CHAPTER 14

THE SOCIOBIOLOGY OF CAPTIVE PROPAGATION

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For the captive propagation of an animal to be successful, one must take into account the species' spatial requirements, dietary specializations, environmental needs (temperature, light cycle, humidity), specific housing requirements and medical problems. This knowledge must be obtained from detailed studies in the natural habitat. Without it, a captive breeding program will proceed on a trial and error basis. Serendipity is at the root of some successful propagation programs, but many species which have particular but unknown requirements have been impossible to maintain or breed in captivity. Historically, they were referred to as "delicate." Improved field techniques (for example, radio telemetry) and a remarkable increase in the amount and quality of field research have provided clues about life history requirements which, in some cases, have made previously "delicate" species prolific breeders.

Knowledge of a species' social requirements has always been considered important for successful captive propagation. A superficial analysis of a species' social system, however, can be misleading and can result in serious errors when establishing captive colonies. For example, two species in nature might live in groups which have an identical age and sex composition, yet have entirely different mating and parental care systems as well as social organizations. Attempts to apply the same captive management techniques to both would probably result in the failure to maintain and propagate one of the species.

Moreover, just as species may differ in their ability to adapt to the absence of specific nutritional or housing requirements, there are unknown species-specific differences in the social lability of animals (for example, the degree to which an abnormal social environment can be accommodated without pathological consequences). Differences in the degree of social lability may have greatly influenced which species have his-

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torically thrived in captive conditions, where there has been ignorance about their social requirements.

Sociobiology has been defined by Wilson (1975) as "the systematic study of the biological basis of all social behavior." As such, it has its roots in modern evolutionary theory, ethology, physiological psychology, population genetics and ecology. The study of social behavior must, therefore, encompass knowledge of a species' phylogenetic history, ecology, life history parameters, population genetics and behavioral adaptations.

Studies of the behavior of captive animals have a long history, but have mainly contributed to the disciplines of ethology and physiological psychology. Because of small sample sizes and restricted conditions, behavioral research in zoological gardens has concentrated on the dynamics of social interactions, animal communication, the evolution of behavior and the analysis of the motivation and function of behavior. Thus, some of the major branches of study within sociobiology have not been explored in zoos. One of the major purposes of this chapter is to suggest not only how studies from other branches of sociobiology may benefit captive propagation programs, but to suggest how studies of captive animals—especially in zoos—may contribute more broadly to the field of sociobiology.

SOCIAL ORGANIZATION

Social organization is an umbrella term which encompasses a number of other characteristics, some—though not all—of which are independent of each other. Subsumed under the term social organization is the mating system of a species, be it monogamous, polygynous, polyandrous or promiscuous. Mating strategies must be differentiated according to whether a particular male-female relationship is constant over several reproductive efforts, or changes with each reproductive effort. For example, numerous bird species are serially monogamous, with partners changing each season, while others form long-term or even lifetime bonds.

Rearing strategy will also affect the ultimate social organization of a species. Most important are: (1) the degree of contact between the mother and young during rearing; (2) the degree to which females will rear young together; and (3) the degree of participation by the male or older nonreproducing offspring in parental care.

Group size is partly affected by mating and rearing strategies, but is also influenced by feeding habits, food distribution and the method of acquisition, shelter requirements, antipredator needs and phylogenetic constraints such as a species' size and mobility.

The successful establishment and maintenance of a species in captivity depends upon detailed knowledge of social organization. For example, the average group size, sex and age composition of a wolf pack *(Canis*

lupus) and a lion pride *(Panthera leo)* might be similar, yet the mating systems, parental care techniques and social organizations of these carnivores differ dramatically (Kleiman and Eisenberg, 1973). These differences will have a major effect on the development of captive breeding programs for these two species. Wolves are essentially monogamous; only the single founding pair will usually reproduce. The adult male and older offspring aid in rearing younger siblings, but the latter are themselves reproductively suppressed. Female wolves are as fiercely competitive as males (perhaps more so) and may have serious conflicts after puberty. Females as well as males are likely to disperse from the natal group (see Kleiman and Brady, 1978).

Several males and several females in a group of lions may reproduce. The males of a pride are typically brothers and must compete with other, unrelated males for control of a pride whose core is a group of related females and their offspring. There is, therefore, considerable turnover in the males from year to year. Young males disperse from the natal pride while females normally remain to reproduce within their natal group. Adult males do not participate in parental care (Schaller, 1972; Bertram, 1976).

In captivity, such differences may be expressed at several stages in the development of a breeding group. A wolf pack is best founded upon a single unrelated pair. A lion pride can probably be established immediately with a group of related, tolerant males and a group of related females. Maturing males and females within a wolf pack may develop conflicts with the father and mother, respectively, while such conflicts will develop mainly among males in lions. Among wolves, the onset of reproduction may result in fighting within each sex; this is rarer among lions. Several female lions can usually raise their litters cooperatively, while such an event is less likely in wolves. Each of these factors has relevance to captive management decisions.

Mating Strategy

Definitions of mating strategies are, to some degree, simplistic. As Jenni (1974) has pointed out, males and females may have different strategies within a single breeding system which may depend on the temporal organization of reproduction. Among mammals, if a female's period of estrous is short, and only one male at a time is likely to mate within a social group (for example Père David's deer, *Elaphurus davidianus* or Hamadryas baboon, *Papio hamadryas*), the female can be considered to be monogamous in her relationship with the male while the male is considered to be polygynous. If the major male breeder changes annually or

every two years, the female could be considered to be serially monogamous. Similar effects of temporal changes in the structure of a species breeding population make it clear that time must be included as part of any definition of a mating system.

The temporal organization of reproduction is important for captive colonies because of the potential genetic consequences. For example, Père David deer males compete for the position of harem master during the breeding season. During the rut, one male is likely to do a majority of the breeding, but other males may also reach the status of harem master when the dominant bull is fatigued. The top position is achieved by fighting among the males which can—and has—led to the death of captive individuals (Wemmer, 1977; Wemmer and Collins, in preparation). The same bull may achieve control of the harem in successive years, but eventually it cannot compete effectively with younger bulls reaching their prime. A management policy which isolates the majority of bulls from the harem during the rut and which allows only one or two males to copulate with the females, prevents intrasexual competition and thus does not permit the natural elimination of potentially unfit males. Although permitting mate selection to develop without excessive interference should be the goal of any long-term propagation program, the potential for mortality from fighting is great. Thus, curators and keepers usually decide which animals will breed.

The process of mate selection may not only result in fighting among males, but may be extremely disruptive to entire social groups. For example, in several langur species (*Presbytis* spp.) all-male groups may periodically take over established breeding units (Rudran, 1973; Sugiyama, 1965; Blaffer-Hrdy, 1977). The phenomenon has also been described for other colobine and cercopithecine monkeys (for example, Struhsaker, 1977), and it is likely to be found in other primate species that tend to live in age-graded male troops or one-male troops (Eisenberg et al., 1972). Takeovers are usually accompanied by great social upheaval and tension —including infant mortality—in part from infanticide by the invading male(s) (Rudran, 1973; Blaffer-Hrdy, 1977).

Rudran (1973) indicated that such takeovers may occur, on the average, every three years in the purple-faced langur, *Presbytis senex,* while Blaffer-Hrdy (1977) estimates that takeovers occurred as often as every 28 months in one population of *Presbytis entellus*. One of the effects of such takeovers is the prevention of inbreeding within a deme.

Clearly, it would be unacceptable to orchestrate such changes in captive colonies of colobines—that is, to permit groups of subadult and adult males to invade established breeding units. More appropriately, the adult male could be replaced with a different male every two to three years. Even such planned replacements, however, might result in juvenile and infant deaths due to aggression from the introduced male; zoological parks should perhaps expect an increased juvenile mortality at such peri-

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ods or decide to delay the introduction of a new male and thus forgo reproduction until most infants and juveniles in a group are weaned. In either case, a management plan for species with this reproductive strategy must include the expectation that there may be no infant cohort every third or fourth year when males are exchanged.

Interestingly, there are reported (via the zoo grapevine) cases among some captive primates of males and other group members killing infants. Documentation of the events surrounding such deaths, including the names of the species in which infanticide has occurred, might aid captive management and contribute to our understanding of the function and evolution of infanticide in wild primate populations.

Although it may be possible to artificially limit intrasexual competition and still achieve the outcrossing benefits of this process by manipulating individuals or groups, some species or individuals may not reproduce adequately without competition. Among the males of some mammals there is a complex feedback system regulating androgen levels through social behavior—for example, the rhesus monkey, *Macaca mulatta* (Rose et al., 1975). This system may affect the strength of the male libido. The performance of socially dominant behaviors (for example, threats and fighting) and the experience of winning aggressive encounters may be essential to achieve hormonal levels adequate for the performance of sexual behavior. The absence of competition may depress male libido sufficiently to inhibit reproduction.

Females may be similarly affected; the absence of male-male competition, for example, could result in somewhat lower androgen levels in a male which in turn could depress female reproductive function. Such a phenomenon could simply be an extension of the "Whitten" effect in which female mice housed in groups without a male exhibit irregular or no reproductive cycle until exposed to a mature male or his odor (Whitten and Bronson, 1970). Thus, a female's estrous cycle may be irregular or depressed in the presence of a male whose urine or other glandular secretions indicate low androgen levels.

Most zoos have experienced situations where a single pair has not reproduced despite every effort to provide adequate housing, diet and other environmental needs. Currently, at the U. S. National Zoological Park there is a single pair of lowland gorilla *(Gorilla gorilla)* and a pair of Indian rhinocerus *(Rhinocerus unicornis)* whose lack of reproduction may be attributable to the absence of male-male competition. In both species there was a single successful reproductive effort followed by a depression of the female estrous cycle and relative disinterest on the part of the male.

The successful propagation of monogamous mammals has posed a

problem for most zoological institutions. First, this mating strategy has been difficult to recognize in the field since monogamous species can exhibit a group size varying from one to 15 individuals, as shown in Figure 1 (Kleiman, 1977; in press, *a*). For example, elephant shrews *(Elephantulus rufescens)* tend to be solitary (G. B. Rathbun, in press) while hunting dog packs *(Lycaon pictus)* are extremely large due to the presence of subadult and adult "helpers" and a normal litter size averaging six to seven (occasionally reaching 15 pups) (Kleiman and Eisenberg, 1973). Both species were originally assumed to be polygamous until detailed field studies revealed the true mating system *(Lycaon:* Kühme, 1965; van Lawick, 1973; Frame et al., in press; *Elephantulus:* G. B. Rathbun, in press).

To propagate monogamous species one must accept the fact that no more than one female will usually breed in a group. Thus, several pairs or family groups should be maintained to ensure that reproduction is not halted with the death of a breeding male or female. This requires extra cage space and keeper efforts as well as attention to appropriate group size, age and sex structure.

Reproduction in monogamous mammals can be negatively affected by problems of mate selection and intrasexual competition. Although one can usually expect a successful mating when a pair is newly established, occasional pairs are incompatible. For example, in rufous elephant shrews, females are typically dominant over males (G. B. Rathbun, in press). In captivity, pairs with reversed dominance status will rarely reproduce successfully (G. B. Rathbun, personal communication). In the absence of detailed observations of pair interactions, failure of reproduction can only be ascertained five to six months after the initial pairing. Even with a successful breeding pair a time lag may occur before the first pregnancy.

With some species, it may be possible to encourage mate selection by permitting one individual to choose between two potential mates. How-


SOLITARY   PAIR OR   NUCLEAR FAMILY   EXTENDED
                  TEMPORARY FAMILY   FAMILY
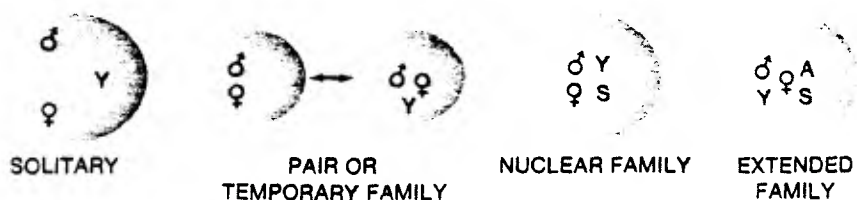
FIGURE 1. Group size and structure in some monogamous mammals. The circles represent joint territory. The placement of the symbols for the breeding male (♂), breeding female (♀), immature offspring (Y), subadult offspring (S) and related adults (A) within a circle indicate the distances between individuals. In the "pair" condition, young may only be with the parents temporarily, until dispersal. There may be more than one Y, S, and A, thus leading to group sizes of 10 to 15 individuals.

FIGURE 2. The monogamous golden lion tamarin *(Leontopithecus rosalia)* is an endangered primate from the southeastern coastal rain forests of Brazil. Males and other relatives aid in parental care by helping to carry young. (Photo by National Zoological Park)

ever, this can only be accomplished where adults of the same sex can be housed together without serious fighting. Among lion tamarins *(Leontopithecus rosalia)*, an endangered primate species from the southeastern coastal rain forests of Brazil, this is more easily accomplished with males (Figure 2). In a study designed to examine the process of mate selection, I housed adult or young adult females with two males. Of ten such trios, only one had to be dissolved due to overt aggression between the males (Figure 3, Trio G). Yet, in the majority of trios only one of the males exhibited sexual behavior (Figure 3). Sexual behavior by the sexu-
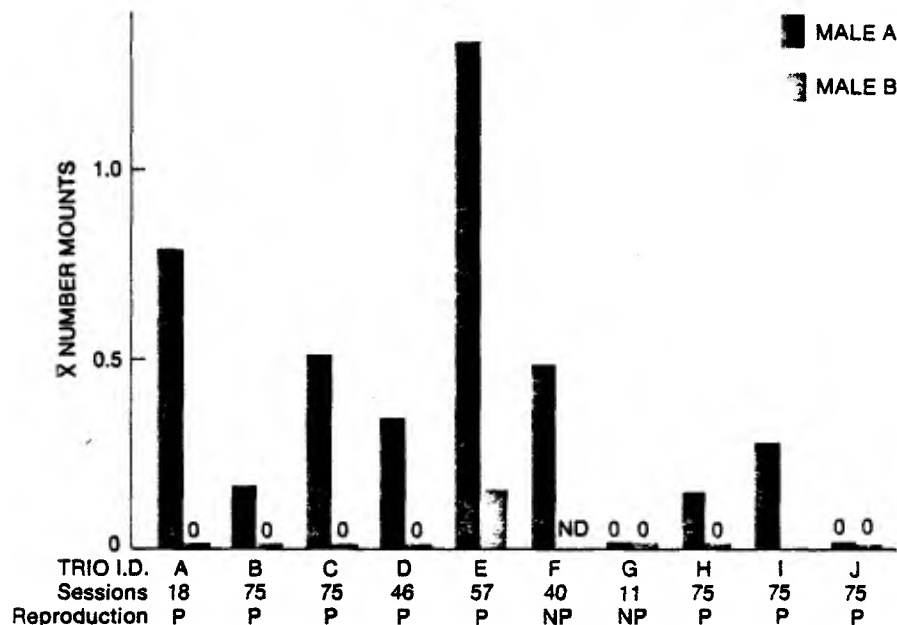
FIGURE 3. The mounting frequency of each male in ten trios of lion tamarins composed of two males and one female. NP : no pregnancy; P : pregnancy occurred during the observations; Sessions refers to the number of half-hour observation periods; ND : no data available.

ally inactive males in Trios E and I often consisted of mounting without pelvic thrusting; thus copulation was certainly not successful. In Trio G, which was dissolved, the female became pregnant by male A soon after observations terminated. In Trio J, male A was known to have impregnated the female soon after the trio was established even though no mounting was observed during formal observations.

There were several other interesting results of this study. First, overt signs of dominance were rarely seen between the males; the sexually inactive male was not isolated from the pair. Indeed, the trio rested and slept as a group. Second, there was only minimal evidence that the female deliberately chose one of the males. Figure 4 details the grooming interactions of the female and males in the ten trios. In the majority of cases, the sexually active male groomed the female significantly more than did the sexually inactive male. In three of the four exceptions, the female was related to the sexually inactive male (sister, Trios H and F; mother, Trio J) and had been living with him and other family members prior to the establishment of the trio. In only four trios did the females preferentially groom the male with whom they mated; in two of these four trios, the female was the sister of the sexually inactive male. Thus, female prefer-

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ence may be more strongly exhibited when a female is choosing between a relative and nonrelative.

The lack of overt male competition and of clear-cut female choice makes some sense in the context of the tamarin social organization. Family groups may include subadult and, perhaps, adult offspring. These and perhaps other relatives aid in the rearing of offspring by carrying infants and feeding weanlings. It is to the advantage of the breeding pair to be tolerant of relatives as long as they do not challenge reproductive dominance since helpers may increase the survivorship of the reproductive pair's offspring. Thus, nonbreeding subadults and adults can be integrated into family activities without aggression from the dominant reproductive pair.
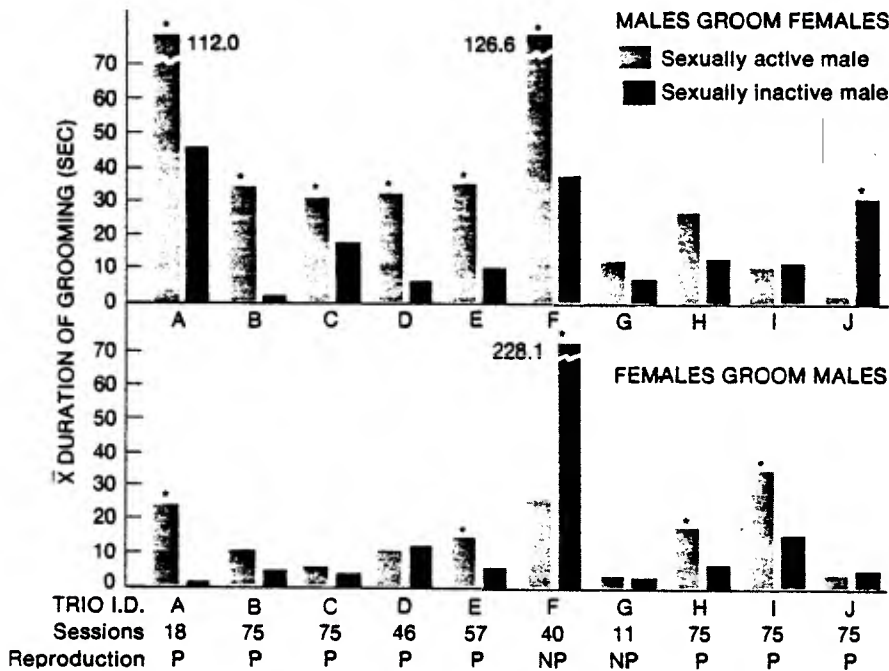
FIGURE 4. Grooming interactions in ten trios of lion tamarins. NP: no pregnancy; P: pregnancy occurred during the observations; Sessions refers to the number of half-hour observation periods. An asterisk indicates a significant difference between the two males of a trio, both in those grooming females and in those being groomed (Wilcoxon Matched Pairs Signed Ranks Test).

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In some monogamous mammals intrasexual competition may be more intense among females than males (Kleiman, in press,a). The competition may be expressed in a conventional manner (by fighting, for example) but differential reproductive success can occur without overt agonistic behavior, thus maintaining the reproductive superiority of a single female. A review of the methods a female uses to maintain reproductive dominance may indicate how subtle some of the mechanisms are (Figure 5).
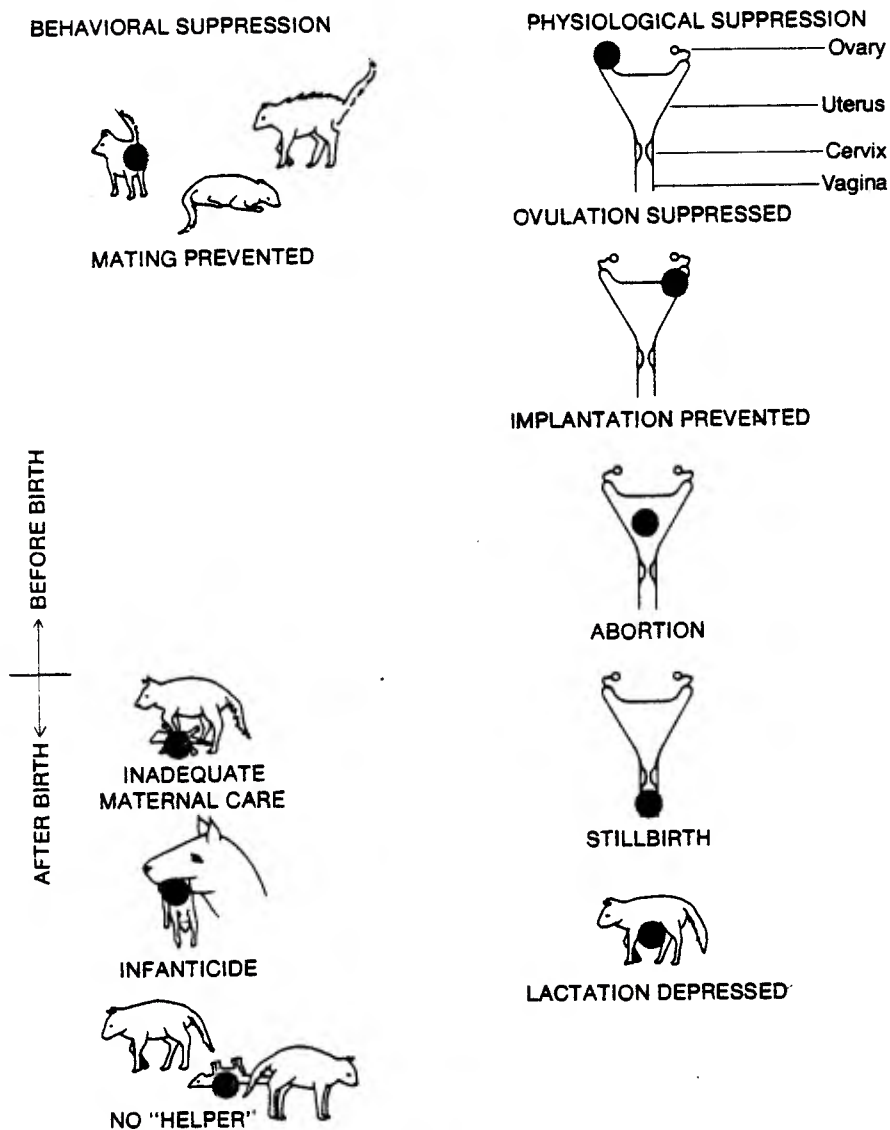
Among common marmosets *(Callithrix jacchus),* only one adult female in a group will exhibit a normal reproductive cycle. In families or artificial groups, the estrous cycles of all females except the dominant one will be suppressed (Hearn, 1977; Lunn, 1978). Among timber wolves *(Canis lupus)* the dominant female may prevent a subdominant female from copulating through overt threats and attacks, which disrupts mating attempts (Rabb et al., 1967). Should a subdominant female of a monogamous species become pregnant, the stress of living with a dominant female can cause abortion and stillbirths. I have noted this form of reproductive inhibition several times in the green acouchi *(Myoprocta pratti).*

Lastly, although subdominants may mate successfully, become pregnant and give birth, the survival of their offspring may be jeopardized by the dominant female. For both wolves and hunting dogs, there are reported cases where dominant females either killed the offspring of a second female or were sufficiently disruptive of the mother-young interaction that the infants died of neglect, starvation or harassment (Altmann, 1974; van Lawick, 1973).

The effect of the dominant female's presence may be subtle, and differential reproductive success may only be noticeable after several reproductive efforts. Dik-diks *(Madoqua kirki)* can be maintained in trios (or even groups) containing several reproductive-age females, all of whom may breed, even though they are monogamous in nature (Hendrichs and Hendrichs, 1972).

At the U.S. National Zoological Park, the death of pre-pubertal juveniles was often attributed to many causes, including severe weather. No one considered that offspring of subdominant females may be under greater stress and therefore more prone to a variety of illnesses. Because of difficulties in identifying the offspring of different females, we cannot say with certainty that mortality was greater in the young of subdominant females. Yet, this is certainly a factor which must be examined in the future.

To summarize, in monogamous species (as well as with other mating strategies) adult females housed with dominant females may be reproductively suppressed by a variety of mechanisms, including estrous cycle disruption or inhibition, mating prevention, pregnancy interference or disruption and mortality of offspring at several postnatal stages. Re-

BEHAVIORAL SUPPRESSION

PHYSIOLOGICAL SUPPRESSION

Ovary

Uterus

Cervix

Vagina

OVULATION SUPPRESSED

MATING PREVENTED

IMPLANTATION PREVENTED

BEFORE BIRTH

AFTER BIRTH

ABORTION

INADEQUATE
MATERNAL CARE

STILLBIRTH

INFANTICIDE

LACTATION DEPRESSED

NO "HELPER"

FIGURE 5. Behavioral and physiological mechanisms involved in the reproductive suppression of subordinate females in mammalian species exhibiting monogamy. Species differ in terms of which mechanisms are most common. Reproductive suppression is also seen in mammals exhibiting other mating systems.

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productive suppression may occur not only as a result of direct action by the dominant female, but also through the subtle effects of her presence. These effects can cause stress in the subdominant female, negatively affecting pregnancy and lactation, or cause stress in her offspring, thereby increasing their susceptibility to disease and decreasing their likelihood of survivorship.

There appear to be species-specific tendencies in the use of different methods of reproductive inhibition among the females of both polygynous and monogamous mammals (Eisenberg, 1967). The study of these differences could be of enormous benefit in defining species limitations, and, thus, in improving the management of mammals in captivity. Such studies must carefully consider the degree to which reproductive suppression may be mediated by the olfactory sense alone. For example, there may be some species in which olfactory contact with reproductively dominant neighbors may be enough to inhibit reproduction in an otherwise adequate pair. This has been suggested for some species of marmosets and tamarins, although it has never been adequately proven. Olfactory control of reproductive processes has recently been reviewed by Doty (1976).

A consideration of mating strategies must include the degree to which inbreeding occurs in each species in nature. In many mammals, father-daughter and mother-son crosses may be prevented by: (1) dispersal of young at puberty or (2) the disappearance, death or reproductive senility of parents before the sexual maturity of offspring. In zoos, such natural phenomena are often prevented by management constraints, yet there are occasional examples. This indicates that there is a suppression of mating in closely related individuals. For example, in a wolf pack derived from a single litter—established in 1963 or 1964 at the London Zoo—there were no pregnancies until 1973, and no young survived from the first two litters (Olney, 1975; 1976). The females would come into heat annually, but no successful copulations occurred, despite the pack being organized into the typical male and female hierarchies (Kleiman, unpublished observations, 1964–1969).

In three trios of lion tamarins *(Leontopithecus rosalia)* in which the female was related (either sister or mother) to one of two males, mating occurred only with the unrelated male, even though the related males were all sexually mature (Figure 3; Kleiman, 1978). Mainardi (1963 *a; b; c*) has shown that young female mice prefer to mate with unfamiliar individuals rather than conspecifics with whom they were raised. This suggests the existence of a behavioral mechanism for suppressing inbreeding. Clearly, the strength of such inhibitions will vary across species and may even be overcome in the absence of an appropriate partner. But the effects of such inhibitions may be felt in captive propagation programs when unrelated individuals are not available for breeding. In any case, inbreeding should be avoided if at all possible (Chapters 8, 9 and 12).

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Group Size and Structure

Knowledge of a species' mating strategy permits sensible decisions about the optimum sex ratio to be maintained in captivity, but does not always provide enough information on the spatial or social needs of a species. For example, although talapoin monkeys *(Miopithecus talapoin)* are polygamous, males and females tend to segregate into sex-specific subgroups; reproduction is poor when the sexes are forced into close contact with each other. Females become extremely aggressive and males may die from the frequent harassment (Rowell, 1973). Talapoins may, therefore, have to be separated by sex except during mating if enclosure sizes are inadequate.

Among monogamous mammals, as already indicated (Figure 1), group size differs from species to species. Management plans must, therefore, take into account such factors as whether a family group can remain socially stable. For example, the captive reproduction of elephant shrews is most successful when weaned offspring are removed from the parents prior to subsequent births; this would be unnecessary and even undesirable in wolves or African wild dogs. In some cases, the need for isolation of the breeding male, female or the pair is not obvious, except for the absence of successful reproduction. Both the cheetah *(Acinonyx jubatus)* and the red panda *(Ailurus fulgens)* can be maintained in groups in captivity without apparent aggression. However, reproduction in cheetahs is most successful when the female is isolated except during the mating period; red panda females reproduce best when either isolated or housed with a single male.

Although there is some information concerning which species need to be isolated—as individuals or pairs—for successful reproduction, less is known about which species need a minimum group size in order to breed. For example, many bat species normally reproduce in large colonies. In two small groups of the long-tongued bat *(Glossophaga soricina)* where only a single female was present, reproduction was poor. In the related short-tailed leaf-nosed bat *(Carollia perspicillata)* two different colonies with 10 to 20 females reproduced successfully under the same environmental conditions. In a small group of *Carollia* (with only three to four females), however, reproduction was erratic (Kleiman, unpublished).

The need for a minimum number of females may have several bases. In some bat species, colonial roosting may act as a heat conservation mechanism. This is especially true for the temperate zone verspertilionids, but may also apply to tropical bats. The duration of pregnancy is known to be affected by temperature in *Pipistrellus pipistrellus* (Racey, 1973), but lactation and the growth of young may also be affected. By

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living in a nursery colony, females and their young may more easily maintain an optimum temperature at a low energy cost.

Anti-predator strategies may be responsible for the females of some species reproducing in large groups. Often this is accompanied by reproductive synchrony. For example, wildebeest *(Connochaetes taurinus)* give birth synchronously in East Africa; it has been shown that this is an adaptation that floods predators with potential prey (wildebeest infants), thus reducing overall infant mortality (Estes, 1976). Although there are no data to indicate that the reproduction of captive wildebeest is reduced without a minimum number of females, there may be certain species in which the evolution of reproductive synchrony as an anti-predator strategy has proceeded to the point where a large female group is essential for adequate reproduction.

Rearing Strategies

The survivorship of offspring may be affected when the rearing strategy of a species is not carefully considered. The females of many mammals rear young cooperatively or communally. The degree to which the isolation of a lactating female influences the development of offspring has not been carefully documented. For example, the young of many species of colobine monkeys are transferred to "aunts" soon after birth (Blaffer-Hrdy, 1976; Horwich and Manski, 1975) and therefore spend limited time with the mother. It is not known whether the mother is simply tolerant of other animals' involvement with her offspring or whether this rearing strategy is so highly specialized that young born to a single isolated female in captivity will have a reduced chance of survival. Data are simply not available to indicate whether there is higher infant mortality in captivity in species like elephants, dolphins and colobine monkeys where "aunts" are an integral part of the rearing system.

A similar problem exists for species where males and juvenile "helpers" aid in rearing the young. Jantschke (1973) documented the importance of the presence of the father for the successful rearing of young by a female bush dog *(Speothos venaticus)*. Undoubtedly, in other monogamous exotic species similar effects will be seen. Dudley (1974) elegantly showed that male *Peromyscus californicus parasiticus* contribute to pup survivorship by keeping the litters warm while the female is absent. However, males may provide other aid, such as feeding weanlings, providing protection from predation or transporting young (Kleiman, 1977).

In lion tamarins, the adult male carries and shares food with the young and aids in their socialization (Hoage, 1977; 1978; Figure 2). Lion tamarins may have one to three young. An analysis of the number of days after birth when the father begins to carry the most recent offspring suggests that fathers exhibit paternal care earlier when the litters are large (Table I). Thus, the timing and degree of parental care by fathers and

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TABLE I. The average number of days after birth when the father begins to carry offspring from different size litters in lion tamarins (*Leontopithecus rosalia*).

	Litter size		
	1	**2**	**3**
Mean	14.2 days	8.6 days	3 days
Range	12–17 days	5–11 days	–
Number of litters	6	9	1

Data are from four females.

other relatives may be dependent on the needs of the mother at any given time.

In many mammals, females rear their young isolated from conspecifics. Forced contact or close confinemment have been shown to reduce infant survivorship in certain species. Martin (1968; 1975) first discovered that a female tree shrew *(Tupaia belangeri)* housed with a single male needed a separate nest box for the young. Tree shrews exhibit an "absentee" parental care system (Eisenberg, 1977); young are cannibalized if the female is forced to nest with them and the male. Similarly, reproduction in red pandas *(Ailurus fulgens)* is nearly always unsuccessful when two or more females are housed together. Although the females become pregnant, the young are inevitably ignored or destroyed. The mating strategy of red pandas is not known, but such findings suggest that red pandas may be monogamous in nature.

THE PROBLEM OF DISPERSAL

One of the least considered problems in the successful maintenance of captive populations is how and when to dispose of adults and offspring while still maintaining an optimal age and sex structure and not disrupting the social dynamics of a group. Little is known about the life history of groups in the wild (their formation, maintenance and dissolution) although such factors may be extremely important in understanding population regulation in a species (Eisenberg et al., 1972).

Field studies on a variety of mammals have recently been concentrating more closely on the long-term changes in groups of known composition, and information on group life histories is beginning to appear. Already such studies have shown that methods of dispersal differ from species to species and may not be entirely predictable from social organization or mating strategy. Moreover, Bekoff (1977) has recently sug-

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gested that individuals of the same species may be behaviorally polymorphic with respect to dispersal strategies. He cites observations of individual differences in coyote litters *(Canis latrans)* which result in both the most dominant and most subordinate littermates being least interactive with siblings. Bekoff suggests that these noninteractive individuals may be most likely to disperse from the natal group even though the reasons for their isolation from littermates are entirely different.

Some recent observations of lion tamarins indicate how difficult it is to predict which animals are likely to disperse (and which, therefore, should be removed from a family group). Adolescent lion tamarin males begin exhibiting signs of sexual maturity, such as scent marking (Kleiman and Mack, in press) and arch displaying (C. D. Rathbun, in press) while still in the family group. By contrast, females do not exhibit signs of sexual maturity until they are removed from the parents and paired with an unrelated male; thus they are socially and reproductively inhibited. However, in both sexes dominance relations are established and can be identified among siblings of the same sex. Dominance relations among sibling males occasionally include fights which result in scratches and minor wounds. The young dominant male may pursue the mother while in heat as well as scent-mark and arch display more than the father, yet still be tolerated by the parents with only minor squabbles.

By contrast, in two family groups a dominant sister was killed; in both cases the mother was strongly implicated in the death. Interestingly, the attacked females were not even sexually mature (both were about a year of age) and both females either had a twin sister or were in a family group where there were several other female offspring. Among young dominant males, there have never been any deaths. A casual observer of a family group might recommend the removal of pubertal males due to their greater sociosexual activity. However, it appears that females are at greater risk and at an earlier age. Presumably, such females would disperse from the family group before being killed. Thus, in this species strife among males seems to be less damaging in the long run and is resolved overtly through squabbles without serious damage.

THE EFFECTS OF CAPTIVITY ON BEHAVIOR

Studies of captive animals or attempts to extrapolate from the behavior of captive animals to the behavior of wild animals (or the reverse) must take into account the long- and short-term effects of captivity on behavior. Right from the initial choice of which animals to bring into captivity, human selection is applied to maintaining and breeding individuals with certain behavioral phenotypes (for example, tractability and tameness). Individuals which exhibit either extreme fear or extreme aggression towards humans are usually weeded out of a breeding pool be-

cause they are difficult to manage. Such human selection may be unconscious.

Regardless of human selection, behavioral types such as easily stressed individuals may not reproduce successfully; thus their contribution to the gene pool will be lost. This may alter the behavioral genotype of the captive population, decreasing the tendency to avoid humans or other predators.

Genotypes which would not survive in nature may be maintained in captivity. Hand-rearing rejected or weak young retains genes in the captive population which might have been eliminated in the wild. A classic case of this is the inbreeding of partially albinistic tigers *(Panthera tigris)* at several zoos. It is not known whether this rare mutant has peculiar behavioral characteristics associated with it, although highly inbred individuals do exhibit abnormalities of the visual system (Guillery and Kaas, 1973).

The behavior of captive animals may be altered permanently by having young reared in inappropriate social or environmental conditions. Hand-rearing often prevents individuals from later forming adequate social attachments. Goldfoot (1977) recently reported that the greater the degree of social deprivation in hand-reared rhesus monkeys *(Macaca mulatta)* during development, the lower the eventual reproductive success. Similar correlations between other complex adult behaviors and deprivation during development have been reported. Predators learn to immobilize and kill prey slowly with the aid of parents and other relatives. Such experience cannot be duplicated once an animal becomes an adult nor can such an "untrained" individual properly "teach" its own offspring. The success of such techniques as artificial insemination and hand-rearing have the potential of increasing the population size of a captive species, but at the expense of the normal behavioral repertoire. With increasing dependence on artificial means of reproduction, it is possible to maintain a captive species in which individuals can neither mate properly, nor rear their young.

A final factor which influences the captive behavior of species is human interference in the normal patterns of mate selection and dispersal of adults or young. Arbitrary decisions based on management considerations may significantly affect the gene pool and result in altered behavioral genotypes.

There are a variety of factors which have long- and short-term effects on the behavioral phenotype of individuals. Some are irreversible. Behavioral alterations may not only be acceptable, but desirable for populations of species which are to be retained in captivity in perpetuity.

However, zoos are breeding certain species with the expressed intent of eventually returning them to the wild. In these cases the unconscious damage to the gene pool and behavior of the captive population may prevent a successful reintroduction. Efforts at the reintroduction of species have been few and of limited success for the most part. Brambell (1977) details some of the considerations which must go into such an effort (see also Chapters 11 and 15).

SUMMARY

Inadequate consideration of mating and rearing systems and of the dispersal of adults and young from breeding groups can negatively affect reproduction in captivity (Eisenberg, 1967). Unfortunately, it is extremely difficult to pinpoint the reasons for a lack of reproduction in a species, especially if the characteristics of the species' life history are poorly understood. Zoos rarely publish an analysis of a propagation program that failed, as a pathologist would publish the results of an autopsy. Zoos do not like to discuss their failures. However, lack of publication is often due to small sample sizes or to the anecdotal nature of the observations. One can never be sure whether a finding from a single individual or group in captivity is representative of a species or idiosyncratic. For example, there may be numerous cases of infanticide in zoo primates which are directly comparable to similar events in the wild. Yet, it would be extremely difficult to locate details in zoo records which might be relevant to our understanding of this phenomenon—such as the age and sex structure of the group and social changes which occurred prior to the infanticide. Moreover, to determine in which primate species infanticide is most likely to occur would require comparative data detailing the prevailing social conditions when infanticide did not occur. Such an analysis could be done, but only with great effort.

Interestingly, a captive propagation program which is a failure may contribute more to sociobiological theory or knowledge than one which is a success. For example, behavioral mechanisms which decrease the likelihood of inbreeding could be analyzed more easily in a zoological park setting. A study of the life history characteristics of species in which mating between close relatives is inhibited could provide comparative information which would be valuable for our understanding of how inbreeding is prevented.

Current knowledge of the mating and rearing strategies of the monogamous marmosets and tamarins is derived from numerous failures to successfully propagate these primates. Zoos and other institutions had attempted to maintain them in artificial groups of unrelated individuals, only to find that no more than a single female would reproduce. Moreover, young which were removed from the parents after weaning, but before a subsequent birth, exhibited improper parental care once they

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themselves reproduced; the young lacked as juveniles the infant care experience which is essential for adequate parental care in adulthood (Hoage, 1977; 1978).

Captive studies can contribute to sociobiology in other ways. Longitudinal studies of species in zoos can provide important information on the social dynamics of groups over several generations. Such an approach has been followed in captive wolf studies (Rabb et al., 1967), and recently with Père David's deer (Wemmer and Collins, in preparation).

Unfortunately, such studies are rarely conducted in zoos because a commitment of a decade or more is required, especially with longer-lived species. However, some of the most important problems in sociobiology relate to the interactions of kin and the degree to which the genetic relationships of individuals affect social behavior. And such problems can effectively be examined in zoo populations.

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