharing	B
C	Food learning	B
C	Late dispersal	B
C	Protection	B
	Social integration	
C	Learn social roles	B
B	Behavioral suppression	C
B	Direct conflict	C
B	Aid relatives	C
	Reproduction	
C	Learn parental care	B
B	Reproductive suppression	C
B	Variance in reproductive success	C

[a] It should be remembered that these are not real costs and benefits since the social structure of a species is assumed to be an adaptive evolved strategy. However, the table points out the differences for infant mammals in developing in an extended vs. a nuclear family.

same-aged littermates. Thus, survivorship among young may be enhanced through greater access to food at all ages, including the preweaning period when the assistance of "helpers" in babysitting and bringing food to the mother may have positive effects on the mother's physical condition (which would positively affect milk production).

In extended families, the young are rarely left alone; thus, they do not need to expend as much energy on thermoregulation. The presence of older animals also protects them against predation. A negative correlation between the number of helpers available and the time left alone has been found by several authors (e.g., for jackals, see Moehlman, 1983). The protection afforded by a social group is significant even in those species in which the adults are still vulnerable to predation (e.g., dwarf mongooses—Rood, 1978). Indeed, because dwarf mongooses are individualistic foragers and feed on only small food items, the selective pressures favoring such large social groups derive mainly from their antipredator benefits.

The dispersal at or before sexual maturity of the young of monogamous species in nuclear families may be costly to those young in terms of their survivorship. They must forage and find protection in unfamiliar terrain and would certainly be the target of aggression by conspecific territorial pairs. Survivorship and successful reproduction ultimately depend on the acquisition as rapidly as possible, of both a mate and a territory.

Social Integration

An infant maturing in an extended family has the opportunity to gain much more complex social experiences than in a nuclear family because the age, sex, and reproductive experience of the group members may vary considerably. Thus, a youngster may learn a variety of social roles and be more socially flexible. Young from nuclear families typically interact only with parents and siblings of one age or reproductive class.

The social variety, however, has its costs. As the infant matures, it may experience behavioral suppression, both from its parents and from other older animals (Kleiman, 1979, 1980). The juvenile or pubertal individual may be cast frequently in a subordinate role that limits its potential for behavioral expression and may produce severe social stress. The same animal may also be the object of direct aggressive behavior, also by parents and other adults. Among wolves *(Canis lupus)* and New World marmosets and tamarins, survivorship may be jeopardized by the aggression of potential reproductive competitors (e.g., see Kleiman, 1979). Typically, this aggression occurs within each sex, and in some species, it is greater among females than among males (Frame *et al.*, 1979; Kleiman, 1979; Malcolm, 1979).

The maturing subadult or mature nonreproductive individual within an extended family typically aids its parents (or other relatives) in the care of their offspring. The cost of providing food and protection to such young is not clear; certainly, there may be some positive benefit if the young are close relatives, such as younger siblings, through an increase in inclusive fitness (Hamilton, 1964). Yet, as already discussed, there are few data available indicating a direct positive effect on infant survivorship due to the activities of helpers, and there are no known data on the costs to the helpers of helping.

Reproduction

Helpers may certainly benefit by gaining experience in parental care techniques. Such benefits through learning have been documented for some species of marmosets and tamarins (Hoage, 1977; Ingram, 1978).

The benefits of parental care experience in terms of the survivorship of the helper's offspring have also been shown in nonmonogamous species (e.g., chimpanzees, *Pan troglodytes;* see Nadler, this volume).

This benefit is, however, offset by two related costs. First, as long as an individual chooses to forgo a reproduction attempt by not risking emigration or not provoking a conflict with the reproductively dominant individual of its sex, it will not reproduce successfully. Methods of reproductive suppression have already been discussed (and see Kleiman, 1980).

Second, in all species in which extended families are the major reproductive unit, there is great variance in individual reproductive success. Indeed, it is likely that some adult individuals in groups may never reproduce during their lifetime—although survivorship may be jeopardized at any time that an animal attempts to improve its reproductive position, through emigration or direct conflict. Thus, although there are considerable benefits associated with development within an extended family, the ultimate cost of forfeiting reproduction is of major importance to an individual's fitness.

SOME CONCLUDING SPECULATIVE COMMENTS

Parental Manipulation

Alexander (1974) discussed the retention of helpers in terms of the parental manipulation of offspring, as the reproductive success and fitness of the parents may be enhanced through the assistance and at the expense of nonreproductive offspring. Thus, the reproductive suppression of offspring may be seen as another example of parent–offspring conflict in which the parent dominates.

Incest Taboos

Although not quantitatively documented, there is some suggestion that parent–offspring and sibling matings are less common in species living in extended families. This may be an evolutionary response to the great variance in individual reproductive success among males and females in extended families and may thus ensure that inbreeding, with its negative consequences, will be rare (Ralls, Brugger, & Ballou, 1979). The mechanisms whereby matings are inhibited among relatives appear to be behavioral; thus, individuals that grow up together from an early age avoid sexual relationships (for an interesting example in the prairie

vole, *Microtus ochrogaster*, see Carter, Getz, Gavish, McDermott, & Arnold, 1983). Exact genetic relations need not be known; the major variable would be in the degree of familiarity from an early age.

Sex Ratios, Polyandry, and Female Conflict

I have already indicated that among some species existing in extended families, female competition and aggression appear to be greater than in males. Such species (e.g., African wild dogs and some marmosets and tamarins) tend to exhibit sex ratios biased toward males among adults in nature and, in some cases, to have sex ratios significantly biased toward males at birth (Kleiman, 1979; Kleiman & Eisenberg, 1973; Malcolm, 1979). Female survivorship may be lower than that of males *in utero*, and again at and after puberty, when females are more often forced to emigrate from their natal group. It is of interest that there have been reports of multiple males mating with the dominant reproductive female in these or related species (Malcolm, 1979), a finding suggesting a polyandrous condition (greater reproductive variance among females than among males). Because of the typically greater parental effort of mammalian females relative to males, polyandry would not be expected to evolve among mammals. Its occurrence may indicate that male assistance in rearing young is sufficiently crucial to a female's reproductive success so that, for both sexes, fitness is enhanced by the increased uncertainty of paternity and a near-polyandrous condition.

Role Differentiation in Fathers and Mothers

Despite the high correlation within the males and the females of a species in the quality and the quantity of parental care behaviors (Hartung & Dewsbury, 1979), fathers and mothers do differ in their interactions with their offspring, as already mentioned. Thus, different parental roles exist. The direction of the difference is likely to be based on evolutionary and ecological constraints, and it needs to be further investigated in light of each species' natural history. For example, whereas marmoset and tamarin males may assist in carrying infants, permitting the female the possibility of unimpeded foraging, a wolf or a wild dog male may take a major responsibility for leading a hunt while the mother remains at the den site and guards the young. Because the male can regurgitate food to the female and the offspring, both the carrying and the hunting strategies of the males serve to maintain the nutritional status of the mate. They do, however, result in major differences in the father's form and frequency of interaction with his offspring.

ACKNOWLEDGMENTS

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