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Sexual Behavior of Maternally Separated Gibbons (*Hylobates*)

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ABSTRACT: The effect of early maternal separation on the sexual behavior of captive gibbons was investigated because (a) maternal separation compromises sexual behavior of some nonhuman primates and (b) adequate sexual behavior is essential to species propagation. Most of the maternally separated gibbons (24/31) were sexually proficient. Sexual behavior overall did not differ significantly in relation to species, sex, origin (wild- vs. captive-born), or type of rearing facility (home vs. zoo). Sexual proficiency was not related to the age at separation from the mother, but it was associated with introduction within 19 months of age to a conspecific of less than 3 years of age and an absolute age difference of less than 2 years. Sexual proficiency was associated with rearing and adult housing in relatively large enclosures. Gibbons that were isolated from conspecifics between 6 months and 2 years of age were strongly attached to humans, but this did not prevent sexual proficiency. A greater proportion of males than females were adversely affected sexually by prolonged early social isolation. Inadequate sexual behavior was associated with fearfulness of conspecifics, which probably interfered with compatible social relationships, including duetting. Inadequate sexual behavior was but one aspect of a more general behavioral deficiency resulting from inadequate early socialization. Early maternal separation in gibbons is compatible with species-typical sexual behavior under the conditions described above. It is not necessary for gibbons to learn sexual and parental behavior by observing experienced adult conspecifics. © 1997 John Wiley & Sons, Inc. *Dev Psychobiol* 31: 149–161, 1997

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INTRODUCTION

Gibbons (*Hylobates*) are generally recognized as belonging to a single genus that contains four subgenera (Marshall & Sugardjito, 1986; Prouty, Buchanan, Pollitzer, & Mootnick, 1983a, 1983b) and

11 species (Geissmann, 1994; Groves, 1993; Mootnick & Sheeran, 1996). All *Hylobates* spp. are endangered (Brockelman & Chivers, 1984; Eudey, 1987) and some are close to extinction, e.g., the moloch gibbon (*H. moloch*) (Kappeler, 1984), Kloss' gibbon (*H. klossii*) (Whitten, 1980), and the Hainan crested gibbon (*H. concolor hainanus*) (Zhang, 1992). For these reasons, it is important to the survival of these species that captive individuals reproduce. A census of captive gibbons re-

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vealed that a considerable number were separated from their mothers at an early age by a variety of techniques due to incompetent mothers or abusive fathers, medical problems, or because zoo personnel were unable to confirm that the infant was suckling (Mootnick, 1984). Very little is known about the sexual competence of such maternally separated gibbons, but sexual behavior of several other nonhuman primates is often compromised by early separation from the mother (e.g., chimpanzees (*Pan troglodytes*), Fritz & Fritz, 1985; King & Mellen, 1994; Riesen, 1971; Rogers & Davenport, 1969; lowland gorillas (*Gorilla*), Beck & Power, 1988; Gold, 1986; Meder, 1995; Nadler, 1984; macaques (*Macaca* spp.), Deutsch & Larson, 1974; Missakian, 1969; Ruppenthal & Sackett, 1974; see Capitanio, 1986, for a comprehensive review of the primate data). Only one preliminary report has been published regarding a pair of maternally separated gibbons that produced an offspring (Poglayen-Neuwall, 1977). The present study for the first time evaluated the influence of rearing procedures on the sexual and social behavior of 31 maternally separated gibbons housed under various types of captive conditions over the past 19 years.

Studies on the other nonhuman primates, cited above (see Capitanio, 1986), suggested a number of hypotheses to be tested. It was hypothesized that the sexual competence of the maternally separated gibbons would be, H_1 : greater for females than for males, H_2 : greater for those maintained in relatively large cages, both H_{2a} : during rearing and H_{2b} : in adulthood, H_3 : directly related to the age at which they were separated from their mothers, H_4 : inversely related to the age at which they were introduced to another conspecific following separation from the mother, H_5 : greater for those introduced to older, female partners, H_6 : less for those with strong human attachments, and that H_7 : inadequate sexual behavior would be just one aspect of a more general syndrome of aberrant behavior and deficient social and parental behavior resulting from inadequate early socialization.

METHOD

Subjects

Data were collected between 1976 and 1994 on 31 maternally separated gibbons from 21 zoos, three research facilities, and 19 private individuals in North America and Scotland, including the Inter-

national Center for Gibbon Studies (ICGS) (Santa Clarita, CA) (Some animals were housed at more than one facility during development.) The ages of wild-born gibbons were estimated from body weight and size, skin color, pelage, and tooth eruption by comparison with normative data obtained at the ICGS. All species of gibbon were included in the survey except the black crested gibbon (*H. concolor*) and Kloss' gibbon (*H. klossii*).

The data were obtained by a questionnaire which included all the items described below. Responses to the questionnaire were obtained by telephone and written correspondence from the relevant individuals, examination of observation records, and personal observation of 11 gibbons at the ICGS.

Questionnaire

Questions (Self-Explanatory). (1) Species of gibbons, (2) sex, (3) origin (wild-born, captive-born), (4) type of rearing facility (private home, zoo), (5) age at separation from the mother, (6) age at time of first introduction to a conspecific, (7) age and sex of the conspecific to whom the subject animal was introduced, (8) other animals (nongibbons) interacted with the subject animal during rearing (yes, no), (9) the extent of human contact and sex of the primary human caretaker during rearing (continuous, infrequent), (10) enclosure size during rearing and (11) during adulthood [large, small (see below)], (12) conspecific contact within the first 6 months of life (yes, no), (13) between 6 months and 2 years (yes, no), (14) between 2 years and 3 years (yes, no), (15) sex of conspecific partners during rearing (male, female), (16) socially attached to humans (yes, no), (17) competent sexual behavior (yes, no), (18) competent parent (yes, no), (19) aggressive toward conspecifics (yes, no), (20) fearful of conspecifics (yes, no), (21) duetted with partner (yes, no), (22) aberrant behavior (yes, no), (23) number of oppositely sexed, sexually proficient adult conspecific partners, (24) number of socially compatible, oppositely sexed, sexually proficient adult conspecific partners, (25) number of years with an oppositely sexed, sexually proficient adult conspecific, and (26) number of pregnancies (females) or impregnations (males). Detailed answers were obtained in addition to the dichotomous ones (see definitions).

Definitions

Maternally separated—Separated from the mother within the first 1.5 years of age.

Enclosure size—Enclosure size, measured in terms of the age-graded arm span of gibbons, was defined in terms of the requirements for brachiation and socialization reflected in the literature (Brockelman, 1984; Carpenter, 1940; Ellefson, 1974; Fleagle, 1974) and in the experience of the first author. The minimal requirements for a large, adequate enclosure was defined as one that permitted approximately four brachiations (six arm-spans) in one horizontal direction and access to at least two vertical levels. In the case of 2 animals, an increase in width of one arm-span was required for unrestricted brachiation and compatible socialization.

Large (adequate) enclosure for 1 gibbon— $2 \times 6 \times 3$ arm-spans high.

Small (inadequate) enclosure for 1 gibbon—less than $2 \times 6 \times 3$ arm-spans high.

Large (adequate) enclosure for 2 gibbons— $3 \times 6 \times 3$ arm-spans high.

Small (inadequate) enclosure for 2 gibbons—less than $3 \times 6 \times 3$ arm-spans high.

Proficient sexual behavior—Copulated with an oppositely sexed conspecific under captive conditions.

Inadequate sexual behavior—Never copulated with an oppositely sexed conspecific despite having the opportunity, though may have displayed sexual behavior toward a human.

Socially attached to human—Solicited and maintained close physical contact (immature gibbons), presented sexually to a human (females only), presented its back or extended an arm for grooming, or masturbated when approached by a human.

Adequate parental behavior—Held, suckled (female only), groomed, shared food, and played with an infant.

Abusive parental behavior—Abandoned an infant (female only), stole an infant (male only), or pulled, bit, dropped, or handled an infant roughly.

Fearful of conspecifics—Avoided, retreated, crouched, grimaced, hid, knocked its forehead on ground, or defecated/urinated when approached by a conspecific.

Aggressive toward conspecifics—Hit, pulled hair, chased, or bit a conspecific.

Duet—vocalized in a species-typical manner with an oppositely sexed conspecific.

Aberrant behavior—Bit its own body, repeatedly knocked its forehead on the ground, inappropriately vocalized in response to specific ambient noises, sucked its thumb, and laid in feces and urine.

Data Analysis

The data for each animal were dichotomized on the basis of several variables, i.e., sexual competence (proficient vs. inadequate), sex, social attachment to humans (yes vs. no), and fearfulness of and/or aggressiveness toward conspecifics (yes vs. no). The significance of differences in proportions of animals with respect to the various questionnaire items was tested by chi square, χ^2 , $df = 1$; Yates' correction for continuity was applied to those tests in which cells had fewer than five expected frequencies (Edwards, 1960). One-way analysis of variance was used to test the significance of differences between means and correlation coefficients were calculated to test the significance of the linear association between variables.

RESULTS

Species, Sex, Origin, Type of Rearing Facility, and Enclosure Size

Life-history data were obtained on 31 maternally separated gibbons representing six species. Twenty of the subjects were white-handed or lar gibbons (*H. lar*), 4 were siamangs, (*H. syndactylus*), 2 each were buff-checked gibbons (*H. gabriellae*), Mueller's gibbons (*H. muelleri*), and pileated gibbons (*H. pileatus*), and 1 was an agile gibbon (*H. agilis*). Sixteen of the animals were female, 15 were male.

Twenty-four of the 31 maternally separated gibbons were sexually proficient, whereas 7 were inadequate, indicating that maternal separation was consistent with sexual proficiency, $\chi^2 = 8.3$, $p = 0.004$. Because of the small number of animals in each of the species other than *H. lar*, the data for those species were combined for all subsequent analyses. When the data were analyzed in this manner, sexual proficiency overall did not differ as a function of species, sex, origin (wild- vs. captive-born), or type of rearing facility (home vs. zoo nursery) (Table 1). There was a sex difference in sexual proficiency, however, related to the duration of social isolation following separation from the mother, supporting H_1 (see below). The 24 sexually proficient animals were all reproductively competent; the number of pregnancies/impregnations ranged from 1–7. The mean ($\pm SD$) number of pregnancies for the females was 2.4 ± 1.4 , the mean ($\pm SD$) number of impregnations for males was 3.7 ± 2.5 .

Sexual behavior differed in relation to enclosure size both during rearing and in adulthood,

Table 1. Sexual Behavior of 31 Maternally Separated Gibbons in Relation to Species, Sex, Origin, Type of Rearing Facility, and Enclosure Size

	Proficient (<i>n</i> = 24)	Inadequate (<i>n</i> = 7)	χ^2	<i>p</i>
Species			0.0	n.s.
Lar	15	5		
Nonlar ^a	9	2		
Sex			0.9	n.s.
Male	10	5		
Female	14	2		
Origin			0.0	n.s.
Wild-born	15	5		
Captive-born	9	2		
Facility			0.0	n.s.
Private home	20	6		
Zoo	4	1		
Enclosure size (rearing)			3.3	0.07 ^b
Large	18	2		
Small	6	5		
Enclosure size (adulthood)			6.9	0.01
Large	22	4		
Small	2	3		

^a*H. syndactylus* (*n* = 4), *H. gabriellae*, *H. muelleri*, and *H. pileatus* (*n* = 2 each), and *H. agilis* (*n* = 1). ^bFisher exact two-tailed probability = 0.04.

supporting H_2 (Table 1). The enclosures of the gibbons varied widely. Some subjects were housed in small cages in zoo nurseries, whereas one zoo used a home environment. In some cases, the home environment allowed access to an entire house and trees. Most of the gibbons that were reared in relatively large enclosures (18/20) were sexually proficient, whereas nearly half of those reared in smaller cages (5/11) were inadequate. Similarly, most of the gibbons that lived in large enclosures as adults (22/26) were sexually proficient, whereas most that lived in smaller enclosures (3/5) were inadequate.

Early Separation from the Mother and Introduction to a Conspecific

Overall, 29 of the 31 gibbons were separated from their mothers within 6 months of age, 11 by 1 month of age. There was no significant difference between the sexually proficient and inadequate gibbons with respect to the mean age at which they were separated from their mothers (Table 2), a failure to support H_3 . The proficient gibbons, however, were placed with conspecifics at a

younger age following separation from their mothers than the inadequate ones, supporting H_4 (Figure 1). In fact, all 17 gibbons that were placed with conspecifics by 19 months of age were sexually proficient, in comparison to only 7/14 that were placed with conspecifics at 2 years of age or older, $\chi^2 = 8.3$, $p = 0.004$. The sexually proficient animals were placed with younger conspecifics than the inadequate ones, a failure to support H_5 . All 17 animals which were placed with conspecifics that were less than 3 years of age were proficient, in comparison to 7/14 animals placed with conspecifics that were 3 years of age or older, $\chi^2 = 8.3$, $p = 0.004$. The duration of social isolation from a conspecific following separation from the mother was highly correlated with the age at which the animals were first introduced to conspecifics, $r = 0.99$, $df = 29$, $p < 0.001$. For the 29 gibbons that were separated by 6 months of age, all 5 males that were socially isolated for 2 years or longer were sexually inadequate, in comparison to only 2 of 8 females, $\chi^2 = 4.3$, $p = 0.04$. The longest period of isolation from conspecifics which was consistent with sexual proficiency was 7.5 years for a female and 4 years for a male. The age difference between the maternally separated animals and the conspecifics with which they were placed was smaller for the sexually proficient animals than the inadequate ones, regardless of whether they were older or younger than the conspecifics. There was no significant difference between the proficient and inadequate animals in the proportion of older and younger conspecifics with which they were placed, $\chi^2 = 0.49$, n.s.). When the absolute age difference was less than 2 years, 16/17 animals were sexually proficient, whereas when the difference was 2 years or more, almost half (6/14) were inadequate, $\chi^2 = 4.1$, $p = 0.04$.

Twenty animals were initially placed with a single oppositely sexed conspecific (9 male, 11 females), 3 with a single same-sexed conspecific, and 8 were placed with two conspecifics, 7 with a male and female, and 1 male with 2 females. Seven of the 23 gibbons that were placed with a single conspecific became sexually inadequate, in comparison to none of the 8 placed with two conspecifics, but the difference in proportions was not significant, $\chi^2 = 1.6$, n.s.).

Early Human Contact, Attachment to Humans, and Adult Behavior

Most of the gibbons for which data were available were reared with other animals, generally a dog,

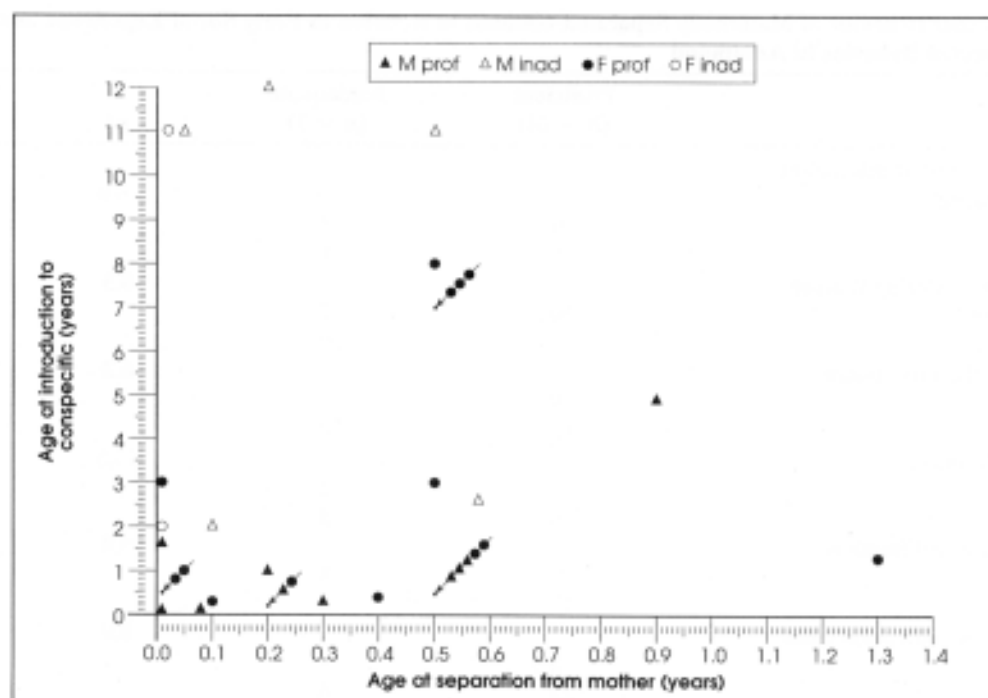


FIGURE 1 Sexual behavior of gibbons in relation to the ages at which they were separated from their mothers and introduced to a conspecific. M = male, F = female, prof = sexually proficient, and inad = sexually inadequate. Arrows indicate multiple data points.

and a large proportion had extensive contact with humans (Table 3). Neither of these conditions was differentially related to sexual proficiency. Despite the lack of a significant difference between the sexually proficient and inadequate animals with respect to the extent of human contact, a greater proportion of the sexually inadequate animals were socially attached to humans, supporting H_6 . Nine females and 7 males were so attached; i.e., there was no significant sex difference in human attachment, $\chi^2 = 0.0$, n.s.

Several analyses were conducted to determine if there was a significant relationship between conspecific contact during *particular* early periods of life and the desire for human contact. The propor-

tion of animals that were strongly attached to humans was determined for those gibbons with and without conspecific contact for each of four age periods, (a) within 6 months of age, (b) 6 months to 2 years, (c) 2 years to 3 years, and (d) the total of the previous three periods. The relationship was significant only for the period of 6 months to 2 years of age, $\chi^2 = 7.3$, $p = 0.007$. Twelve of 15 animals that were isolated from conspecifics during this period showed strong attachment to humans, whereas only 4/16 that lived with conspecifics during this stage of their lives showed such attachment. There was no significant relationship for the period of less than 6 months of age, $\chi^2 = 2.6$, n.s., the period between 2 years and 3 years

Table 2. Early Separation of Gibbons From Their Mothers and Placement with Conspecifics: Relation to Sexual Behavior in Adulthood

	Proficient ^a (n = 24)	Inadequate ^a (n = 7)	F(1,29)	p
Age separated from the mother (mos)	4.4 ± 3.7	2.5 ± 2.8	1.5	n.s.
Age placed with a new conspecific (yrs)	2.0 ± 2.6	7.4 ± 4.9	14.8	<0.001
Age of the new conspecific (yrs)	2.1 ± 2.2	5.0 ± 1.7	10.3	0.003
Age difference with conspecific (yrs)	1.6 ± 1.5	3.9 ± 2.6	9.4	0.005

^aMean ± SD.

Table 3. Sexual Behavior of Maternally Separated Gibbons in Relation to Early Social Experience and Social and Self-Directed Behavior in Adulthood

	Proficient (<i>n</i> = 24)	Inadequate (<i>n</i> = 7)	χ^2	<i>p</i>
Animal (nongibbon) interaction during rearing ^a			0.0	n.s.
Yes	9	3		
No	5	1		
Human contact during rearing			0.3	n.s.
Continuous	20	7		
Infrequent	4	0		
Socially attached to human			6.2	0.01
Yes	9	7		
No	15	0		
Duetted with partner			15.5	<0.001
Yes	24	2		
No	0	5		
Aggressive toward humans			0.0	n.s.
Yes	7	3		
No	17	4		
Aggressive toward conspecifics			0.0	n.s.
Yes	2	1		
No	22	6		
Fearful of conspecifics			15.5	<0.001
Yes	0	5		
No	24	2		
Abusive toward self ^b			4.2	0.04
Yes	1	3		
No	23	4		

^aNo data were available on 10 proficient and 3 inadequate animals. ^bBit itself habitually, repeatedly knocked its forehead on the ground, laid in feces/urine.

of age, $\chi^2 = 2.2$, n.s., or the total of all three periods, $\chi^2 = 2.6$, n.s. Similarly, the comparison between those animals with conspecific contact during two and three of those periods and those that had such contact during none or only one such period was significant, but it did not improve the relationship over that found for the period of 6 months to 2 years only, $\chi^2 = 5.6$, $p = 0.02$.

Analyses were also conducted to determine if there were significant relationships between the sex of the primary caretaker during the gibbons' first 2 years of life and the behavior of the gibbons as adults. Most of the primary caretakers were women (23/31); as a result, most of the males (11/15) had caretakers of the opposite sex, whereas most of the females (12/16) had caretakers of the same sex. A greater proportion of the gibbons whose primary caretakers were men (7/8) in comparison to women (9/23) developed strong human attachments, $\chi^2 = 3.8$, $p = 0.05$. A greater proportion of the gibbons whose caretakers were men (4/8) in comparison to women (3/23) were sexually

inadequate, but this result was only of borderline significance, $\chi^2 = 2.8$, $p = 0.10$; Fisher exact one-tailed probability = 0.05. A clearer relationship to sexual behavior of the gibbons, albeit with a small number of animals, was found in the males whose primary caretakers were men; a greater proportion (3/4) of these male gibbons became sexually inadequate in comparison to females that were reared by women (1/12), $\chi^2 = 4.0$, $p = 0.05$. There was no significant difference in sexual proficiency, however, between the males that were reared by same-sexed caretakers (1/4) and those reared by oppositely sexed caretakers (9/11), $\chi^2 = 2.1$, n.s.

There was no significant relationship between aggression toward humans and sexual behavior with conspecifics (Table 3). Ten animals displayed aggression toward humans, 4 males and 6 females; there was no significant sex difference, $\chi^2 = 0.1$, n.s. Eight of the animals became aggressive when they solicited but were denied human contact and 2 regardless of soliciting. Three of the females after reaching sexual maturity became aggressive

toward sexually mature women, including the women who reared them. In fact, most of the females that were socially attached to humans (6/9) became aggressive toward the humans postpubertally in comparison to few (2/7) of the males, but the sex difference was not significant, $\chi^2 = 1.0$, n.s.

Social, Parental, and Aberrant Behavior

The modal number of conspecific partners with which the maternally separated gibbons ever lived was one and there was no significant difference between the mean number of partners for the proficient (1.7 ± 0.8) and the inadequate (2.3 ± 2.4) animals, $F(1,29) = 1.1$, n.s. There was a significant difference between the two groups, however, in the number of conspecific partners with which they were socially compatible, $F(1,29) = 4.7$, $p = 0.04$. The sexually proficient animals had a greater number of partners with which they were compatible (1.6 ± 0.9) than the inadequate animals (0.7 ± 1.1). The sexually proficient animals also spent more time with other sexually proficient animals than did the inadequate animals, 7.2 ± 4.2 years and 3.6 ± 4.1 years, respectively, $F(1,29) = 4.0$, $p = 0.04$. Only 3 of the 24 sexually proficient gibbons were neglectful or abusive parents, 1 male *H. muelleri*, and 2 female *H. syndactylus*, i.e., most of the animals that mated were adequate parents, failing to support this aspect of H_7 .

As adults, 26 of the 31 maternally separated gibbons duetted with their partners (Table 3). All 5 of the animals that failed to duet were sexually inadequate, $\chi^2 = 15.5$, $p < 0.001$, supporting H_7 . Only 3 gibbons displayed aggressiveness toward conspecifics, all females. This was not related to sexual behavior; 2 were proficient, 1 was inadequate. Fearfulness toward conspecifics, however, was related to sexual inadequacy. All 5 of the fearful animals were sexually inadequate, whereas 24 of the 26 other animals were proficient, supporting H_7 . Of the 5 fearful animals, only 1 developed socially compatible relationships with conspecific partners. Moreover, the 8 animals that were either aggressive toward or fearful of conspecifics differed in several ways from the animals that were neither aggressive nor fearful. The fearful and aggressive animals were separated from their mothers at a somewhat earlier age on average, 2 ± 3 months versus 5 ± 4 months, $F(1,29) = 4.5$, $p = 0.04$, and were introduced to conspecifics at a much later age, (5.6 ± 4.8 years versus 2.4 ± 3.3 years, $F(1,29) = 4.3$, $p = 0.05$). As a result, the fearful or aggressive animals were socially isolated from

conspecifics for a longer period of time than the other animals, 5.4 ± 4.9 years versus 2.0 ± 3.2 years, $F(1,29) = 5.1$, $p = 0.03$. For 2 males that were socially isolated for shorter periods of time, fearfulness developed during early placement with an older conspecific that behaved aggressively toward them. All 8 of the aggressive or fearful animals were incompatible with at least one conspecific partner, in comparison to only 1 of the 23 animals that were neither aggressive nor fearful, $\chi^2 = 21.9$, $p < 0.001$. Compatibility, of course, depends on the behavior of both animals in a pair, a factor which must be considered in interpreting all the data on social compatibility.

Although other types of aberrant behavior were relatively rare among the maternally separated gibbons, certain ones occurred in a greater proportion of the sexually inadequate animals (Table 3), consistent with H_7 . In situations judged to be stressful by their caretakers, 3 animals knocked their foreheads on the ground, physically abused (bit) themselves, and laid in their feces and urine. These aberrant behaviors did not cease during adulthood, even when the animals were housed in large enclosures. Thumb-sucking occurred in 2 sexually proficient animals (1 male and 1 female) and 1 female that was inadequate. Another behavior observed in 3 females (2 proficient and 1 inadequate) was a territorial vocalization that occurred only when humans conversed near their enclosures. Only the more destructive types of aberrant behavior (Table 3), therefore, were associated with sexual inadequacy.

DISCUSSION

Species, Sex, Origin, Type of Rearing Facility, and Enclosure Size

Most of the maternally separated gibbons considered in this article were sexually proficient, reproductively competent, and parentally adequate. Their sexual proficiency overall was not influenced by their species, sex, origin, or type of rearing facility (But see discussion of a sex difference, below.) Sexual proficiency was facilitated, however, by living in relatively large enclosures, a phenomenon also observed in some nonprimate species (e.g., domestic cats; Mellen, 1988). The term *relatively large* is used in the sense of an *adequate* enclosure, one in which the enclosure size is related to the size of the animal, the animal's typical mode of locomotion, and its characteristic form of

social spacing. Although consideration of locomotor behavior in determining enclosure size is relevant to the behavioral welfare of all primates, it is especially important for gibbons, which typically brachiate over large distances (Brockelman, 1984; Carpenter, 1940; Dahl, 1989; Ellefson, 1974). Appropriate objects and apparatus are also important to the behavioral welfare of gibbons in that they permit more complete utilization of the available space (Dahl, 1989; Mootnick, Haimoff, & Nyunt-Lwin, 1987).

Early Separation From the Mother and Introduction to a Conspecific

The results suggest that the presence of another young and sexually inexperienced conspecific counteracted the adverse effects on sexual and social behavior resulting from early separation from the mother, similar to data on rhesus monkeys (Bercovitch, Roy, Sladky, & Goy, 1988; Capitanio, 1986; Wallen, Goldfoot, & Goy, 1981). In the case of the gibbons, such conspecific companionship was most important prior to 2 years of age, a finding which varies among species as a function of species-typical rates of maturation. Males were more adversely affected sexually than females by relatively long periods of social isolation following early separation from the mother. This result is consistent with the data on rhesus monkeys (Mason, 1960; Mason, Davenport, & Menzel, 1968; Missakian, 1969), chimpanzees (King & Mellen, 1994; Nissen, 1954; Riesen, 1971; Rogers & Davenport, 1969), and gorillas (Meder, 1995). The sex difference is likely related to the different behavioral requirements on males and females for sexual interaction and the greater complexity of the male copulatory pattern. Although a female may be sexually inadequate in some sense, it can be induced to present sexually by a proficient and dominant male. It is much less likely that a sexually inadequate male can be induced by a female to mount, intromit, and thrust to ejaculation.

It should be noted that the age at separation from the mother was similar for most of the animals (29/31), i.e., within 6 months. As a result, the age at introduction to a conspecific was highly correlated with the duration of social isolation. Comparative research on other nonhuman primates, however, strongly suggests that it is the age per se, during which animals are socially isolated that is most relevant to deficient socialization (Capitanio, 1986; Mason et al., 1968; Rogers & Davenport, 1969).

It was noteworthy that the animals placed with conspecifics of comparable age (and those of less than 3 years of age) became sexually proficient rather than those placed with older conspecifics, as was hypothesized. It was thought that an older female conspecific, i.e., an "aunt," would better substitute for the mother. Being caged with older conspecifics, however, was more closely associated with the development of fearfulness (see below). This finding is reminiscent of research which showed that socially deficient adult rhesus monkeys were rehabilitated when they were housed with young conspecifics, apparently because the socially deficient animals were less fearful of the youngsters than they were of older and large animals (Mitchell, Maple, & Erwin, 1979; also see Harlow, Harlow & Suomi, 1971). The data on the gibbons suggest that a comparable interpretation applies to these species.

The idea that early social experience has a profound influence on adult sexual behavior of nonhuman primates was first proposed by H. C. Bingham (1928) following his visit to the chimpanzee colony maintained at the Abreu estate in Cuba. Bingham was particularly curious about the sexual indifference of one captive-born adult male and speculated that its lack of sexual responsiveness might have resulted from a failure during development in captivity to observe copulation by experienced adults. His subsequent research with 4 young maternally separated chimpanzees reared together as a group changed his perspective and his opinion. As a result, Bingham proposed that proficiency in sexual behavior developed through an association between certain aspects of early social interaction, especially those involving bodily contact, and the increase in sexual responsiveness that occurs with physical maturation. That those young chimpanzees eventually developed sexual competence was demonstrated by their inclusion in the first experimental laboratory study of sexual behavior conducted with this species (Yerkes & Elder, 1936). The data on the gibbons support the hypothesis that proficient sexual behavior can develop in total isolation from experienced adults, presumably through the reinforcing properties of sexual stimulation combined with trial-and-error learning carried out with another young, inexperienced, but socially compatible conspecific. Clearly, it is not necessary for gibbons to observe sexual behavior of adult conspecifics in order to become sexually proficient, though such observation may facilitate the development of sexual proficiency (Meder, 1995).

Early Human Contact, Attachment to Humans, and Adult Behavior

The development of strong social attachments to humans by the maternally separated gibbons was associated with social isolation from conspecifics during the specific period of 6 months to 2 years of age and occurred disproportionately in the sexually inadequate animals. Attachment to humans was reported to interfere with the development of species-typical sexual behavior of some maternally separated chimpanzees (Nissen, 1954; J. Fritz, personal communication), but not others (Lemmon, 1971; Rogers & Davenport, 1969). Lemmon (1971) differentiated between maternally separated male chimpanzees on the basis of the *quality* of their human relations. Those males that were judged to have had "good human relationships" copulated adequately as adults with sexually responsive adult female chimpanzees the very first time they were introduced! It was not possible to evaluate the quality of the human relations of the maternally separated gibbons in the present study, but most (9/16) of those with strong human attachments nevertheless became sexually proficient, i.e., human attachment was compatible with sexual proficiency. There was some suggestion that both human attachment and sexual inadequacy were greater for those gibbons whose primary caretakers were men, particularly so for the male gibbons. Because the numbers of animals in these relationships were small and the significance levels relatively low, no interpretation is presented for the data. Additional data are being sought to determine if these relationships persist.

It is apparent from the analyses presented above that the period from 6 months to 2 years of age was important for the development of both sexual proficiency with conspecifics and human attachments. There is no compelling evidence that these social attachments are mutually exclusive, either for the gibbons or other nonhuman primates. It is the absence of social experience with conspecifics which is most deleterious to the socialization of nonhuman primates, a condition which is frequently confounded with, but in some cases probably ameliorated by, human contact.

Some of the maternally separated gibbons became aggressive toward sexually mature humans when they themselves reached sexual maturity, similar to other captive gibbons (Carpenter, 1940; van Gulik, 1967). Among the maternally separated gibbons, the aggression was frequently directed toward humans of the same sex. Of a related na-

ture were reports on wild gibbons that it was the parent of the same sex that generally used aggression to peripheralize sexually mature offspring from the family group (Chivers & Raemaekers, 1980; Tenaza, 1975; Tilson, 1979). One of the maternally separated males sexually solicited the woman who reared him, but aggressively threatened men. Three other males became aggressive toward their sexual partners when the latter interacted with humans (personal observations). Some of the maternally separated gibbons directed sexual solicitations and masturbation toward humans (also see Mootnick & Baker, 1994), and they acted to prevent contact between their sexual partners and humans. These types of observations, though limited in number, suggest that maternally separated gibbons may respond to humans as if the humans were conspecifics.

Although the consequences of strong social attachment to humans are somewhat controversial, aggression toward humans may represent a natural initial response of the maternally separated gibbons. Aggressive behavior toward humans occurs during initial contacts in captive mother-reared (personal observations) and wild-born gibbons (Finn, 1929; Harlan, 1834; Kuhnert et al., 1902), but it readily declines over time with positive human interaction.

Social, Parental, and Aberrant Behavior

There was a clear association between several aspects of social behavior and sexual inadequacy in the maternally separated gibbons, suggesting a causal relation. The sexually inadequate animals were disproportionately fearful of conspecifics, a condition which likely contributed to their incompatibility with conspecifics, their lack of duetting, and thereby, their deficient sexual behavior. Others speculated that fearfulness and sexual inadequacy in some captive gibbons may have resulted from early social deprivation (Berkson & Chai-cumpa, 1969; Brody & Brody, 1974), a relationship strongly supported by the current data. A variety of artificial "mother surrogates" were used to counteract the effects of early social deprivation in some maternally separated, nonhuman primate infants (Harlow et al., 1971; Deutsch & Larsson, 1974), including gibbons (Sasaki, 1962; Kawakami & Kollias, 1984), but most, including those used with the gibbons (Breznock, Porter, Harold, & Kawakami, 1979), did not adequately substitute for a living animal. Mobile mother surrogates were somewhat superior to stationary ones

with respect to certain aspects of behavior in rhesus monkeys (Anderson, Kenney, & Mason, 1977), but a comparably aged, socially compatible conspecific is the maternal replacement of choice with respect to the development of sexual behavior.

Aggressiveness toward conspecifics also occurred among the gibbons, but it was relatively uncommon (3 of 16 females, no males) and was not directly related to sexual proficiency. Both aggressiveness toward and fearfulness of conspecifics, however, were associated with social incompatibility. All 3 of the gibbons that were aggressive toward conspecifics developed compatible social relations with at least one partner, but only 1 of the fearful animals did so. Those gibbons that were either fearful of or aggressive toward conspecifics were socially isolated for a relatively long period of time early in life, more than twice as long on average as the other gibbons. Fearfulness of conspecifics, aggressiveness, and sexual inadequacy have long been recognized as the hallmarks of early social deprivation in other nonhuman primates (Capitanio, 1986; Harlow et al., 1971; Mason, 1960; Mason et al., 1968). Another factor that may have induced fearfulness in 2 of the maternally separated gibbons was early abuse by an older and aggressive conspecific partner.

Most of the sexually proficient animals (22/24) were adequate parents, a finding which provides some insight into the contrary findings on monkeys (Harlow et al., 1971; Suomi, 1978) and chimpanzees (Nadler, 1981) reared in isolation from conspecifics and gorillas reared with peers only (Nadler, 1975, 1984). The presence of peers during early development in the gibbons likely accounts for their more adequate parental behavior in comparison to the monkeys and chimpanzees, and the presence of a conspecific (the male partner) at the time of parturition perhaps accounts for the difference with the gorillas. Among captive gorillas which were reared with peers, most females that gave birth for the first time *within a social group* cared adequately for their offspring, whereas most of those that were socially isolated from conspecifics prior to their first parturition neglected or abused their offspring. As was true for gorillas, the development of adequate maternal behavior in the gibbons did not require prior observation of maternal behavior in experienced adults. Those gibbons that learned species-appropriate *social interaction* apparently learned the essential requirements of parenting within a short period of time after their first parturition.

The maternally separated gibbons exhibited

several types of aberrant behavior, similar to other nonhuman primates separated from their mothers early in life (Capitanio, 1986; Harlow et al., Mason, 1960; Mason et al., 1968). Relatively benign aberrancies, such as thumb-sucking and inappropriate vocalizing, were compatible with sexual proficiency, whereas self-abusive behaviors, such as biting oneself, were more frequently associated with sexual inadequacy. The results suggest that early separation of gibbons from their mothers results in a spectrum of behavioral deficiencies, similar but not identical to those found in other nonhuman primates. None of the gibbons, for example, showed the stereotyped rocking which was characteristic of monkeys and chimpanzees that were socially isolated early in life (Lemmon, 1971; Mason, 1960; Mason et al., 1968; Rogers & Davenport, 1969). The similarities among the species in aberrant behavior and deficient social, sexual, and parental behavior apparently reflect a common primate response to early maternal separation, a behavioral syndrome which is ameliorated or prevented altogether by relatively rapid housing with a conspecific peer following separation from the mother.

CONCLUSIONS

1. Maternal separation in gibbons is compatible with the development of sexual proficiency under certain conditions, but not others.

2. Sexual proficiency of gibbons is compromised by early rearing in the absence of conspecific contact, similar to other nonhuman primates.

3. Sexual proficiency of maternally separated gibbons is facilitated by introduction within 2 years of age to a socially compatible conspecific of comparable age, in contrast to introduction at a later age or to an older conspecific.

4. Sexual proficiency of maternally separated gibbons is facilitated by rearing and maintenance in relatively large enclosures in contrast to small ones.

5. Maternally separated, but sexually proficient gibbons, are likely to be reproductively competent and parentally adequate.

6. Gibbons, like the other apes, need not learn sexual or parental behavior by observing experienced adult conspecifics. Given adequate socialization during infancy, they acquire important social skills which then facilitate the acquisition of sexual and parental competence when the opportunities for these activities first arise in adulthood.

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