

RESEARCH ARTICLES

Effects of Early Rearing Experience on Subsequent Adult Sexual Behavior Using Domestic Cats (*Felis catus*) as a Model for Exotic Small Felids

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Zoo professionals generally believe that maternal rearing of zoo animals is preferable to human/nursery raising. The lack of consistent reproductive success in small captive exotic felids has been partially attributed to an excess of human-raised individuals. To investigate experimentally the effects of human/nursery rearing on adult sexual behavior, domestic cats were used as a model for small captive exotic felids. Three groups of female domestic cats were reared under three different conditions (intended to mimic typical zoo rearing situations) and then paired at sexual maturity with sexually experienced males. Cats in Condition I were Human-Raised Alone, i.e., had no physical or visual contact with conspecifics until sexual maturity; cats in Condition II were Human-Raised with a Sibling, i.e., had no physical or visual contact with any conspecifics except their respective sibling until sexual maturity; cats in Condition 3 were Maternally Raised with a female sibling, but had no other physical or visual contact with other conspecifics until sexual maturity. Individuals in Condition 3 copulated significantly more often than did the individuals in Condition 1. The individuals in Condition 1 were distinguished by the extreme aggression they displayed toward both the males with which they were paired and their human-caretakers. Data suggest that human-reared female cats are less likely to reproduce than are their maternally-reared counterparts. These results suggest that, whenever possible, nursery-raising of small exotic felids should be avoided.

Key words: *Felis* spp., reproductive failure, reproductive behavior

INTRODUCTION

The influence of early rearing experience on adult sexual behavior has been examined in a variety of mammalian species. This area of research has focused

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predominantly on rodents [e.g., Beach, 1942, 1958; Duffy and Hendricks, 1973; Larsson, 1978], food animals [e.g., Signoret, 1970; Hemsworth et al., 1977; Zenchak and Anderson, 1980], domestic dogs [e.g., Beach, 1968], and most predominantly on non-human primates [e.g., Mason, 1960; Harlow, 1965; Mitchell et al., 1966]. Briefly summarized, early isolation rearing in these species appears to have a lasting effect on subsequent sexual behavior. Further, the above research demonstrates that isolation is more debilitating to males than to females.

Studies in which early rearing experience was varied in domestic cats [e.g., Seitz, 1959; Kuo, 1960; Kling et al., 1969; Baerends-van Roon and Baerends, 1979] have demonstrated that the raising of cats in the absence of conspecifics has profound effects on their behavior. These effects persist into adulthood: 1) cats raised alone and then tested as adults were described as "suspicious, fearful, and aggressive" towards other cats [Seitz, 1959; Kuo, 1960], 2) males raised alone showed a reduced ability to copulate [Rosenblatt, 1968], and, 3) kittens raised only with a surrogate "brooder" were termed "hypergregarious" by Guyot, Cross, and Bennett [1980].

Zoo professionals generally believe that maternal rearing of animals is preferable to human- (hand) raising [Kleiman, 1975; Eaton, 1977a, 1984; Brambell and Jones, 1977; Meier, 1986]. Most feel that handling by humans early in development may have an adverse effect on subsequent adult behavior. There has been substantial conjecture about optimal rearing conditions among many exotic animals, including those in the family Felidae. Maternally raised kittens are presumed to be healthier and gain weight more rapidly than are human-raised kittens [Eaton, 1977b; Eaton and Velandar, 1977]. Hand-raised cats are thought to become sexually imprinted on humans [Hediger, 1950, 1955; Klinghammer, 1973; Eaton, 1974, 1977a; Freeman, 1977; Leyhausen, 1979]. Also, human-raised exotic felids are thought to have lower reproductive success and show inadequate maternal care [Kleiman, 1975, 1980; Eaton, 1974, 1977a]. Nevertheless, many human-raised individuals breed just as well as maternally raised felids [Quillen, 1981; Eaton, 1984] and these tamer animals are easier to treat when ill [Eaton, 1974, 1977a]. Other confounding issues include the possibility that adult human-raised females that abandon or cannibalize their litters may do so in response to external disruptions or genetically deficient kittens and not, in fact, because of an inability to care adequately for their offspring.

In the present study, domestic kittens were raised under the various conditions typically occurring in zoos, i.e., Human-Raised Alone, Human-Raised with a Sibling (these two conditions simulating typical zoo nursery-rearing), and Maternally Raised with a Sibling (this condition simulating typical mother-rearing of zoo felids). In order to ascertain potential for reproductive success, the domestic female cats at maturity were systematically paired with experienced males and their behaviors recorded. Thus, female domestic cats were used as a model for small exotic felids. Early rearing experience was systematically varied in ways to mimic typical zoo conditions for small exotic felids and their subsequent ability to copulate was measured.

MATERIALS AND METHODS

Subjects, Housing, and Care

The subjects were 21 female domestic cats (*Felis catus*). The cats were acquired in two ways. The kittens that were human-raised (Conditions 1 and 2—see below) were donated. Owners of non-purebred pregnant cats of average size were asked to

notify the author immediately after their cats gave birth. Two female kittens were removed from each mother at 48-hour post-partum and randomly assigned to either Condition 1 or 2. A 48-hour post-partum time period was chosen because the kittens had received maternal antibodies from the colostrum and yet had had minimal interaction with conspecifics. A total of 15 kittens were obtained in this manner, seven in Condition 1 and eight in Condition 2.

The third group of kittens (for Condition 3—see below) was obtained through the breeding of barn cats donated to this project. Barn cats were used because they presumably represented a better model for exotic cats than tamer house cats (i.e., pets). Each of four female barn cats was placed with one of two male barn cats when she showed signs of being in estrus. Each estrous female was placed daily with a male for 30 minutes or until three copulations had occurred. This process was continued until conception occurred. Forty-eight hours after the birth of each litter, all but two female kittens were removed (excess kittens were cross-fostered or human-raised, but were not used in this experiment). Thus, each of the four female barn cats raised two female kittens. Eight kittens were obtained in this manner.

One of the subjects raised under the second condition died at eleven months of age, leaving a total of seven individuals in Condition 2; one of the subjects in Condition 3 was mis-sexed and at 154 days of age was separated from *his* female sibling. Thus, a total of 21 female cats, 7 in each of three groups, were studied.

The two male barn cats used to sire the kittens in Condition 3 were maintained throughout the study and subsequently used for the experimental pairings with each of the females in Conditions 1, 2, and 3. Each of the two males was separately housed in "breeding" enclosures each measuring 3.05 m $\times$ 1.83 m $\times$ 2.44 m, made of wood supports and chicken wire. Each enclosure contained two wooden den boxes, each measuring 0.61 m $\times$ 0.305 m $\times$ 0.305 m, plus several perching areas and logs, a litter pan, food and water dishes and several cat toys. The experimental pairings occurred in these two "breeding" pens, as Michael [1961] and Leyhausen [1979] suggest that tom cats are most likely to breed in a familiar area.

The kittens in Conditions 1 and 2 remained in the author's home until 12 weeks of age. At that time the individuals in Condition 1 and the pairs in Condition 2 were moved to the outdoor enclosures at the Washington Park Zoo, Portland, Oregon. Each hand-reared kitten was bottle-fed Borden's Kitten Milk Replacement (KMR)[®] and then gradually weaned onto solid food. Throughout the remainder of the study, individuals in Condition 1, pairs in Condition 2, and mother-infant trios in Condition 3 were housed in individual plywood and hardware cloth cages measuring 1.22 m $\times$ 0.915 m $\times$ 1.22 m with a heated den box measuring 0.61 m $\times$ 0.305 m $\times$ 0.305 m (mother-reared cats were born and raised in these cages). These cages, as well as those of the males, were located in an outdoor, off-exhibit area at the Washington Park Zoo. At sexual maturity, i.e., once estrous behavior was noted in the females in Conditions 2 and 3, all 21 female cats were individually housed in the 1.22 m $\times$ 0.915 m $\times$ 1.22 m plywood and hardware cloth enclosures.

One of four caretakers, including the author, checked the experimental cats daily for signs of estrus, i.e., Lordosis, Tail to One Side, Treading with Hind Feet, vocalizations, Cheek Rubbing, Rolling on Back, and increased "friendly" behavior. (Occurrence of estrous behavior was confirmed by the author prior to all experimental pairings). During routine cleaning periods and on an irregular basis, each of the 21 females was also given access to a large exercise pen.

Human-Raised Females—Conditions 1 and 2

Fifteen kittens were randomly assigned to Condition 1 or 2. Kittens assigned to Condition 1 were raised by humans beginning at 2 days of age and had no physical contact with conspecifics until sexually maturity. Throughout the study visual contact with conspecifics was minimal, although auditory and olfactory contact occurred. The eight kittens assigned to Condition 2 were four sibling pairs of females. These females were removed from their respective mothers at two days of age and were raised by humans. These pairs were housed together until one member of the pair reached sexual maturity, i.e., showed signs of estrus. At that time, the members of each pair were housed separately. As with the individuals in Condition 1, visual contact with all conspecifics (except its sibling) was minimal, although auditory and olfactory contact occurred. As mentioned above, one of the subjects in Condition 2 died at 11 months of age; the death of this individual occurred after her sister came into estrus for the first time.

Maternally Raised Females—Condition 3

As described above, four female barn cats each raised two kittens. Human interaction with the mothers and kittens were minimal, involving only routine cleaning, feeding, and health and weight checks. The mothers were removed from their kittens when the kittens were 20 weeks old. These pairs of maternally raised kittens were housed together until one member of the pair reached sexual maturity, i.e., showed signs of estrus. At that time, the members of each pair were housed separately. As with the individuals in Conditions 1 and 2, visual contact with all conspecifics (except with mother and sibling) was minimal.

Experimental Design

Sexual maturity was defined by each cat's first estrous period. Individuals in Conditions 2 and 3 (Human-Raised with a Sib and Maternally Raised with a Sib) were separated from their respective littermates at first estrus. For all three groups, each female was placed with one of two males on four consecutive days, beginning with the second time she came into estrus. Two males were used, in case mating success was related to mate preference [Leyhausen, 1979; Voith, 1980]. The two males were alternated during four days of each female's estrous period; the male used on Day 1 was randomly determined. On each of the 4 days, the female was placed in the male's area (the breeding pen) until three copulations occurred. Exceptions to this procedure were as follows: if no copulation occurred the trial was terminated (typically after 30 minutes), or, if injury to either animal appeared imminent, the trial was discontinued immediately. This procedure was followed until copulation occurred or through five estrous periods. Thus, the maximum number of 30-minute pairing periods was 20 (one 30-minute session on each of four consecutive days per estrous period over five estrous cycles). During each estrous cycle, the female was allowed four consecutive daily pairings whether or not copulation occurred. If copulation occurred, that female's part in the experiment was complete. She was not paired again during any subsequent estrous cycles. The purpose of this procedure was to give each male equal opportunity for matings and to determine if one male was more successful than the other. Table 1 illustrates this experimental design indicating alternate pairings with each of the male cats, "Chunk" and "Spencer."

TABLE 1. Sample schedule for pairing of each female domestic cat with two male cats (named "Chunk" and "Spencer")*

	Day 1	Day 2	Day 3	Day 4
1st estrus	Chunk	Spencer	Chunk	Spencer
2nd estrus	Spencer	Chunk	Spencer	Chunk
3rd estrus	Chunk	Spencer	Chunk	Spencer
4th estrus	Spencer	Chunk	Spencer	Chunk
5th estrus	Chunk	Spencer	Chunk	Spencer

*Each experimental pairing ended after three copulations occurred, after approximately 30 minutes *or* if injury to either animal appeared imminent.

During the pairings, the frequency of a variety of behaviors associated with reproductive behavior in felids was recorded. These are listed and defined in Table 2.

RESULTS

Of the seven females in each group, two of seven in the Human-Raised Alone condition copulated, three of seven in the Human-Raised with Sibling group copulated, and six of seven in the Maternally Raised with Sib condition copulated.

Relative Reproductive Success of Each Male

As stated earlier, females were alternately placed with one of two males while in estrus. Two males were used in this experiment to reduce any preference effect a female might show for a single male. To determine if there was a significant difference between the relative success in copulations by the two males, a chi-square goodness-of-fit test [Conover, 1980] was used to assess both the total number of females bred by each male and the total number of intromissions achieved. Neither the total number of females bred ($\chi^2 = 0.1037$, $df = 1$, $P > 0.250$) nor the total number of intromissions achieved ($\chi^2 = 0.08$, $df = 1$, $P > 0.250$) differed significantly when the two males were compared.

The males were remarkably resilient and patient in approaching the females and attempting to copulate with them. Each male was paired in excess of 100 hours with females from the various groups, many of whom responded with extreme aggression to Approaches and Attempted Mounts by the males. Yet, in those 100+ hours, each male successfully copulated only 26 and 24 times, respectively.

Comparisons of Rates of Behavior Among the Three Groups

Table 3 presents the average rates of behaviors for each group of females; Table 4 presents the average rates of behaviors exhibited by the two males while paired with the females in each particular group. All behaviors associated with copulation were highest in the Maternally Raised with Sib group of females. (Rates of selected behaviors were statistically analyzed to test for differences between groups. Statistical analyses were not performed on all behaviors because of the substantial number of behaviors monitored. If all behaviors were tested for significance, presumably some test results would be significant, simply by chance.) Two behaviors associated with copulation, Rolling on Back and Neck Rubbing, were found to be statistically higher in the Maternally Raised with Sib group (see Table 2). With the exception of one

TABLE 2. Behaviors of domestic cats during experimental pairings of differentially reared females with males

Behavior	Description
Social Sniffing	Cat sniffs any region other than the anogenital region of another cat
Follow/Chase	Rapidly follows within one body length for a distance of at least two body lengths
Social Grooming	Licking, chewing, and/or cleaning the fur of another
Approach	Approaches the other within one body length
Social Head Rubbing	"Forehead" of one cat rubbed against another
Anogenital Sniffing	Sniffs the anogenital region of another
Lordosis	Female elevates hind quarters while resting most of weight on forepaws and chest
Treading	While in a lordosis posture, female "steps" in place with hind feet
Tail to Side	While in a lordosis posture, female deflects her tail laterally away from anogenital region
Copulatory Cry	Loud, sharp vocalization by the female associated with mounting and usually assumed to indicate intromission
Nape Bite	Male grasps back of female's neck with his teeth
Mounts with Front Feet	Male straddles female with his front legs
Mounts with Hind Feet	Male straddles female with both his front and hind legs
Stepping	While mounting female, male makes stepping motions with hind feet, usually rubbing the sides of the female
"Pelvic" Thrusting*	While mounting, male makes searching/thrusting movements with pelvic region contacting the anogenital region of the female
Intromission	Determined indirectly by the copulatory cry of the female (intromission and ejaculation were assumed to have occurred if the female emitted a copulatory cry)
Roll on Back	Vigorously writhes on back
Anogenital Self-Grooming	Cat grooms own genitals for at least four seconds
Cheek Rubbing	Cheek rubbed against an inanimate object
Neck Rubbing	Vigorously rubs or scrapes lateral portions of neck against inanimate object or along substrate
"Sharpening" Claws	Claws of front paws are used to scratch some surface (usually wood)
Urine Marking	Urinating on vertical surface
Flehmen	Open-mouth grimace following the sniffing of an object or cat
Hiss Vocalization	Orients to another cat and emits a hissing vocalization
Growl Vocalization	Orients to another cat and emits a growl
Strike at	Strikes at another with its paw, but no contact is made
Arch Threat	"Halloween" cat posture, i.e., with arched back
Strike with Paw	Strikes another with its paw
Biting	As implied.

*Using Lanier and Dewsbury's classification [1976], domestic cats do not pelvic thrust. The behavior, instead, appears to be a "searching" motion and occurs prior to intromission.

behavior, Striking at with Paw, the Maternally Raised with Sib group had the lowest rate of aggression towards the males. Rates of Hissing and Growling were examined for statistical significance, but no differences were found (Table 2). Urine Marking was observed in only one female (from the Human-Raised with Sibling group). "Sharpening" Claws occurred at a lower rate in the Maternally Raised with Sib group than in either of the Human-Raised groups. Head rubbing, generally considered to be a greeting or amicable behavior, was never observed in any of the females during pairings with the males. Females from the Maternally Raised with Sib group copu-

Table 3. Mean rates of behavior per hour ($\pm$ standard error) for behaviors exhibited by females in different treatments*

Behavior	Alone (A) N = 7	Sibling (S) N = 7	Parent (P) N = 7	Value ^a	Alpha	Follow-up test		
						A:P	A:S	S:P
Social Sniffing	0.48 $\pm$ 0.33	0.21 $\pm$ 0.09	2.21 $\pm$ 0.81					
Follow/Chase	0.03 $\pm$ 0.03	0.11 $\pm$ 0.09	0.11 $\pm$ 0.08					
Social Grooming	0.00 $\pm$ 0.00	0.07 $\pm$ 0.07	0.00 $\pm$ 0.00					
Anogenital Sniffing	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.18 $\pm$ 0.10					
Approach Male	2.96 $\pm$ 1.49	1.88 $\pm$ 0.92	6.07 $\pm$ 2.01					
Head Rubs Male	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Lordosis	0.48 $\pm$ 0.31	1.05 $\pm$ 0.64	3.08 $\pm$ 1.43					
Treading	0.43 $\pm$ 0.28	0.96 $\pm$ 0.59	2.02 $\pm$ 0.64					
Tail to Side	0.39 $\pm$ 0.25	0.76 $\pm$ 0.45	1.56 $\pm$ 0.48					
Copulatory Cry	0.10 $\pm$ 0.07	0.50 $\pm$ 0.34	1.35 $\pm$ 0.57					
Threat After Copulation	0.07 $\pm$ 0.07	0.42 $\pm$ 0.37	0.51 $\pm$ 0.30					
Rolls on Back	2.33 $\pm$ 1.20	9.82 $\pm$ 4.82	18.91 $\pm$ 4.06	9.92	$P \leq 0.005$	$z = 10.43; P \leq 0.05$	$z = 5.43; n.s.$	$z = 5.00; n.s.$
Anogenital Groom	0.18 $\pm$ 0.10	0.81 $\pm$ 0.48	1.43 $\pm$ 0.45					
Neck Rubbing	1.53 $\pm$ 1.17	6.60 $\pm$ 4.36	19.58 $\pm$ 8.99	6.55	$P \leq 0.05$	$z = 8.43; P \leq 0.05$	$z = 4.43; n.s.$	$z = 4.00; n.s.$
Cheek Rubbing	1.97 $\pm$ 1.41	1.10 $\pm$ 0.48	5.12 $\pm$ 2.03					
Flehmen	0.13 $\pm$ 0.10	0.21 $\pm$ 0.07	0.55 $\pm$ 0.31					
Urine Marking	0.00 $\pm$ 0.00	0.06 $\pm$ 0.04	0.00 $\pm$ 0.00					
Sharpen Claws	0.72 $\pm$ 0.41	0.81 $\pm$ 0.40	0.33 $\pm$ 0.13					
Hissing	12.27 $\pm$ 4.47	9.13 $\pm$ 1.62	4.17 $\pm$ 2.54	4.06	$0.10 \leq P \leq 0.25$			
Growing	8.38 $\pm$ 3.32	0.46 $\pm$ 0.13	1.28 $\pm$ 0.67	4.85	$0.05 \leq P \leq 0.10$			
Strike at with Paw	6.21 $\pm$ 2.72	2.19 $\pm$ 0.74	9.82 $\pm$ 2.64					
Arch Back	0.19 $\pm$ 0.12	0.40 $\pm$ 0.30	0.00 $\pm$ 0.00					
Striking with Paw	0.17 $\pm$ 0.06	0.52 $\pm$ 0.31	1.46 $\pm$ 0.79					
Bites at Male	0.00 $\pm$ 0.00	0.32 $\pm$ 0.32	0.33 $\pm$ 0.33					

*Only those behaviors in **bold** were tested for significance.

^aKruskal-Wallis Test [Conover, 1980] (df = 2, N = 21).

TABLE 4. Mean rates of behavior per hour ($\pm$ standard error) for behaviors exhibited by two males when paired with females in different treatments*

Behavior	Alone (A) N = 7	Sibling (S) N = 7	Parent (P) N = 7	Value ^a	Alpha	Follow-up test		
						A:P	A:S	S:P
Social Sniffing	2.01 $\pm$ 0.54	1.60 $\pm$ 0.30	8.02 $\pm$ 2.66					
Chase	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.37 $\pm$ 0.27					
Social Grooming	0.00 $\pm$ 0.00	0.09 $\pm$ 0.09	0.12 $\pm$ 0.07					
Poke with Paw	0.10 $\pm$ 0.06	0.07 $\pm$ 0.04	1.49 $\pm$ 0.63					
Head Rubbing	0.06 $\pm$ 0.06	0.03 $\pm$ 0.03	0.01 $\pm$ 0.01					
Approach Female	24.40 $\pm$ 3.66	21.91 $\pm$ 1.90	42.82 $\pm$ 3.22	11.96	$P \leq 0.005$	$z = 9.14$; $P \leq 0.05$	$z = 1.43$; n.s.	$z = 10.57$; $P \leq 0.05$
Anogenital Sniffing	0.71 $\pm$ 0.31	0.68 $\pm$ 0.20	5.03 $\pm$ 1.23	10.34	$P \leq 0.005$	$z = 9.57$; $P \leq 0.05$	$z = 0.72$; n.s.	$z = 8.85$; $P \leq 0.05$
Follows Female	2.90 $\pm$ 1.02	1.84 $\pm$ 0.36	10.00 $\pm$ 1.80	12.38	$P \leq 0.005$	$z = 8.57$; $P \leq 0.05$	$z = 2.57$; n.s.	$z = 11.14$; $P \leq 0.05$
"Chirp" Vocalization	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Nape Bite	1.75 $\pm$ 1.02	1.38 $\pm$ 0.74	4.60 $\pm$ 1.58					
Mount with Front Legs	1.00 $\pm$ 0.42	1.35 $\pm$ 0.76	2.50 $\pm$ 0.69					
Mount with Hind Legs	0.58 $\pm$ 0.39	1.24 $\pm$ 0.74	1.95 $\pm$ 0.59					
Forepaw Rubbing	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Stepping	0.41 $\pm$ 0.27	0.98 $\pm$ 0.59	1.39 $\pm$ 0.42					
'Pelvic Thrusting'	0.51 $\pm$ 0.36	1.11 $\pm$ 0.67	1.69 $\pm$ 0.52					
Intromission	0.10 $\pm$ 0.07	0.53 $\pm$ 0.35	1.37 $\pm$ 0.56	8.16	$P \leq 0.05$	$z = 8.04$; $P \leq 0.05$	$z = 2.43$; n.s.	$z = 4.86$; n.s.
Anogenital Grooming	0.58 $\pm$ 0.16	0.36 $\pm$ 0.07	1.03 $\pm$ 0.32					
Rolling on Back	0.27 $\pm$ 0.21	0.27 $\pm$ 0.14	0.24 $\pm$ 0.10					
Neck Rubbing	0.56 $\pm$ 0.29	1.13 $\pm$ 0.57	0.67 $\pm$ 0.31					
Cheek Rubbing	4.76 $\pm$ 2.40	6.19 $\pm$ 1.63	4.47 $\pm$ 2.03					
Flehmen	0.85 $\pm$ 0.29	0.97 $\pm$ 0.20	0.89 $\pm$ 0.35					
Urine Marking	0.01 $\pm$ 0.01	0.03 $\pm$ 0.02	0.00 $\pm$ 0.00					
Sharpening Claws	0.58 $\pm$ 0.18	0.38 $\pm$ 0.10	0.48 $\pm$ 0.16					
Chin Rubbing	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Hissing	0.00 $\pm$ 0.00	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02					
Growling	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Strike at with Paw	3.71 $\pm$ 1.92	0.56 $\pm$ 0.27	6.06 $\pm$ 2.05					
Arch Back	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00					
Striking with Paw	0.24 $\pm$ 0.10	0.01 $\pm$ 0.001	0.26 $\pm$ 0.72					

*Only those behaviors in **bold** were tested for significance.

^aKruskal-Wallis Test [Conover, 1980] (df = 2, N = 21).

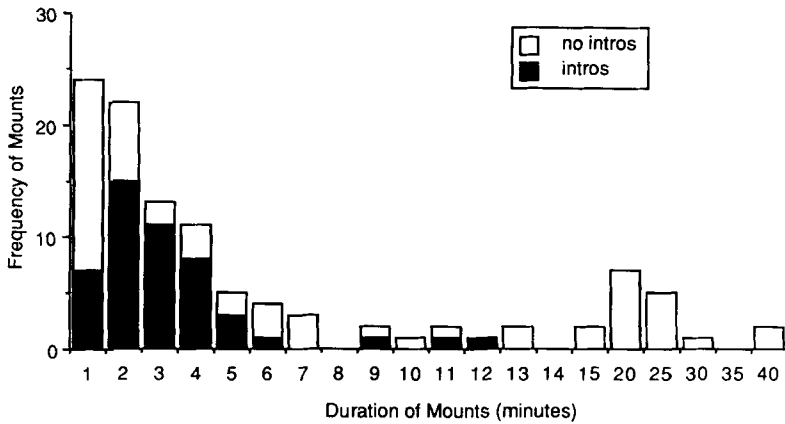


Fig. 1. Duration of all mounts by male domestic cats paired with differentially reared females. Results are based on 48 mounts in which there was intromission and on 59 mounts in which there was no intromission.

lated (as measured by the number of Intromissions) significantly more often than did the females which were Human-Raised Alone (see Tables 3, 4). In addition to the average rate of Intromission, Table 3 shows that the males Approached, Followed, and Sniffed the Anogenital Region of females in the Maternally Raised with Sib group significantly more often than the Human-Raised Alone females. As with the behavior of the females, the males' rates of those behaviors associated with copulation were all highest when they were paired with the Maternally Raised with Sib females (Table 4). The rates of aggression initiated by the males were very low for all three groups and males were remarkably tolerant to threats and attacks by females. The aggressive behavior, Strike at with Paw, virtually always occurred in response to a threat or an attack by a female. Rates of Flehmen were practically identical for the males in response to all three groups of females (Table 4).

Duration of Mounts: A Comparison of the Three Groups of Females

During the course of this study it became apparent that mounts lasting more than about 5 minutes seldom resulted in intromission. Figure 1 details the number of mounts relative to their duration. Only 4 of 48 mounts (8.33%) lasting more than five minutes resulted in intromission. Also, mounts of very short duration did not result in intromission. The shortest mount that resulted in an intromission lasted 20 seconds.

The duration of mounts was also assessed in terms of the average length of mounts for each group of females. The average length of mounts was 9.62 minutes ($n = 31$) for the Human-Raised Alone group, 5.52 minutes for Human-Raised with Sibling group ($n = 21$), and 3.63 minutes for the Maternally Raised with Sib group ($n = 55$). See Figure 2.

There was a significant difference in the duration of mounts among the three groups ($F = 6.72$; $df = 2, 104$; $P < 0.01$). Post-hoc tests indicated that the difference occurred again between the Human-Raised Alone group and the Maternally Raised with Sib group ($P < 0.05$). These data suggest that there may be subtle differences in the various females' positions/postures that facilitated successful copulations, i.e.,

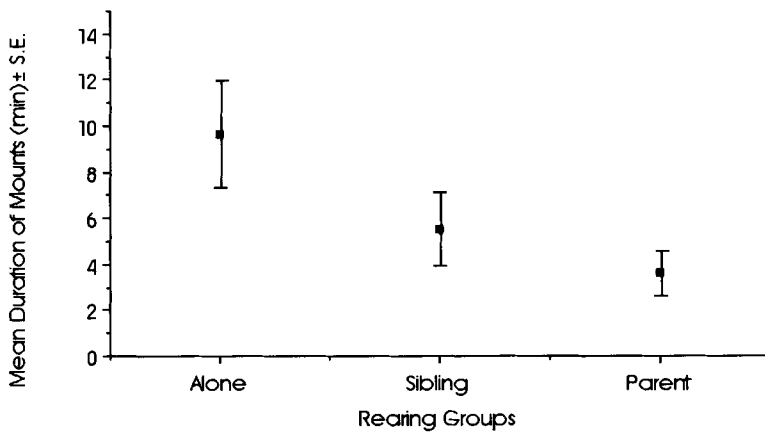


Fig. 2. Mean duration of all mounts by male domestic cats ($\pm$ standard error) with three groups of differentially reared females.

Intromission. However, in situations in which the females were overtly “cooperating” with a male during a mount, i.e., in Lordosis with Tail to One Side and Treading, the author could discern no difference in the positions/postures of females who successfully copulated as compared with those which did not.

Qualitative Differences Among the Three Groups of Females

Although no systematic assessments were made of the females’ behavior while in their home cages (other than signs of estrus and health considerations), it became obvious that the “personalities” of the cats in each group were profoundly different. The females in the Maternally Raised with Sib group (Condition III) could be described as calm and friendly toward their human caretakers. Routine husbandry procedures like replacing a flea collar presented no problem for the caretaker. However, it was very difficult to determine when these females were in estrus as they did not direct sexual behavior such as Rubbing, Rolling, and Lordosis towards humans. During pairings with the males, these females appeared playful and calm.

The behavior of the Human-Raised Alone group (Condition I) differed dramatically in many respects. Although these females appeared to be interested in the activities and approaches of their human caretakers, many individuals were extremely aggressive. They usually responded aggressively (Biting, Striking with Paws, Growling) to almost any type of direct human handling. For example, changing flea collars was very difficult, as was placing them in the transfer case. With one female, it was necessary to wear leather animal handling gloves in order to reach safely into the cage to change the litter pan. Another female frequently sat with the top of her head against the side of her enclosure, growling. The females in this group, however, were substantially friendlier while in estrus (as compared to their behavior when not in estrus) and directed pronounced sexual behavior towards humans (Rubbing, Rolling on Back, and Lordosis). In the presence of a male (during the experimental pairings), they appeared to be somewhat attracted to the male, but responded very aggressively to any approach or movements by him.

The Human-Raised with Sib group (Condition 2) was intermediate in behavior when compared to the other two groups. These females were somewhat more difficult to handle than the Maternally Raised females, but were not excessively aggressive; their personalities could be described as "nervous" or "flighty." This group also directed sexual behavior towards humans. In general, their behavior towards the males was mildly aggressive.

Upon completion of this experiment and while homes were being found for the animals, members of various groups were allowed to interact (in other words, the doors to many of the cages were opened simultaneously, allowing interactions in a large, common area). In general, the Maternally Raised with Sib females attempted to interact with other cats and humans, in most cases, in a friendly manner. The Human-Raised Alone individuals seemed not to initiate any interactions (human or feline). Approaches by other cats were responded to by Hissing, Growling, or Striking at with Paw. They tended to run away from or ignore humans. The Human-Raised with Sibling females seemed to prefer familiar people but not other cats.

DISCUSSION

Effects of Early Rearing Experience on Subsequent Adult Behavior

In this study, the Human-Raised Alone group (Condition 1) was more aggressive and exhibited the least number of behaviors associated with courtship/amicable behaviors as well as the fewest copulatory behaviors. These results are in agreement with those of Baerends van Roon and Baerends [1979]. The behavior of the Human-Raised Alone group towards their human caretakers was characterized by extremes of approach and avoidance. When in estrus, they cheek-rubbed and appeared to solicit attention, but once approached were difficult to handle. Any sudden move or any minor change was responded to by extreme aggression—claws out, growling, biting, and an uninhibited attempt to flee. When paired with males (and at peak estrus), their behavior was very interesting. They rubbed against inanimate objects, rolled, and appeared interested in the male. However, if the male approached a Human-Raised Alone female or even appeared to begin to move towards her, she usually hissed, growled, or moved away. It was as if these females were attracted to some aspect of the male, but had no social skills or experience to deal with his approaches. This is in agreement with Kleiman's belief that "... infants of some species when raised in isolation from conspecifics display inadequate social, sexual, . . . behavior when adult. The more severe the isolation, the more disturbed is the reproductive behavior" [1975, p. 172]. The general descriptions of the "personalities" of the cats parallel those of Seitz [1959] who separated kittens from conspecifics at 2 weeks of age.

With regard to the Human-Raised with Sibling group (Condition 2), the role of the sibling in the rearing experience remains enigmatic. In virtually all behavioral measures, this group was intermediate to the two other groups and in most instances, although significant differences were found between the Human-Raised Alone group and the Maternally Raised with Sib group, the Human-Raised with a Sibling group was significantly different from *neither* group. The results of this study contrast with those of Koepke and Pribram [1971], who concluded that an active mother is not necessary for the development of normal social relationships as long as kittens can interact with littermates regularly. In terms of the effect on reproductive behavior, the number of intromissions for this group was intermediate between the other two

groups, but was not significantly different from either. This group of females seemed fearful of the males, but did not respond hyperaggressively like the Human-Raised Alone group did. These results are somewhat comparable to those obtained from peer-reared ("together-together") monkeys from Harry Harlow's laboratory [Harlow and Harlow, 1962; Chamove et al., 1973]. These monkeys were much better socially adjusted than individuals raised alone, but nevertheless their social behavior was substantially impaired as compared to more normally reared monkeys. Peer-reared female rhesus monkeys (*Macaca mulatta*), as adults, showed impaired sexual behavior, e.g., an inadequate support pattern when mounted. Further, Goldfoot [1977] suggested that for eventual reproductive potential to develop, rhesus infants need a complex social environment. Rhesus raised only with peers showed high rates of play behavior, but were still deficient in sexual behavior. Goldfoot suggests that normal rearing eliminates excessive fear of peers and provides opportunities to develop affectional relationships, i.e., "to learn to trust." For these animals, mother provides security and proper social stimulation as do peers. Certainly, the Human-Raised Alone cats in the present study could be described as lacking "trust" in both their human caretakers and the males with whom they were paired.

Obviously, the primary difference between the Human-Raised with Sibling group (Condition 2) and the control group (Condition 3) was the presence/absence of a mother. Through interactions with mothers, kittens may also learn not to be afraid of conspecifics larger than themselves. (In the present study the males were substantially larger than most of the females.)

From the results of this study, it is unclear as to whether or not the non-copulating Human-Raised with Sib cats would ever have successfully copulated. Perhaps moving them to a new environment and/or providing them with yet another male would have resulted in matings. A female caracal (*Felis caracal*) who had been human-raised with a sibling exhibited responses to the male's attempts at copulation similar to those of comparably-raised the domestic cats in the present study. She later successfully copulated when moved to a new enclosure when paired with a reproductively successful male at the Sacramento Zoo (pers. observ.). Certainly, the Human-Raised with Sibling cats (Condition II) in the present study seemed better able to adjust to their environment than the Human-Raised Alone group and thus, human-raising with a sibling would seem a preferred zoo nursery regime.

It is still unclear whether this atypical social behavior was due to the absence of the mother, absence of the littermates, or both. Guyot et al. [1980] further believe that the development of social play is affected by isolation and that social play is necessary for appropriate adult social behavior [but see Martin, 1984; Martin and Caro, 1985]. Whether because of lack of social play or an inability to perceive accurately the communication of conspecifics, isolate-reared animals seem to behave inappropriately in social situations, especially in agonistic ones [e.g., Mason, 1960]. Early deprivation may have a more general effect due to a lack of experience with conspecifics; thus, these animals are unable to behave appropriately in agonistic conflicts. In the present study, the Human-Raised Alone females (Condition 1) were hyperaggressive in their behavior towards males. The males' lack of successful copulations with the Human-Raised Alone females may have been due to an inability to approach and contact, i.e., begin to mount, because the females responded so aggressively to any movement by the males. Mating in felids is thought to be "dangerous" to both parties because cats possess the ability to injure one another seriously and because

aggressive tendencies must be overcome during courtship [Wemmer and Scow, 1977]. Baerends van Roon and Baerends [1979] felt that through social play, cats learn an harmonious equilibrium between the tendencies to attack and to flee, important in copulation behavior.

Previous studies on the effects of isolate rearing on subsequent adult sexual behavior have suggested that males become more impaired than females [Duffy and Hendricks [1973], rats; Signoret [1970], pigs; Mason, 1960; Harlow, 1965; Mitchell, 1979, rhesus macaques]. Further, the male domestic cat shows some independence from hormonal control of sexual behavior [Rosenblatt and Aronson, 1958a,b], while females are totally dependent on hormones for manifestations of sexual receptivity [Michael, 1961]. Additionally, Leyhausen [1979] suggests that "during the actual copulation the female has a completely passive role as regards orientation and correct body orientation is purely the concern of the male" p. 262 [see also Larsson, 1978, pp. 80–81]. However, in rhesus macaques, Mason [1960] found that the presentation posture of isolate-reared females differed from normally reared females and Goldfoot [1977] found that female rhesus failed to support a mount or did not accommodate intromission attempts.

Data on the duration of mounts in the present study suggest that differences in early rearing experience may also result in subtle differences in the lordosis posture of female domestic cats. The average duration of mounts for the two Human-Raised groups was over 5 minutes and yet most successful mounts (with intromission) were less than 5 minutes in length. So, even if the male is successful in overcoming the higher level of aggression shown by these females, he may still be unable to complete a mount successfully because of slight postural abnormalities of the female.

Application to the Management of Exotic Cats in Captivity

Most zoo personnel believe that human raising should be considered as an alternative only when maternal neglect is obvious and cannibalism is considered a threat (one of the most common causes of death in neonates is maternal neglect [Meier, 1986]). The results of the present study, however suggest that Human-Raised Alone females are less likely to breed successfully than controls raised with both mother and sibling.

The results of this study suggest that a developmental endpoint, successful copulation, could not be reached by animals from the Human-Raised Alone group. Thus, this rearing condition would appear to be *below* the threshold required for eventual reproductive success and is therefore an undesirable approach to raising individuals earmarked for captive propagation programs. Unfortunately, zoo personnel, faced with human-raising a single individual of an exotic species of cat, sometimes must attempt to provide an environment that *is* adequate for the development of a single individual. How then can that environment be enriched? The Human-Raised with Sibling group in the present study was intended to approximate another common rearing condition in zoos—human-raising of littermates (or presumably with domestic cats as surrogate siblings) together and to test whether the presence of a peer would compensate for more normal rearing conditions [see, e.g., Yarusso, 1990]. Unfortunately, the results of this study did not conclusively demonstrate the efficacy of such a practice. The Human-Raised with Sibling group was not statistically different from either of the other two groups, and so it cannot be said conclusively that the presence of a sibling in a human-raised situation significantly improves the likelihood

of reproductive success. These animals were, however, capable of somewhat more "normal" interactions with conspecific males. Other factors must be examined as possible facilitators to reproductive success [e.g., see Mellen, 1989, 1991].

Thus, a more varied environment might compensate for a lack of conspecifics. This richer environment may provide the inertia to bring the human-raised animal above a threshold necessary for successful reproduction. Alternative rearing strategies (e.g., keepers taking the nursery-reared animal home at night allowing the animal to experience a more complex environment, including children, dogs, cats, and back-yard play areas) may result in a successfully reproducing adult.

CONCLUSIONS

1. Using domestic cats as a model for small captive exotic felids, data suggest that non-mother-raised female cats are less likely to copulate successfully as adults.
2. If zoo-nursery rearing (i.e., human rearing) is necessary, data suggest (but are not conclusive) that the presence of a sibling, conspecific, or congener may facilitate more normal development of social and sexual behaviors.
3. To counteract the inability of human-reared cats to exhibit normative adult social behavior, it is suggested that nursery-reared exotic felids be provided with a rich and varied environment, often lacking in the traditional zoo nursery setting.

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