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Correlations Among Life History Characteristics of Mammalian Species Exhibiting Two Extreme Forms of Monogamy

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INTRODUCTION

The form of social organization exhibited by monogamous mammals ranges from a dispersed social system (the pair is rarely seen together or with the young) to a pair bonded condition (the pair is usually seen together, with the nuclear family a temporary phenomenon) to a permanent nuclear or extended family (the pair is always seen together with different-aged offspring and sometimes other kin) (see Figure 20–1). The purpose of this paper is to examine the similarities and differences in the behavior of monogamous mammals, to determine whether there are correlations among different behavioral characteristics, depending upon the form of social organization exhibited. The chief behavioral characteristics to be discussed here include the form, intensity, and direction of interactions between and within the sexes, the condition of young at birth and during ontogeny, parental care systems, dispersal mechanisms, and sex differences in territorial behaviors such as scent marking.

BACKGROUND

A recent merging of evolutionary and ecological theory has produced testable hypotheses concerning the factors promoting the evolution of different mating systems (for recent reviews see Emlen and Oring, 1977; Clutton-Brock and Harvey, 1978). It has been suggested that monogamy may evolve when males cannot defend either groups of females or monopolize those resources sufficiently to attract several females. Such conditions are most likely to occur when essential resources are sparse but evenly distributed, thus leading to a wide dispersion of females. The ecological adaptations of many monogamous mammals generally support this hypothesis. For example, callitrichids are frugivore/omnivores, depending on small packets of high-energy foods such as fruits, insects, and small vertebrates that are relatively evenly dispersed in space and time (Dawson 1977; Izawa 1978). The monogamous elephant shrews (Macroscelididae) and dik-diks (*Madoqua* spp.) depend on invertebrates and high-quality browse, respectively (Rathbun, 1979; Hendrichs and Hendrichs, 1971), high-energy diets that are also dispersed in small packets.

The evolution of a modal group size, social tolerance, and ultimate social organization is, however, influenced by factors independent of the mating system itself. For example, social tolerance may be negatively influenced by the following factors:

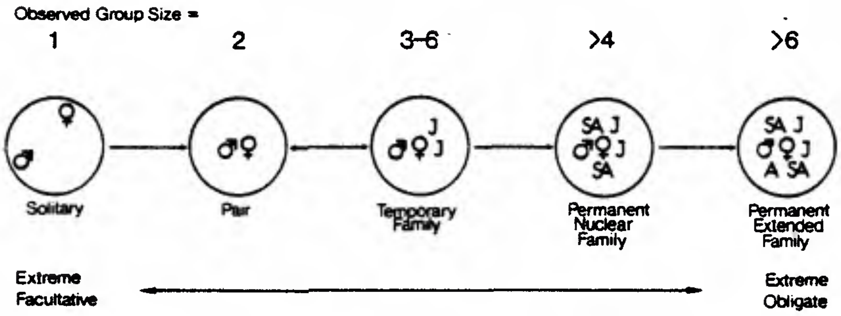

Figure 20–1. Observed group size and composition in different forms of monogamy ranging from the facultative (dispersed social system) to the obligate (cohesive social system) type. Note that the pair may temporarily become a nuclear family, depending upon reproduction. ♂ and ♀ represent the reproductively active male and female. J refers to juvenile offspring, SA to subadult offspring, and A to adult offspring or other adult relatives of the breeding pair.

1. Intersexual competition: Social tolerance may be selected against if the sexes must themselves compete for limited resources. For example, rufous elephant shrew females (*Elephantulus rufescens*), although monogamous, aggressively defend from males (including the mate) areas of termite surface activity; these concentrations of foraging termites occur erratically (Rathbun, 1979) but are a temporarily rich food resource.
2. Cryptic anti-predator strategy: For species that depend on crypsis to avoid predation, social contact may be disadvantageous to all individuals (Eisenberg and McKay, 1974). The monogamous elephant shrews and agoutis (*Dasyprocta punctata*) are cursorial species, which are heavily preyed upon by a variety of small predators (Rathbun, 1978; Smythe, 1978). Presumably, susceptibility to predation would be increased with a larger group size. Selection against a social group has even influenced the form of maternal care in these species, in that mother-young contact is rare, with neonates spending the majority of time in isolation, hiding.

Although group foraging and feeding is usually more disadvantageous than advantageous, thus promoting social intolerance, food acquisition and defense may in some cases be improved by a larger group size (Eisenberg, 1966; Alexander, 1974). In some of the smaller monogamous canid species, cooperative hunting *may* occasionally improve foraging success, thus benefiting more than one individual (Kleiman and Eisenberg, 1973). This would result in selection for greater social tolerance. Another condition that would select for greater social tolerance is an anti-predator strategy based on group defense.

Given that there are factors that independently select for and against social tolerance, variations in group size and social structure in monogamous mammals should parallel the variation seen in polygynous mammals. Indeed, among monogamous mammals, group size may vary from 1 to 15 individuals while social structure ranges from an essentially solitary condition to extended families in which several adult males and females as well as juveniles and sub-adults co-exist (Figure 20–1).

Examples of relatively asocial monogamous species include the elephant shrews (Macroscelididae) (Rathbun, 1976, 1979) and dik-diks (*Madoqua* spp.) (Hendrichs and Hendrichs, 1971) where individuals are usually seen alone or as pairs, and young usually disperse from the parental home range before a subsequent birth. In the more social monogamous mammals, the group is essentially a nuclear family, although in some species siblings of the reproductive pair (and perhaps other close relatives) are also part of the social group, resulting in an extended family with only one set of reproductive adults. Offspring may not disperse until after puberty, thus young of different ages may be present simultaneously. Examples of species exhibiting this form of monogamy may be found in the primate family Callitrichidae, the marmosets and tamarins (Epple, 1975a; Rothe, 1975); pack-hunting canids like the wolf, *Canis lupus*, and hunting dog, *Lycaon pictus*, also show these characteristics (Mech, 1970; van Lawick, 1971; Frame and Frame, 1976; Kleiman and Brady, 1978).

I have previously termed the two most extreme forms of monogamy in mammals facultative (asocial) and obligate (highly social) (Kleiman, 1977a). The adjective facultative is defined by *Webster's New Collegiate Dictionary* (1977) as "showing the typical life style under some environmental conditions but not under others." The use of this qualifier reflects the probability that polygyny in asocial monogamous mammals is prevented by ecological constraints, i.e., the dispersion of resources in an average environment reduces the probability that a male can defend the territories (or home ranges) of more than one female and thus increase his reproductive success. Obligate is defined as "restricted to one particular mode of life" (Webster's, 1977). As used here, it suggests that polygyny is prevented less by ecological constraints than by the reduced probability that a female can rear young successfully without the *direct* aid of a male. Thus, direct male parental care appears to have less effect on female reproductive success in asocial monogamous mammals than on female reproductive success in the highly social species despite the fact that the monogamy is still the modal mating system, i.e., a male and female tend to mate exclusively with each other through several reproductive efforts.

This implies that the quality and quantity of parental investment by males, like the degree of social tolerance, are influenced by factors other than the mating system itself. For example, the degree of close contact between a male and female should affect the frequency and type of parental investment by males. Where social tolerance is high and pair mates interact frequently, direct paternal care by males is more likely as paternity is more certain. In relatively asocial species, paternity may be in question because the pair mates are rarely in contact. Thus, one would expect less active paternal care. Finally, the quality and quantity of parental care will be influenced by the degree to which such behavior is advantageous in the rearing of offspring.

Correlated Life History Characteristics and their Analysis

In Table 20–1, I suggest the probable correlations among eight life history characteristics in extreme facultative and extreme obligate monogamy. These correlations are based on a combination of expectations from theory and known facts. The function of these correlations is to provide a framework whereby comparisons can be made, with the same questions being asked of many different species.

A. Behavior towards adult conspecifics

1. Relationship within the bonded pair:

The term "pair bond" is a frequently and loosely used phrase for which there is not yet an operational definition. For example, Wilson (1975), in his glossary, defines "pair bonding" as "a close and long-lasting association formed between a male and female" (p. 590). This definition, however, does not specify the character of the association or its duration. Nor has there been an attempt to do so by most authors, even though intuitively, both ethologists and others recognize that pair bond "strength" varies from species to species and that there should be a method of quantifying such variability (see Eisenberg, 1966).

Among species exhibiting facultative monogamy where there may be selection against social tolerance, one would expect a "weaker" pair bond. Among species with obligate monogamy, where there is either no selection against social tolerance or selection favoring social tolerance, pair bonds should be "stronger." To examine differences in pair bond

Table 20–1. Correlations of behavioral characteristics in extreme facultative and extreme obligate monogamy.

	Facultative Monogamy	Obligate Monogamy
1. Behavior towards adult conspecifics		
a. Relationship between bonded pair	weak pair bond; more aggressive than affiliative behaviors; female aggressive to male?	strong pair bond; more affiliative than aggressive behaviors; female aggressive to male?
b. Behavior towards other adults	male–male aggression greater than female–female aggression; occasional polygamy	female–female aggression equal to or greater than male–male aggresson; polygamy uncommon
2. Relation to space and time		
a. Distribution of territorial behaviors between mates	males more than females	males and females equal
b. Synchrony of pair activities	asynchronous	synchronous
3. Quality and quantity of parental care		
a. Paternal care	less developed, mainly indirect	well-developed, mainly direct
b. Parental care by juveniles	not present	present
4. Ontogeny		
a. Sequence of development	rapid social weaning; early puberty	late social weaning; delayed puberty
b. Mechanisms of dispersal	parental aggression towards young	sibling aggression; parental aggression rarer

"strength," the following characteristics could be investigated.

(a) Paired individuals could exhibit both agonistic and affiliative behaviors towards each other, regardless of the interaction rate. One would expect that the ratio of affiliative to agonistic behaviors would be higher, the stronger the bond between the pair. Weakly bonded individuals would be expected to exhibit relatively higher rates of agonistic or conflict behavior and avoidance. Affiliative behaviors would include (i) those that promote proximity between paired individuals, e.g., courtship displays and vocal signals that maintain auditory contact during independent foraging and (ii) those involving long periods of body contact, such as sleeping together, huddling, allogrooming, and sexual contacts.

(b) The process of pair-bond formation as measured by the length of time it takes for pair interactions to reach an equilibrium as well as the degree to which reproduction (i.e., sexual activity) alters that equilibrium could also be an indicator of pair-bond quality. In weakly bonded species pair interactions might be expected to reach an equilibrium rapidly but be more easily altered or upset than in strongly bonded species. Moreover, species in which only weak bonds are formed might exhibit relatively higher levels of courtship behavior by the male prior to sexual activity because of the generally low levels of interactive behavior at other times. Increased courtship prior to copulation would also aid in ensuring paternity because the female would be monopolized during the receptive period. Fewer changes in interactions before mating might characterize species with a stronger bonding tendency.

(c) The degree of synchrony in routine daily activities could also be used to distinguish between strong and weak pair bonds. Species exhibiting strong pair bonds are likely to be characterized by a high level of synchrony in such activities as foraging, feeding, scent marking, nest-building, etc., with the reverse true for weakly bonded species.

(d) The duration of the pair's association may be a measure of pair-bond strength.

However, this characteristic must be related to longevity and frequency of reproduction and can only be determined from long-term field observations. It is likely that in more strongly bonded species, mate changes will be relatively less frequent.

In species exhibiting facultative monogamy, where social tolerance may be disadvantageous for ecological reasons, pair bonds may be weak and I would predict that pairs would exhibit a higher ratio of agonistic and conflict behavior relative to affiliative behavior, less behavioral synchrony, and would reach an interaction equilibrium faster after pair bond formation than in obligate monogamy. Data already available seem to confirm this expectation. For example, in the rufous elephant shrew, *Elephantulus rufescens*, interactions between pair mates are characterized by agonistic behavior or avoidance, except before the female's estrus. Pairs infrequently sleep at the same location and never forage together (Rathbun, 1979). Similar observations have been reported by Smythe (1978) for the agouti, *Dasyprocta punctata*. Females rarely permit the pair mates to approach and also become extremely aggressive shortly after birth. Smythe observed very rare cases of affiliative behavior, such as mutual grooming of the ear region. Foraging was conducted independently, and pairs did not sleep in contact, although they were occasionally in close proximity.

By contrast, pair interactions are of a more affiliative nature in species exhibiting obligate monogamy. For example, among lion tamarins (*Leontopithecus rosalia*), which live in nuclear or extended family groups, agonistic interactions are rarely seen within the members of a pair. Moreover, pair mates regularly rest and sleep in close body contact and allogroom on a regular basis (Kleiman, 1977b). There is synchrony in feeding and resting behavior, and pairs are rarely out of visual or vocal contact with each other. Courtship behavior by the males during estrus is inconspicuous relative to the driving behavior described for elephant shrews (Rathbun, 1979) and agoutis (Smythe, 1978).

There are species in which pair bonds appear to be intermediate in "strength," suggesting that the gradation in group size reflects a gradation in the degree of social tolerance among monogamous mammals. Such variability undoubtedly depends on the strength of the various ecological pressures, e.g., feeding strategies, either favoring or selecting against social tolerance.

A species intermediate in pair bond strength is the crab-eating fox *(Cerdocyon thous)* where pairs are usually seen together although they may forage separately and exhibit intermediate levels of close body contact and affiliative behaviors. Agonistic interactions occur mainly during the early stages of pair bond formation (Kleiman and Brady, 1978). Courtship is conspicuous, as in elephant shrews and agoutis.

One characteristic of a pair bond that is unrelated to group size and social structure is the dominance relationship within a pair. I have already suggested that in some monogamous mammals, females appear to be more assertive and aggressive than males in heterosexual interactions (Kleiman, 1977a), a characteristic that is rare in polygynous mammals. If monogamous females compete with males for scarce resources, and these resources are critical for the female's reproductive success, one would predict a reversal of the more typical form of male-dominated heterosexual interaction. Such a condition need not be specific to monogamous mammals but may be accentuated with this reproductive strategy as the male's reproductive success is closely aligned with the female's reproductive success. Such critical resources might include a burrow system, cached food, or food resources that are rich but sparsely distributed in the home range. The scattered food hoards of the agouti are such a resource (Smythe, 1978), and female agoutis tend to dominate the mate.

The female also tends to be dominant over the male in rufous elephant shrews (Rathbun, 1979), bush dogs *(Speothos venaticus)* (Drüwa 1976, 1977), beavers *(Castor fiber)* (Wilsson, 1971), and green acouchis *(Myoprocta pratti)* (Kleiman, 1977a) although it is not known whether the causes of the female dominance are the same in all cases. Female dominance may be associated with females being nearly as large or larger than males, although this is not the case in dik-diks, *Madoqua* (Ralls, pers. comm.)

2. Relationship with adults other than the mate:

With a monogamous reproductive strategy, male-male competition should be less intense than in polygyny. However, there may still be considerable variation in the degree of intrasexual competition among both males and females in monogamous mammals, and these may derive from differences in group size and social tolerance. Moreover, the degree of exclusivity of the mating relationship may differ. I would expect that in species exhibiting facultative monogamy where pair members are dispersed, the degree of intrasexual competition will be greater in males than in females and will parallel what is seen in polygynous mammals because of the relatively lower certainty of paternity. By contrast, in species exhibiting obligate monogamy where the certainty of paternity is higher, males and females will be more similar in the degree of aggression shown towards same-sexed conspecifics. This trend will be paralleled by a tendency for facultative species to have potentially less exclusive mating relationships (although still with a high percentage of monogamous matings) while mating outside the pair bond may be rarer in obligate species.

In species exhibiting facultative monogamy, males seem to be more aggressive to male strangers than females are to female strangers, e.g., dik-dik, *Madoqua kirki* (Hendrichs and Hendrichs, 1971), elephant shrews, *Rhynchocyon chrysopygus* (Rathbun, 1979), and agoutis, *Dasyprocta punctata* (Smythe, 1978). Females do, however, defend the territory against female strangers.

Among some mammals exhibiting obligate monogamy, it has been reported that competition or aggression among females is more intense than among males, e.g., saddle-backed tamarin, *Saguinus fuscicollis*, (Epple, 1977); wolf, *Canis lupus*, (Zimen, 1975); hunting dog, *Lycaon pictus*, (van Lawick, 1971, 1973; Frame and Frame, 1976, 1977; Frame et al., 1980). This reversal of the normal mammalian pattern of intense male–male competition is predicted to occur only in species where males are the limiting sex, i.e., in polyandry where males have a greater parental investment than females. With internal gestation and lactation female mammals always provide more parental investment than males and therefore are the limiting sex. The intense female–female competition in some monogamous mammals suggests that females may be competing for groups of males that exhibit good paternal care even though only a single male may contribute gametes to the future offspring. Such a condition is more likely where the males are genetically related, e.g., brothers, and does appear to exist among hunting dogs, *Lycaon pictus*, where females (usually sisters) compete intensely for the loyalty of groups of related males (Frame and Frame, 1976, 1977). Groups of related males are usually monopolized by and rear the offspring of a single dominant female who apparently only mates with the most dominant male. Other females are prevented from achieving reproductive success by (1) the dominant female's aggression during estrus that prevents copulations, (2) the dominant female destroying the offspring of sisters and (3) males refusing to feed a subordinate female and her litter. Competition among females also results in females being the primary dispersers from social groups (Frame and Frame, 1976, 1977; Frame et al., 1979; van Lawick, 1971, 1973).

Since facultative monogamy involves little assurance of paternity because of the low levels of social tolerance, it is likely that males may opportunistically try to mate with other females. However, aggression from the female pair-mate towards other transient or neighboring female adults may limit the success of such attempts. Observations of elephant shrews (Rathbun, 1979) suggest that intersexual relations among neighbors are usually amicable. Rathbun did observe an *R. chrysopygus* male attempting to mate with a neighboring female who had lost her mate.

In obligate monogamy, attempts to mate outside the pair bond may be much rarer, since pairs are in close association and usually jointly attack territorial intruders (e.g., tamarins, Dawson 1977; Neyman, 1977; wolves, Mech, 1970). Among family members, the dominant pair suppresses reproduction in siblings or offspring by both behavioral and physiological means. In marmosets and tamarins, it is already clear that sexual behavior is restricted to the bonded pair in families and artificial groups (Epple, 1972; Rothe, 1975; Kleiman, 1979) without aggression being common between same-sexed adults *if* they have been previously habituated to each other. Hearn (1977) has shown that daughters will not exhibit an ovarian cycle as long as they remain in the presence of their mother. Among wolves and dwarf mongooses (*Helogale undulata*), matings of subdominant animals may be prevented by direct aggression (Rabb et al., 1967; Rasa, 1973a), and in African wild dogs, reproductive dominance occasionally may be achieved through killing the offspring born to a subordinate female (van Lawick, 1973).

Clearly, in assessing how and why mating exclusivity is achieved, one must determine (1) whether mating outside the pair bond occurs and (2) if not, whether it is prevented by the pair-mate or simply not attempted. There are no data available on the frequency of polygyny (or polyandry) for any typically monogamous mammal.

B. Behavior with respect to space and time

1. Distribution of territorial behaviors between mates:

Mammals may use a variety of behavior patterns to indicate their presence to conspecifics without a direct confrontation. These include signals such as scent marking and long-distance vocalizations that probably provide information about an individual or group's identity and location.

The majority of monogamous mammals appear to be territorial in that they defend exclusive use of an area from neighboring conspecifics and advertise their presence by scent marking and vocalizing.

The greater degree of intra-male aggression suggested for species exhibiting facultative monogamy should be paralleled by sex differences in the frequency of "territorial" behaviors such as scent marking, with males exhibiting more marking than females. Among elephant shrews (Rathbun, 1979), dik-diks (Hendrichs and Hendrichs, 1971; Kranz, unpublished), and agoutis (Smythe, 1978), this is indeed the case.

In obligate monogamy, sex differences in these behaviors should be reduced. Among several species of marmosets and tamarins, males and females tend to scent mark at similar frequencies (Kleiman and Mack, 1980; Epple, 1977; Box, 1977a), and females occasionally scent-mark more than males. Although Rasa (1973b) reports that in dwarf mongooses the dominant male marks significantly more than the dominant female (p. 300), these results were obtained during experimental tests, and Figure 6 in Rasa (1973b) suggests that there is little sex difference with longitudinal observations. Among bush dogs the female consistently urine-marks at much higher levels than the male (Drüwa, 1976, 1977; Kleiman and Brady, unpublished), indicating a reversal of the typical sex role and paralleling the high levels of intrasexual competition among females in this species.

With respect to long-distance vocalizations, hylobatid males and females jointly vocalize on a daily basis. The calls of males and females differ, with the female's great call dominating the duet in some species (Marshall and Marshall, 1976).

2. Synchrony of pair activities

Because the males and females of species exhibiting facultative monogamy are not often in contact, it is likely that they will carry out most maintenance activities alone and will rarely jointly perform behavior patterns that promote spacing.

Under obligate monogamy, pairs should synchronize their activities, including foraging and feeding, resting, and the execution of "territorial" behaviors. Such synchronous activity has been remarked upon by many authors for species such as siamangs (*Symphalangus syndactylus*) (Chivers, 1975) and titi monkeys (*Callicebus* spp.) (Robinson, 1979; Kinzey et al., 1977). Long-distance vocalizations may be performed as duets (e.g., lion tamarins, McLanahan and Green, 1977; some hylobatids, Marshall and Marshall, 1976; titi monkeys, Robinson, 1979; Kinzey et al., 1977), and scent-marking may be performed in alternation (or sequentially) at the same location (canids, Kleiman and Brady, 1978; Golani and Keller, 1975; Frame et al., 1979; marmosets and tamarins, Mack and Kleiman, 1979). Wolf howls, although performed by an entire family, are undoubtedly derived from the joint calling of the dominant breeding male and female of a pack.

Among species exhibiting facultative monogamy, pairs appear to carry out most maintenance activities alone and rarely perform together behavior patterns that promote spacing. This trend has already been noted for scent-marking in elephant shrews (Rathbun, 1976, 1979), agoutis (Smythe, 1978), and dik-diks (Hendrichs and Hendrichs, 1971).

C. Quality and quantity of parental care

1. Paternal investment:

A critical expectation already mentioned is that the males of species exhibiting facultative monogamy will exhibit less parental care than males of species exhibiting obligate monogamy, because the former are less assured of paternity as a result of their asocial tendencies. Unfortunately, it is difficult to compare species directly with respect to parental investment by both sexes because one must consider, for each type of behavior pattern, the time and energy output, the cost or risk to the parent (with respect to future reproduction) of such an activity, and the contribution to the survivorship of offspring by the behavior. Moreover, indirect forms of parental care, such as territorial defense, that contribute to survivorship of young must be considered in addition to direct forms of investment such as feeding young (Ralls, 1977). Finally, physical differences must be considered as some species cannot provide a form of parental care that is common in others. However, the time devoted to specific behavior patterns could be compared among species and the *relative* contribution by males and females to rearing young within each species can be roughly assessed. It is clear that an individual female mammal will assume a greater parental burden than a single male regardless of the species' reproductive strategy because female mammals both gestate young and feed them with milk until the time of weaning.

The total time in contact with young is a minimal measure of potential contribution to an infant's survival. Whether and how often young are fed (by males and females after weaning), played with, or carried are also important measures.

Changes in the degree of intolerance to strange conspecifics in both adult sexes when young are born may also indicate the degree to which a male or female becomes more territorial during reproduction. This may be an important measure of parental investment for facultative species.

I have already suggested that male parental investment is highest in obligate monogamy although the index used was somewhat arbitrary because of the sketchy data (Kleiman, 1977a). In species showing facultative monogamy, although the male's direct contribution appears low, total parental investment by males cannot easily be determined since indirect investment may be considerable. In facultative species, males expend considerable time and energy in patrolling the territory. Protectiveness towards the young has also been reported (e.g., in elephant shrews, Rathbun, 1979, and dik-diks, Simonetta, 1966). It is worth noticing that many of the species exhibiting facultative monogamy produce precocial young that are "hiders" during the early post-natal period. Thus, lack of close contact between the male and his offspring or direct paternal care is paralleled by reduced mother–young contact or maternal care.

The heavy parental investment by males in species exhibiting obligate monogamy has been documented in several species, e.g. marmosets and tamarins (Epple, 1975b; Hoage, 1977; Box, 1977b), dwarf mongooses (Rasa, 1977), and canids (van Lawick, 1971, 1973; Mech, 1970; Moehlman, 1979) and may be correlated with larger and/or heavier litters as well as more altricial young.

2. "Parental" investment by kin:

One of the basic differences between the two extreme forms of monogamy is that older juveniles may remain with the parents after weaning (and even puberty) in the obligate condition and aid in rearing the young of subsequent litters of their parents (Kleiman, 1977a). In facultative monogamy young tend to disperse prior to the next birth or at least avoid the parents after weaning (e.g., elephant shrews, Rathbun, 1979) if they remain on the parental territory. There are differences, however, within obligate monogamy in whether a nuclear or extended family is maintained. For example, among golden and black-backed jackals

(*Canis aureus, C. mesomelas*) (van Lawick, 1971; Moehlman, 1979), the helpers all appear to be offspring of the adult pair while among wolves (Mech, 1970), African wild dogs (van Lawick, 1971, 1973; Frame and Frame, 1976) and possibly marmosets and tamarins (Dawson, 1977), other kin may aid in rearing infants. Group size and composition seem to be positively correlated with the breeding female's reproductive success, both within and between species. Two mammalian families in which such predictions could be examined are the Canidae and Callitrichidae.

For direct parental investment by kin to be possible, several behavioral traits are required. First, parents must exhibit continued tolerance towards weaned young (or brothers and sisters) so that there is an opportunity for them to interact with infants, and second, the older juveniles (or other kin) must have a positive attraction for young. Third, reproductive activity in kin must be suppressed. For these behavioral traits to evolve, there must be clear benefits to both parents and relatives. These benefits have recently been discussed by Blaffer–Hrdy (1976), mainly for polygynous primates. The benefits to parents include increased reproductive success, i.e., survival of more offspring (this has been shown for the black-backed jackal by Moehlman, 1979). The helpers benefit by gaining experience in parental care, gaining protection and access to resources while remaining in the family, and helping in the survivorship of close relatives, which increases their inclusive fitness (Hamilton, 1964).

D. Ontogeny

1. Sequence of development:

The condition of neonates, e.g., altricial or precocial, and ontogenetic parameters were not found to be correlated with a monogamous reproductive strategy in any specific way (Kleiman, 1977a). However, Rathbun (1979) has suggested that facultative species that are cursorial as an anti-predator strategy tend to bear more precocial young. Correlated with this characteristic are rapid development, early weaning, and early puberty.

In species exhibiting obligate monogamy young may remain dependent on the parents long after nutritional weaning, which would be expected if young are to remain with the parents beyond a subsequent birth. Moreover, sociosexual maturity should be delayed in reproductive-age animals as long as they are in the presence of their parents. Delayed puberty or reproductive suppression have been reported for callitrichids (Epple, 1975), dwarf mongooses (Rasa, 1973a), and canids (Mech, 1970; Kleiman and Brady, 1978).

A comparison of the two extreme forms of monogamy with respect to aspects of behavioral development such as delayed puberty requires data on growth rates, earliest and typical age at first reproduction, reproductive cycle, litter size, and age at reproductive senility (i.e., total lifetime productivity). These data are not yet available for many species (but see Eisenberg, in press).

2. Mechanisms of dispersal:

A comparison of this behavioral characteristic in monogamous species is of major importance because a determination of when and why young leave their parents is essential to understanding how a nuclear or extended family can develop and persist.

Among species exhibiting facultative monogamy, it is expected that young will disperse after the development of social intolerance by the parents, when young begin to compete for essential resources. The young may be expected to remain on the parental territory as long as the parents tolerate them, despite a lack of parent-offspring contact. Among elephant shrews, parental aggression towards young and dispersal have been observed in *Elephantulus rufescens* but in *Rhynchocyon chrysopygus*, occasional young were tolerated on the parental territory without aggression for as long as seven months (Rathbun, 1979). In both species, young rarely interact with parents after a subsequent birth. Among agoutis, parental aggression to older offspring tends to be sex specific and exacerbated by food scarcity. Older juveniles appear to be chased out of the parental territory unless fruit is abundant (Smythe, 1978). Among dik-diks, Hendrichs and Hendrichs (1971) have also described parents chasing offspring from the territory. In all of the above species, the post-weaning period is one of the greatest periods of mortality—until juveniles and subadults gain access to their own territory.

In extreme obligate monogamy, parental aggression towards young should be rare as long as offspring (or other kin) "help" with rearing subsequent litters and do not threaten the reproductive dominance of the pair. However, as young mature and as the carrying capacity of the family group's home range is approached, conflicts should develop. The nature of the conflicts is likely to depend on the age and sex composition of the family group, and the result will depend on the available options for the non-reproductive kin. Offspring may often remain within the family group because helping to raise younger siblings increases their inclusive fitness and decreases their potential mortality. In general, however, I suggest that sibling conflict may be a greater promoter of dispersal than parent-offspring conflict since siblings not only increase their inclusive fitness by remaining but have the potential to achieve breeding status if a parent dies.

Clearly, conflict will be within each sex class, and heterosexual fighting should be rare. Conflict should also be more common within each age class, as at any given point the reproductive value of littermates is similar. Offspring should not challenge parents until parents approach reproductive senescence and their reproductive future is uncertain. The decision to remain with the family or disperse will depend on the degree of competition within the family balanced with other available options. Options will differ depending upon the overall population density and the degree of saturation of the habitat. Females should have more serious conflicts than males because they may be competing for "helpers" as well as mates.

There is already evidence that competition among same-sexed, same-aged siblings is high in obligate forms. In common marmosets, *Callithrix jacchus*, twin same-sexed siblings are reported to fight as juveniles (Sutcliffe, 1979; Rothe, 1979), while in lion tamarins, *Leontopithecus rosalia*, it has been noted that aggression within family groups often can be traced to sibling interactions (Kleiman, 1979), usually at the time of the mother's estrus. Conflict is more commonly expressed among twin or sibling males in *Leontopithecus*, although conflict between twin females is more serious and has resulted in fatal attacks on females with the mother strongly implicated in the deaths (Kleiman, 1979).

Captive studies may distort the nature of family conflict, depending on a researcher's measures of conflict. For example, among lion tamarins, conflict among males has been observed most frequently, both between father and sons and between siblings. Yet, the only deaths resulting from family conflict were of females. This suggests that real conflict is greater among females than males. Neyman's (1977) field study indicates that more females (*Saguinus oedipus*) than males are transient or leave groups, which supports the above suggestion.

Among wild dogs, sibling competition is also most severe among female littermates and results in an initial dispersal of females from the natal pack and a secondary dispersal of non-reproductive sisters when one female sibling in a group begins reproducing (Frame and Frame, 1977; Frame, et al., 1979).

SUMMARY

Evidence from mammals indicates that there are two extreme forms of monogamy in this class, with gradations based on the degree of sociality in a species. In facultative monogamy (dispersed social system), the pair bond is weak and polygyny may occasionally occur when opportunities arise. Mated pairs interact rarely and occasionally are antagonistic. Parental investment by males is mainly indirect, i.e., the male defends the essential resources of the home range from conspecifics. Development of young is rapid, and maturing juveniles leave the parental territory and reach reproductive maturity at a relatively early age. Although there is little sexual dimorphism in size, males and females exhibit sex role differences, with males exhibiting higher levels of intrasexual aggression and territorial behaviors. Parent-offspring conflict is mainly responsible for juvenile dispersal.

Within extreme obligate monogamy, sex role differences are smaller and in some species sex roles are almost reversed, especially with respect to intrasexual competition (females may be more aggressive than males) and territorial maintenance (females may be more active than males). In comparing facultative and obligate monogamy it appears that the lack of sexual dimorphism in size, a general characteristic of both types, is not a good indicator of the degree of sex role differentiation.

In obligate monogamy, males exhibit parental care, as do many juveniles and siblings of the breeding pair. Young remain dependent but also help their parents, often beyond the age of sexual maturity. The pair bond is strong and characterized by synchronous behavior of the pair members and the frequent display of affiliative behaviors such as mutual grooming. Sexual infidelity may be prevented by intrasexual aggression towards strangers but also by the reproductive inhibition of juveniles and siblings of the breeding pair, both behaviorally and physiologically. Dispersal of young may be initiated mainly through intrasexual sibling aggression.

Species exhibiting facultative monogamy were often thought to be solitary and polygynous in nature while obligate forms appeared to be social and polygynous. In both cases, the mating system has only become apparent after detailed field and laboratory studies. Clearly, a species' mating system cannot be deduced only from data on group size and composition.

The major force promoting monogamy in mammals is the inability of a male to defend groups of reproducing females. The group size and therefore type of monogamy in mammals depends on the interaction of several factors selecting for and against sociality. In some cases, obligate monogamy may have evolved from the need for increased paternal investment.

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