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Reproductive behavior of small captive exotic cats (*Felis* spp.)

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Reproductive Behavior of Small Captive Exotic Cats (*Felis* spp.)

By

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DISSERTATION

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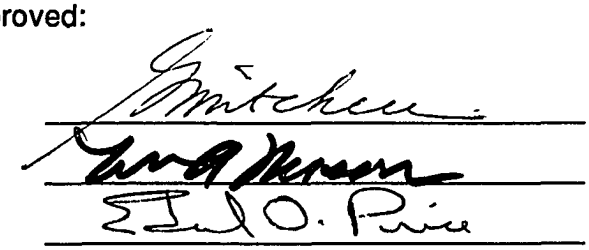

Committee in Charge

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CONTENTS

INTRODUCTION

General Characteristics of Family Felidae

In spite of considerable size differences, cats are a very uniform animal group. All felids can readily be recognized at "cats" (Weigel, 1972). Their jaws are relatively short and the long canines are adapted for grabbing prey; their molars are not adapted for crushing like most carnivores, but instead the shearing action of the carnassials are used for cutting through skin and muscle. All felids have retractile claws except cheetahs (*Acinonyx*) and fishing cats (*Felis viverrina*) (Gonyea and Ashworth, 1975). The major sensory modality is vision; cats have the largest eyes of all carnivores. Some cats have a vertically slit pupil; all have a reflective layer of cells, tapetum lucidum, behind the retina. These modifications aid in night vision (Guggisberg, 1975). The Family Felidae is characterized by its members' style of hunting: the stealthy approach, pounce, and strike. Felids usually kill their prey by either separating neck vertebrae or suffocation. Most live in a forested habitat and are solitary hunters and feeders (Kleiman and Eisenberg, 1973). Their lifestyle is generally one of inactivity punctuated by bouts of hunting (Wright and Walter, 1980). They are cosmopolitan in their distribution with the exception of Australia (Ewer, 1973).

Social Structure

With the exception of the lion (*Panthera leo*) and cheetah, felids are considered solitary (Guggisberg, 1975). In the solitary species, the only affiliative behavior is exhibited during parental care (typically a female and her cubs) and mating. The most common form of social organization is one in which a male's larger territory encompasses the smaller territories of several females. Thus, a male may not contribute directly in the rearing of offspring, but he may reduce competition for females with cubs within his territory by defending against encroaching males (Ewer, 1973). Field studies on bobcats

(*Felis rufus*), cougars (*Felis concolor*), Canadian lynx (*Felis lynx canadensis*), leopards (*Panthera pardus*), and domestic cats (*Felis catus*) have determined this social organization (reviewed by Kleiman and Eisenberg, 1973; Liberg, 1980).

Although most felids are categorized as "solitary," a certain degree of flexibility in social structure may exist (Leyhausen, 1965; Ewer, 1973). Further evidence of flexibility comes from Kleiman and Malcolm (1981) who document some direct male care of offspring in quite a few felid species under captive conditions.

Evolutionary History

An initial radiation by the felids occurred during the Oligocene, giving rise to the sabre-toothed cats; this was followed by an evolutionary line in the Miocene from which the modern genera (*Panthera*, *Acinonyx*, *Neofelis*, and *Felis*) evolved (Kleiman and Eisenberg, 1973). Early members of the Family Felidae appear to have evolved primarily in the tropical forest habitat and diversifying from there. The cheetah (*Acinonyx*) was the first of the felids to exploit the open savanna and represents the oldest living member of the Family Felidae (King, 1986). *Panthera* appeared to have evolved later than the other felid genera, during the Pliocene (Hemmer, 1966). The adaptive radiation of the genus *Panthera* seemed to accompany a similar explosive radiation by the Artiodactyla, which in turn accompanied the appearance of extensive grassland during the late Miocene and Pliocene periods. The relative small size in the genera *Felis* and *Neofelis* may have been selected to exploit small rodent prey items, render them less conspicuous to larger predators, and for some of them to utilize an arboreal niche (Kleiman and Eisenberg, 1973). To this end, most felids have evolved primarily as solitary hunters and feeders.

Taxonomy

The general taxonomy of the Family Felidae is a matter of some controversy (Leyhausen, 1969; Ewer, 1973; Guggisberg, 1975; Eisenberg, 1981; Honacki, Kinman, and Koeppl, 1982). Most taxonomists recognize a total of 38 species of cats (including domestic cats as a distinct species), but there is some disagreement concerning the number of genera into which these species are grouped. One general division is based upon size. The larger cats (lion, leopard, tiger, jaguar, snow leopard, and clouded leopard) possess a hyoid bone which is partially cartilaginous. As a result, the larynx can expand. This correlates with the cats' ability to roar. The large roaring cats are generally grouped into the genus *Panthera* (Wright and Walters, 1980). (However, Peters (1978) disputes this thesis and feels that the genus *Panthera* should be restricted to leopards, lions, and jaguars (*P. pardus, leo, onca*)). The cheetah is distinct in many respects (e.g., only partially retractile claws) from other large cats and is generally placed in a separate genus, *Acinonyx* (Eisenberg, 1981). Additionally, the clouded leopard, with the longest canine length in relation to skull size has also been placed in its own genus, *Neofelis* (Ewer, 1973). The clouded leopard, because of its general body size and behavior, is thought to be representative of a transition between the large and small cats (Weigel, 1972).

The smaller cats, in addition to being characterized by their reduced stature, possess a fully ossified hyoid bone, and do not roar. These cats are generally classified as *Felis* (Wright and Walter, 1980). However, the lynxes with their short tail, tufted ears, and total dental number of 28 (two less than other felids) are often grouped into the genus *Lynx* (Wright and Walter, 1980; Eisenberg, 1981). Additionally, a number of the small cats from South America are sometimes separated into genus *Leopardus* because they have 36

chromosomes (spp. *colocolo, geoffroyi, tigrina, pardalis*, and *wiedi*); all other cats have 38 chromosomes. Robinson's examination (1976) of the karyotypes of felids with respect to taxonomy lends some support to such a generic separation. He suggests that on the basis of distinctive karyotypes and geographic location, the above five species plus *yagouroundi* could be placed in a separate genus, with the remaining small cats in *Felis*. However, he cautions that karyotypic grouping would also place the clouded leopard (*nebulosa*) in the genus *Felis* as well as the lion, jaguar, leopard, and snow leopard (*leo, onca, pardus*, and *uncia*, respectively). Hemmer (1978), after reviewing morphological, physiological, and ethological characteristics of felids, views the living cat species as composed of ten major evolutionary lines and genera. For the purpose of this paper, a relatively conservative nomenclature of four genera was used: *Panthera*, *Acinonyx*, *Neofelis*, and *Felis*.

Purpose of this Dissertation Research

The focus of this dissertation was on species in the genus, *Felis*, maintained in captivity. With the exception of the domestic cat, all species of small cats (*Felis*) are threatened or endangered in at least some portion of their original range and although captive propagation of some groups of animals has facilitated their preservation, zoos have not been particularly successful in breeding small cats. These felids reproduce inconsistently, at best, in captivity. The purpose of this dissertation research was to examine behavioral aspects of reproduction of small cats (*Felis*) in a captive environment, to determine why reproductive success is limited, and to offer suggestions for improving their reproductive potential.

Part I of the dissertation examined whether or not estrus could be detected and monitored solely through systematic behavioral observations. The behavior of 61 individuals representing 15 species of felids housed at 7 zoological

institutions was systematically recorded for a total of 485 hours. Estrus was detectable using behavioral observations. In addition, it was found that compatibility of a pair and specific behavioral indicators of estrus could be determined through behavioral observations. Other reproductive parameters, e.g., length of estrus and gestation, birth season, litter size, and age at maturity, were gleaned from zoo records. Information on size of captive populations and level of inbreeding for these species was also collected and analyzed.

In Part II of this dissertation, the effects of early rearing experience on subsequent adult sexual behavior were examined. It is a pervasive opinion among zoo professionals that hand/human-raised felids are less likely to reproduce than are maternally-raised cats. However, numerous exceptions, i.e., hand-raised cats, have reproduced. An experiment was conducted to examine the effects of hand-rearing on adult sexual behavior, using domestic cats as a model for captive small exotic cats. Results from this experiment demonstrate that hand-rearing substantially reduces the cats' ability to reproduce. Implications for rearing techniques in zoo nurseries are discussed.

Part III of this dissertation presents suggestions for the management of these cats in captivity, both at the level of the individual (husbandry protocol) and at the level of the captive population (population management).

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Part I. Reproductive Behavior of Small Felids (*Felis*) in Captivity

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Abstract. Most members of the Family Felidae are in danger of extinction in at least some portion of their original range. Zoos have contributed to their preservation through captive propagation programs. However, zoos to date, have focused their efforts on the larger cats (*Panthera*, *Acinonyx*, *Neofelis*). At least with the *Panthera* spp., zoos have had considerable success in breeding these large cats and in most cases are managing self-sustaining, captive populations. In contrast, small cats do not breed well in captivity and the captive populations are, for the most part, very small. Invasive techniques such as artificial insemination and embryo transfer have not, to date, been very successful in aiding in the captive propagation of small felids. Further, other invasive techniques to simply monitor reproductive parameters such as estrus have been difficult to utilize because of difficulty in handling this group of animals. Non-invasive, immunoassay techniques for measuring hormones in urine or feces have yet to be developed. The purpose of this study was to determine if estrus could be detected via systematic behavioral observations on adult pairs of small cats housed in zoos. It was found that reproductively successful pairs of cats exhibit detectable changes in their behavior. Information was also obtained on copulatory behavior, communication, and scent-marking through these observations. Review of zoo records provided additional information on other reproductive parameters such as length of estrus, gestation, and age at sexual maturity. Reasons for the absence of reproductive activity in many of the pairs observed were obscured by differences in husbandry techniques between zoos and alarmingly low population numbers which in some cases were documented to have high inbreeding coefficients.

INTRODUCTION

Members of the Family Felidae are in peril throughout most of their original range. Their demise is due mainly to loss of habitat, competition with humans, the fur trade, the pet trade, and to the fact that some are considered to be "highly edible" (Guggisberg, 1979). Zoos now play a much stronger and more active role in the conservation of this and other groups of animals by building and maintaining captive populations as a way of preserving some of the genetic diversity (Foose, 1987). However, zoos have tended to focus on the larger species of cats (*Panthera, Acinonyx, and Neofelis*): the "charismatic megavertebrates." With the exception of the cheetah and clouded leopard, all of the larger cats breed well in captivity. The smaller cats (*Felis*) have not fared as well. At best, they reproduce inconsistently in captivity.

Practical and reliable methods for monitoring reproductive status are essential for any work designed to enhance the captive breeding of rare or endangered species (Hodges, 1986). A definite need exists to increase our knowledge regarding the reproductive biology of small felids in order to facilitate their captive propagation. The ability to provide an objective assessment of reproductive conditions strengthens our ability to effectively manage any captive population. Such assessment should preferably be non-invasive as small cats are usually intractable and appear to be easily stressed. Invasive methods that require repeated handling, restraint, or anaesthetization such as in obtaining vaginal smear/lavage, blood or saliva sample, palpation, ultrasonography, or laparoscopy would seem untenable for most cats and thus these methods are not viable approaches. A notable exception is work done at the San Diego Zoo in which researchers have been able to collect daily vaginal smears from a hand-raised clouded leopard

(Yamada, 1987). This animal may represent that rare exception of a hand-raised animal that is handleable, yet breeds and raises its cubs.

Non-invasive methods include the use of radio immunoassay techniques for the measurement of hormones in urine and feces. However, identifiable estrogenic components are not excreted in measurable levels in the urine of domestic cats (used as a model for exotic cats) and a reliable analysis of steroids in feces has yet to be developed (Shille, Wing, Lasley, and Banks, 1984).

Thus, it would appear that to date, the most useful measure of monitoring the reproductive status of small felids in captivity may be through systematic behavioral observations. It has been suggested that estrus in large felids can be determined via behavioral observations (e.g., Kleiman, 1974; Freeman, 1983). Schmidt, Hess, Schmidt, Smith, and Lewis (1988) have demonstrated that although not all periods of estrus are detected using only behavioral cues, during all instances in which estrous behavior (e.g., rolling, head rubbing, lordosis, increased vocalization and urination) was observed, it was accompanied by elevation of serum concentrations of estradiol. Similar data on behavioral and endocrine correlates of estrus in felids are presented in Schmidt, Nadal, Schmidt, and Beamer (1979) and Seal, Tilson, Plotka, Reindl, and Seal (1987).

Behavioral observations confer an additional advantage not available using any other method - information regarding compatibility of a pair of cats. Regardless of the reproductive potential of any animal, if a pair of cats is not compatible, natural breeding is not likely to occur. Since artificial means of propagating felids (large or small) have to date been largely unsuccessful (Wildt et al., 1987), we must for the moment rely solely on natural breeding.

The purpose of this study was to systematically examine the behavioral biology of small cats in captivity to assess whether the reproductive status of pairs of small cats could be determined via non-invasive (behavioral) observations. This "reproductive cycle profile" (d'Souza, 1978) is an evaluation of the relative changes occurring during the various stages of reproductive activity of a pair of mature animals in which the female is non-pregnant and non-lactating. Specifically, it was the intention of this study to determine whether there are consistent and measurable behavioral signs of estrus in captive small felids. Since the behavior of many species of small cats has not been systematically studied, additional information is also provided with regard to inter-species comparisons of percentage of time spent in various activities, scent-marking, and some other modes of communication.

METHODS

Data were collected on 17 species of small felids (*Felis*) at a total of seven zoological institutions. All individuals observed were assumed to be sexually mature adults. Information on species and number of animals observed, as well as where, when, and for how long is included in Table 1. Table 1 also provides information on the size and type of enclosure (i.e., naturalistic, traditional, or off-exhibit). With regard to the types of enclosures in which the cats were housed, "Off-exhibit" refers to enclosures not open to public viewing. In all instances these were cages made of hardware cloth and metal or wooden supports containing a few perching shelves and having a concrete floor. "Traditional" housing refers to enclosures in which the cats were viewed by public and were typified by a chain-link, metal support cage containing several logs, several shelves and few or no live plants.

Table 1. History of Cats Studied

Common name	Scientific Name	Location [1]	Dates Observed	Hours Observed	Size of Exhibit (m 3)	Type of Exhibit [2]
Asian Cats						
Pallas cat	*Felis manul*	Brkfld	Jun 24-Aug 18, 1984	25.50	781.72	Naturalistic
sand cat	*F. margarita*	Brkfld	Jun 24-Aug 18, 1984	21.85	228.8	Naturalistic
		Brkfld (B&#5)	Jun 24-Jul 27, 1984	16.59	14.53	Off-Exhibit
		Brkfld (F&#8)	Jun 24-Jul 27, 1984	14.37	7.26	Off-Exhibit
		WPZ	Feb 23-May 10, 1986	21.71	61.74	Trad/Natrl
fishing cat	*F. viverrina*	WPZ	Mar 2-May 10, 1986	17.05	94.42	Trad/Natrl
		San Diego	Mar 30-Apr 9, 1988	7.50	77.76	Naturalistic
		Cincin	[historical data only]	0.00	37.45	
Temminck's golden cat	*F. temmincki*	WPZ	Jun 23-Aug 29, 1987	21.92	82.55	Trad/Natrl
jungle cat	*F. chaus*	Sacto	Feb 17-Apr 27, 1985	37.47	11.59	Traditional
rusty-spotted cat	F. rubiginosus	Cincin	Oct 17-Oct 28, 1988	4.50	6.13	Off-Exhibit
African Cats						
serval	*F. serval*	WPZ	Jan 18-Mar 28, 1987	13.15	501.34	Naturalistic
		San Diego	Mar 30-Apr 9, 1988	6.00	77.76	Trad/Natrl
		Sacto	Feb 15-Apr 25, 1985	32.73	11.59	Traditional
		NZP	Jul 1-Sep 8, 1985	31.03	621.02	Naturalistic
caracal	*F. caracal*	Sacto (C&G)	Apr 3-May 17, 1985	22.84	11.59	Traditional
		Sacto (L&R)	Feb 24-May 18, 1985	35.52	11.59	Traditional
		Cincin	Oct 17-Oct 28, 1988	3.42	35.89	Trad/Natrl
black-footed cat	*F. nigripes*	San Diego	[historical data only]	0.00	13.95	Traditional
		Cincin	Oct 17-Oct 28, 1988	4.00	37.45	Trad/Natrl
South American Cats						
Geoffroy's cat	*F. geoffroyi*	WPZ	Nov 2, 1986-Jan 10, 1987	25.63	64.69	Trad/Natrl
		Sacto	Jan 31-Mar 6, 1985	26.86	13.69	Traditional
		NZP	Jul 7-Sep 5, 1985	27.69	17.75	Traditional
jaguarundi	*F. yagouarundi*	ASDM	Jan 26-Feb 5, 1988	8.97	124.84	Naturalistic
		Cincin	Oct 17-Oct 28, 1988	3.25	44.26	Trad/Natrl
ocelot	*F. pardalis*	ASDM	Jan 27-Feb 5, 1988	6.00	130.24	Naturalistic
		Cincin	Oct 17-Oct 28, 1988	3.90	40.57	Trad/Natrl
margay	*F. wiedi*	ASDM	[historical data only]	0.00	150.77	Naturalistic
		San Diego	[historical data only]	0.00	27.89	Traditional
		Sacto	[historical data only]	0.00	11.59	Traditional
Pampas cat	*F. colocolo*	Cincin	Oct 17-Oct 28, 1988	3.25	26.53	Trad/Natrl
		Cincin	Oct 17-Oct 28, 1988	4.17	6.13	Off-Exhibit
European Cats						
Scottish wildcat	*F. sylvestris grampia*	San Diego	Mar 30-Apr 9, 1988	6.00	77.76	Trad/Natrl
North American Cats						
Canadian lynx	*F. lynx canadensis*	Sacto	Mar 3-May 18, 1985	31.75	11.59	Traditional
Worldwide						
domestic cat	*F. catus*	WPZ		168.40	7.26	Off-Exhibit
			Total Number of Hour	653.02		

[1] Brkfld = Chicago Zoological Park, Brookfield, IL
NZP = National Zoological Park, Washington, D.C.
WPZ = Washington Park Zoo, Portland, OR
Sacto = Sacramento Zoo, Sacramento, CA
ASDM = Arizona-Sonora Desert Museum, Tucson, AZ
SanDiego = San Diego Zoo, San Diego, CA
Cincin = Cincinnati Zoological Garden, Cincinnati, OH

[2] see text for detail

"Naturalistic" enclosures were typified by an exhibit in which the public was presented with a representation of the animal's native habitat. It has numerous places in which the animal could hide and numerous live plants, deadfall logs, and usually large pools. Exhibits that contained naturalistic rockwork (gunite), but were relatively small and contained few places for concealment and few or no live plants were termed "Traditional/Naturalistic."

Behavioral data as well as other information pertaining to the species' reproductive profiles were collected at four zoos: Chicago Zoological Park, Brookfield, Illinois; Sacramento Zoo (Sacto), Sacramento, California; National Zoological Park (NZP), Washington, D.C.; and, Washington Park Zoo (WPZ), Portland, Oregon. Data were collected for 8-12 weeks at these institutions and are referred to as "long-term observations." Some behavioral data, as well as other information pertaining to the species' reproductive profiles, were obtained from three additional institutions: Arizona-Sonora Desert Museum (ASDM), Tucson, Arizona; San Diego Zoo (S.D.), San Diego, California; and, Cincinnati Zoological Park, Cincinnati, Ohio. These data were collected over a two-week period and are referred to as "short-term observations."

Behavioral Data

Behavioral data for both the long-term and short-term observations were collected via direct observation using a combination of a scan sampling and all occurrences of selected behaviors sampling methods (Altmann, 1974). Definitions of behaviors recorded using the scan sampling technique are in Table 2; definitions of behaviors recorded using the all occurrences of selected behaviors technique are in Table 3. Behavioral observations were made during regular visitor hours at the respective zoos, between 09:00 - 17:00 local time.

Table 2. Ethogram for *Felis* in zoos - scan sampling with a 30-second interval.

Behavior	Description
Resting	sitting or lying down with eyes closed and not exhibiting any other behavior
Rest-Alert	sitting or lying down with eyes open and apparently orienting
Standing	quadrapedal or bipedal stance
Locomoting	directional movement
Pacing	repetitive movement, i.e., the same area is traversed repeatedly
Self-grooming	licking, chewing, and/or cleaning own fur; scratching self with hind paws
Eating/Drinking	as implied; includes chewing on bones
Urinating/Defecating	as implied; this includes urinating both on a horizontal and a verticle surface
Inanimate Sniffing	orienting to and apparently sniffing an inanimate object, i.e., anything but another cat
Other Solitary	any other non-social behavior not listed above
Social Behavior	any social behavior, i.e., any behavior involving another cat; this includes sexual, agonistic, or amicable interactions
Not Visible	cat not visible to observer; behavior of cat not visible

Table 3. Ethogram for *Felis* in zoos - all occurrences of some behaviors

Behavior	Description
Solitary Behaviors	
Cheek rubbing	cheek of cat rubbed against an inanimate object
Head rubbing (inanimate)	head (forehead region) of cat rubbed against an inanimate object
Neck rubbing	cat vigorously rubs/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)
Flehmen	open-mouth grimace following the sniffing of an object or cat
Urine marking	urinating on verticle surface, tail is usually held straight up and sometimes the distal one-third of the tail is vibrated or appears to quiver; behavior sometimes includes scraping substrate with hind feet
Anogenital self-grooming	cat grooms its own genitals for a least four seconds
Rolling on Back	as implied
Flehmen	open mouth grimace following the sniffing of an object or another cat
Social Behaviors	
"Spit" vocalization	cat orients to another cat and emits an explosive sounding "spit" vocalization
Hiss vocalization	cat orients to another cat and emits a hissing vocalization
Growl vocalization	cat orients to another cat and emits a growl
Strike at	cat strikes at another with its paw, but no contact is made
Strike with paw	cat strikes another with its paw

Table 3. (continued) Ethogram for *Felis* in zoos - all occurrences of some behaviors

Biting	as implied
Mounting	dorso-ventral mounting with nape bite and straddling of female with both front feet and hinds feet; presence or absence of "pelvic" thrusting, stepping with hind feet, and/or intromission noted in the male; lorsosis posture, treading with hind feet, tail to one side, and "copulatory cry" noted in the female
Attempted Mount	male nape bites, but does not straddle female with both front and hind feet
Lordosis	female lowers her forequarters while elevating her hindquarters; tail is often moved to one side
Social head rubbing	head (forehead region) rubbed against another cat
Social Grooming	one cat licks and/or nibbles on the fur of another cat
Anogenital sniffing	cat sniffs the anogenital region of another
Social sniffing	cat sniffs any region other than the anogenital region of another cat
Following	cat follows with two body lengths other cat for a distance of at least two body lengths
Displacing	cat directly approaches another cat (within one body length) and within five seconds of the approach, the second cat moves away at least one body length
Approaching	cat directly approaches another cat (within one body length) and the cat approached does not move away
Chasing	one cat runs at or after another cat
Face-Off	both cats simultaneously face on another (usually both are in a sitting position); cats are within one to two body length of each other and stare intently at each other; this behavior is usually preceded and/or followed by an agonistic interaction; duration is variable (10 seconds to 2 minutes).

Long-term data collected using the scan sampling technique were converted to average percentage of time spent in each of the behavioral categories (Wilson, 1978) and selected behavioral categories were graphed over time. Data collected using the all occurrences of selected behaviors technique were converted to weekly rates per hour for each behavior (Wilson, 1978) and graphed over time.

Total rates per hour as well as standard error for behaviors associated with scent-marking behavior were obtained by averaging weekly totals. Short-term data were collected in the same manner as described above except data were converted to daily rates per hour as opposed to weekly.

With the exception of some data collected at the Sacramento Zoo, all data were collected by the author. At the Sacramento Zoo, five undergraduate students from the University of California at Davis assisted the author in data collection and all were trained by her. Interobserver reliability was measured by producing a 30-minute video tape of a pair of cats at the Sacramento Zoo and then reviewing it numerous times and in slow-motion to establish a standard. This standard was then compared with the data collected by each of the six observers (including the author). Interobserver reliability was calculated using Cohen's Kappa (see Lehner, 1979, p. 133). Mean Kappa value for the six observers was 88.00.

Reproductive Data

Data on a variety of reproductive parameters were obtained by reviewing zoo records at the various institutions. They were obtained from direct observations, ISIS records (International Species Inventory System), keeper records, and/or medical records. These parameters included:

1) length of estrus, defined here as the period of receptivity by the female and/or a pronounced increase in interest in the female by the male
2) length of estrous cycle, i.e., the inter-estrus interval or the number of days between the midpoint of one estrus to the midpoint of the next estrus
3) gestation, measured from the last day copulations were observed to the date of parturition
4) birth season, i.e., evaluating the number of litters produced per month for season peaks
5) litter size, i.e., mean litter ± standard error
6) sex ratio of kittens produced, i.e., the number of males, females, and kittens of unknown sex
7) age at sexual maturity, defined as age of the cat (both male and female) when first litter was born
8) whether or not females observed in the present study had successfully reared offspring, i.e., kittens survived to six weeks of age under the care of their mother) and whether or not the cats observed in the present study represented second-generation, captive-born offspring.

In addition to the above parameters, keepers were asked whether or not the female cats under their care showed overt signs of estrus and to describe those signs.

RESULTS AND DISCUSSION

Behavioral Profiles

Wright and Walters (1980) described the behavior of felids as "generally one of inactivity punctuated by forays in search of food" p. 13. Average percentages of time spent by each species in various activity categories are presented in Figure 1 for cats observed in the present study. These data demonstrate that in captivity, small cats' behavior may be described generally as one of inactivity punctuated by brief bouts of scent-marking and even briefer bouts of social interaction.

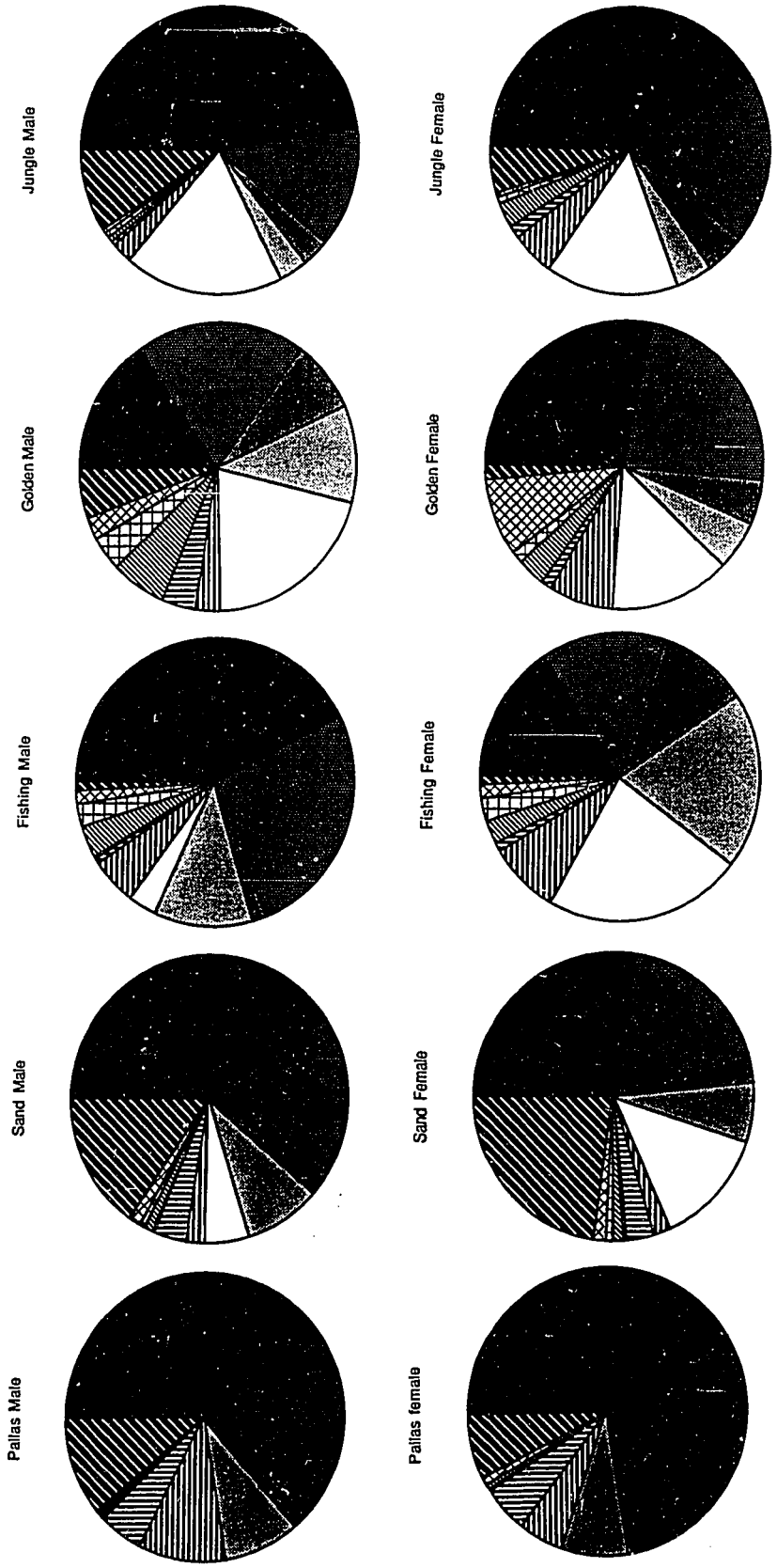


Figure 1. Average percent time spent in various activities by cats observed in this study

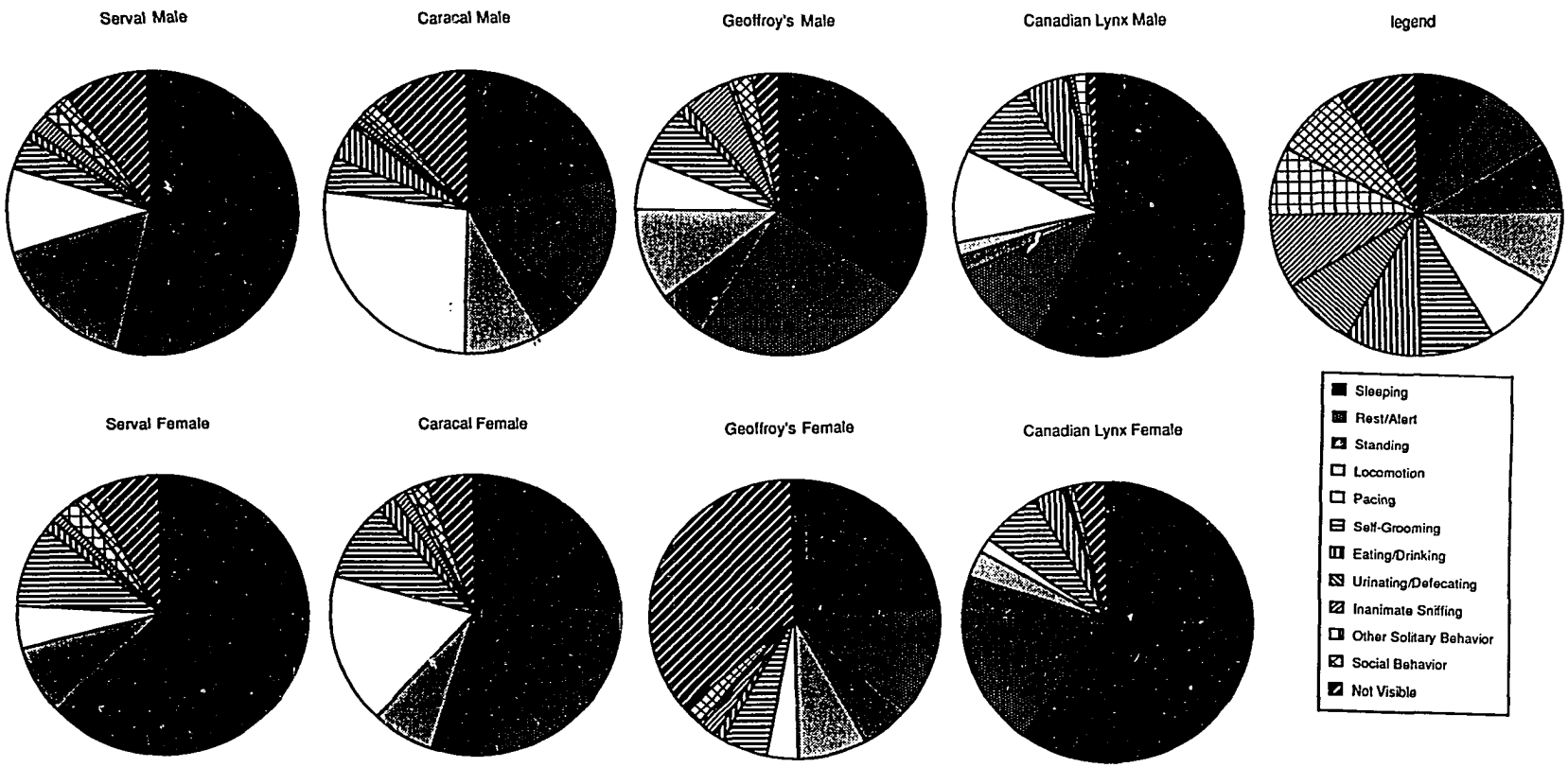


Figure 1. (continued) Average percent time spent in various activities by cats observed in this study

Behaviors Associated with Scent-Marking

Urine, feces, and glandular excretions presumably carry chemical information. Scent-marking behavior may function not only to deposit information-laden odors, but the scent may be delivered in such a way as to be visually conspicuous, e.g., scraping with hind feet (Wemmer and Scow, 1977). A summary of data on behaviors associated with scent-marking are presented in Tables 4a (males) and 4b (females). Average rates of these behavior are presented for those cats that were studied for 8-12 weeks (long-term). Further, if a particular behavior associated with scent-marking was observed outside of formal observations (and thus not quantified), their observed occurrence is indicated by a plus (+) sign. Rates of behaviors for species that were observed during brief two-week visits (short-term) are not presented, but if a particular behavior was observed it is indicated as such in Table 4 as having been observed with a plus (+) sign. These data are meant to serve as an overview of scent-marking behavior for these species of cats.

Figure 2 presents additional information on selected behaviors associated with scent-marking which will allow comparisons of those individuals (studied long-term) that demonstrated reproductive activity to non-reproductive individuals. The following females were assumed to have been in estrus during some portion of the time they were observed: WPZ sand cat, WPZ golden cat, Sacramento jungle cat, WPZ serval, Sacramento caracal (L&R pair), NZP Geoffroy's cat, and WPZ domestic cats. With the exception of the WPZ serval and some of the domestic cats, estrus was assumed because mounting was observed. Reasons for the assumption that the WPZ female serval and the WPZ domestic cats were also in estrus are discussed at length in a subsequent section of this paper (Part I of dissertation) and Part II of this dissertation, respectively. None of the sand cats observed at Brookfield

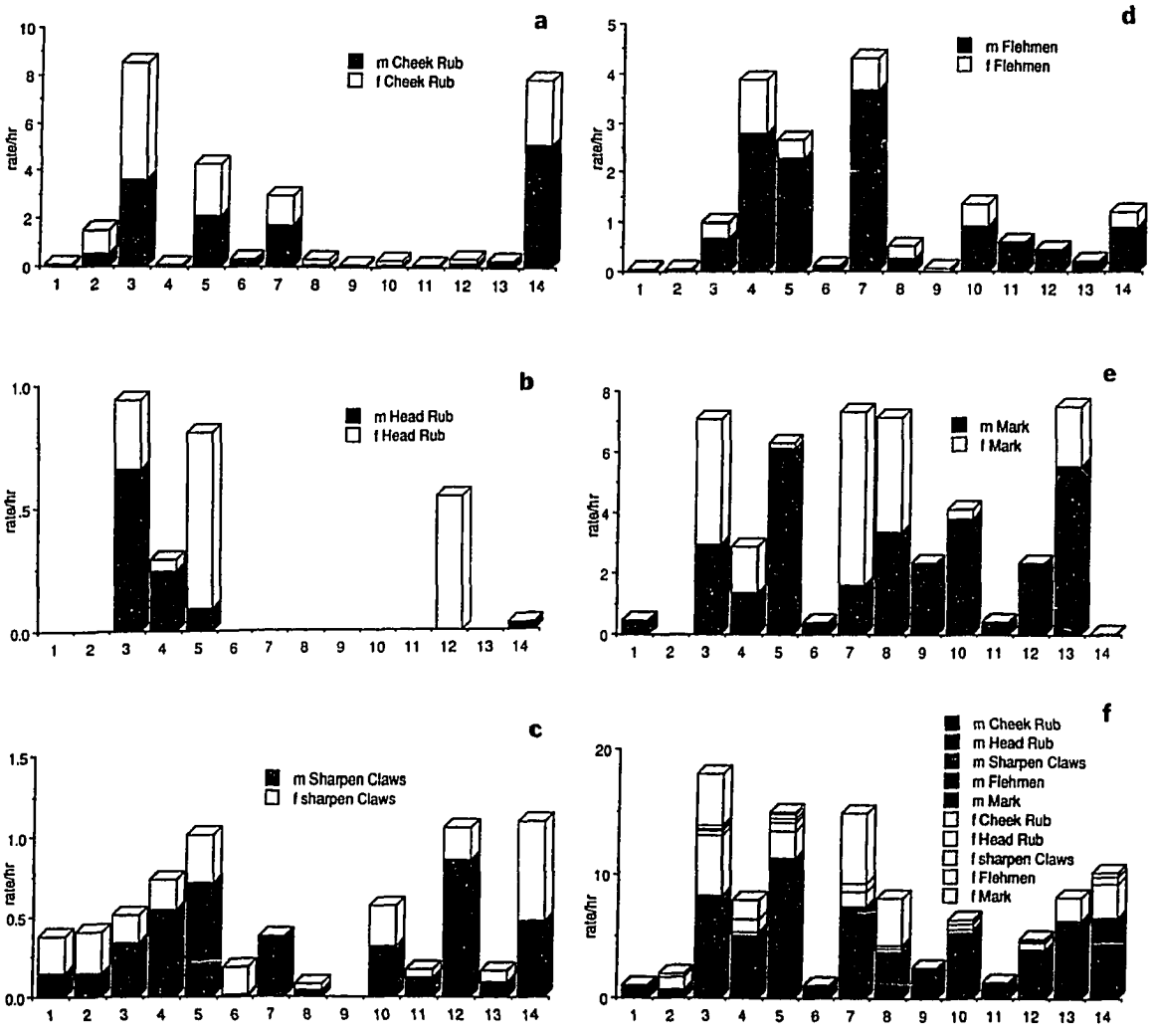
Table 4. Marking Behavior for Male and Female Captive Small Felids

a

Males	Scientific Name	Cheek Rub	± SE	Head Rub Inanimate	± SE	Chin Rub	Neck Rub	Sharpen Claws	± SE	Flehmen	± SE	Mark	± SE	Scrape with Hind Feet	Tail Quiver	N=
Asian Cats																
Pallas cat	*Felis manul*							0.15	0.12	0.03	0.03	0.47	0.21	+		1
sand cat	*F. margarita*	1.83	0.53	0.26	0.15			0.23	0.07	0.26	0.12	1.17	0.47			4
fishing cat	*F. viverrina*	0.05	0.05	0.24	0.12			0.54	0.21	2.77	0.54	1.39	0.20			1
Temminck's golden cat	*F. temmincki*	2.10	0.71	0.09	0.09	+	+	0.72	0.24	2.26	0.36	6.14	0.97	+		1
jungle cat	*F. chaus*	0.22	0.12					0.01	0.01	0.10	0.08	0.40	0.23			1
rusty-spotted cat	*F. rubiginosus*							+		+		+				1
African Cats																
serval	*F. serval*	0.65	0.37			+		0.15	0.08	1.39	0.61	2.81	0.75	+	+	3
caracal	*F. caracal*	0.05	0.03					0.18	0.07	0.53	0.27	3.08	0.71		+	2
black-footed cat	*F. nigripes*	+				+	+			+		+			+	2
South American Cats																
Geoffroy's cat	*F. geoffroyi*	0.07	0.04			+	+	0.40	0.13	0.45	0.12	1.05	0.33	+	+	3
jaguarundi	*F. yagouarundi*	+					+	+		+		+		+		2
ocelot	*F. pardalis*	+		+		+	+	+		+		+		+		2
Pampas cat	*F. colocolo*	+				+				+		+		+	+	2
European Cats																
Scottish wildcat	*F. sylvestris grampia*											+			+	1
North American Cats																
Canadian lynx	*F.lynx canadensis*	0.16	0.07	+				0.09	0.05	0.21	0.10	5.57	2.36		+	1
World Wide Distribution																
domestic cat	*F. catus*	5.14		0.03		0.01	0.79	0.48		0.90		0.01		+		2

b

Females	Scientific Name	Cheek Rub	± SE	Head Rub Inanimate	± SE	Chin Rub	Neck Rub	Sharpen Claws	± SE	Flehmen	± SE	Mark	± SE	Scrape with Hind Feet	Tail Quiver	N=
Asian Cats																
Pallas cat	*Felis manul*	0.11	0.06					0.23	0.07	0.02	0.02					2
sand cat	*F. margarita*	2.25	0.63	0.09	0.07		+	0.25	0.07	0.10	0.04	1.29	0.93			5
fishing cat	*F. viverrina*	0.05	0.05	0.05	0.05			0.20	0.08	1.09	0.46	1.50	0.43			1
Temminck's golden cat	*F. temmincki*	2.17	1.81	0.71	0.52		+	0.30	0.13	0.39	0.23	0.17	0.12			1
jungle cat	*F. chaus*	0.11	0.11					0.17	0.11	+						1
rusty-spotted cat	*F. rubiginosus*						+			+		+				1
African Cats																
serval	*F. serval*	0.54	0.20			+		0.05	0.02	0.39	0.12	4.89	1.86	+	+	3
caracal	*F. caracal*	0.14	0.09					0.14	0.06	0.27	0.15	0.21	0.11			2
black-footed cat	*F. nigripes*											+			+	2
South American Cats																
Geoffroy's cat	*F. geoffroyi*	0.10	0.06	0.20	0.16	+	+	0.10	0.04	0.01	0.01	0.03	0.03	+		3
jaguarundi	*F. yagouarundi*						+	+		+				+		3
ocelot	*F. pardalis*	+		+			+	+		+				+		2
Pampas cat	*F. colocolo*															2
European Cats																
Scottish wildcat	*F. sylvestris grampia*	+		+			+	+								2
North American Cats																
Canadian lynx	*F.lynx canadensis*	0.13	0.09					0.08	0.04			1.96	0.91		+	1
World Wide Distribution																
domestic cat	*F. catus*	2.73		0.00		0.00	9.24	0.62		0.30		0.02				21



1 Pallas cat
2 sand cat -Brookfield
3 sand cat - WPZ
4 fishing cat
5 golden cat
6 jungle cat
7 serval - WPZ
8 serval - NZP, Sacto
9 caracal - Sacto (C&G)
10 caracal - Sacto (L&R)
11 Geoffroy's cat - WPZ
12 Geoffroy's cat - NZP
13 Canadian lynx
14 domestic cat - WPZ

Bold print indicates data from those pairs in which the female was in estrus during some portion of the observation set

Figure 2. Average rates of selected scent-marking behaviors which allow for comparisons of those individuals that demonstrated reproductive activity to those individuals that were not reproductively active. m = male; f = female

showed any reproductive activity during the time in which they were observed so the males' data and the females' data were respectively pooled; the data for the two female Pallas cats and the NZP and Sacramento servals were also pooled for the same reason.

Cheek Rubbing. With the exception of the trio of Pallas cats, all species of cats observed on the present study were seen to cheek rub (Table 4) and the rate at which cheek rubbing occurred was about equal for both males and females (Figure 2a). In general, a higher rate of of cheek rubbing was seen in those pairs demonstrating reproductive activity (Figure 2a). Cats presumably rub saliva onto inanimate objects via cheek rubbing (Ewer, 1973; Fox, 1974; Wemmer and Scow, 1977). They also cheek rub against objects which have previously been sprayed with urine (Wemmer and Scow, 1977). Male domestic cats can apparently differentiate phases of the estrous cycle of females from cheek gland secretions (Verberne and de Boer, 1976). Reiger (1979) and Reiger and Walzthonz (1979) contend that cheek rubbing in Felidae functions not as a "marking" behavior, i.e., laying down a scent, but to pick up scent from the substrate. They further suggest that cheek rubbing serves as a visual display. From data collected during the present study (both Parts I and II of this dissertation), it would appear that cheek rubbing serves to deposit a scent (saliva), to pick up scent (by cheek rubbing against urine marks), and as a visual display (males frequently oriented to estrous females and repeatedly cheek rubbed).

Head Rubbing. When data from Table 4 are compared to those compiled by Wemmer and Scow (pp. 754-755, 1977), head rubbing was observed in relatively fewer species in the present study. However, Wemmer and Scow (1977) describe head rubbing, as well as recumbent head rubbing, to be evoked by strong, novel odors such as carrion, vomit, feces of strange

animals, and catnip. Since the pairs observed in the present study had little contact with novel odors, the probability of observing these behaviors was reduced. No trends were apparent with regard to the relative rates of head rubbing between sexes or between reproductively active versus inactive individuals (Figure 2b).

Neck Rubbing. The behavior termed "neck rubbing" in the present study appears to be similar to Wemmer and Scow's description (1977) of recumbent head rubbing and was observed in apparent response to urine marks of a mate. Additionally, this behavior was frequently seen in both males and females during introductions of pairs (e.g., see description of jaguarundi in Part I of this dissertation) and when a female was in estrus (see Courtship Behavior of Domestic Cats in Part II of this dissertation).

"Sharpening" Claws. This behavior was observed in most species in both the present study (Table 4) and in Wemmer and Scow's study (1977). Data from the present study show that it is exhibited at a somewhat higher rate in males than females and its relative occurrence does not seem to be related to reproductive activity alone (Figure 2c). This behavior is thought not to function to "sharpen" claws *per se*, but instead may function to remove loosened claw sheaths and it probably also serves to leave a visual signal by modifying or disturbing the substrate (Wemmer and Scow, 1977). In the present study, it was a commonly observed behavior, seen both as a part of scent-marking behavior (e.g., occurring in the same areas as urine marking) and as an apparent "displacement" behavior when a male was repeatedly and vigorously threatened by an estrous female (see Part II of this dissertation).

Flehmen. Observations made during the present study support the general description and sequence of occurrence described elsewhere (e.g., Wemmer and Scow, 1977; Wright and Walters, 1980; Hart and Hart, 1985). Typically, a

urine spot is approached, sniffed, and then the cat exhibits a flehmen response. When a cat flehms, it raises its head with mouth half open; the upper lip is slightly withdrawn and the bottom jaw is lowered slightly. The cat appears almost immobilized, has a staring look, and breathes slowly. The flehmen response, its relationship to the vomeronasal organ (VNO), and the role of the VNO have been systematically investigated in domestic cats by Verberne (1976). Via the flehmen response, an animal utilizes the VNO, an accessory olfactory system, to examine the urine (or other substances) for the presence of nonvolatile chemical substances. Flehmen and the use of the VNO system appear to be involved in confirming or refining olfactory discrimination by the primary olfactory system.

Ewer (1973) suggested that a flehmen response may be universal among Felidae. With the exception of the trio of Scottish wildcats and the female Canadian lynx, all species observed (both male and female) in the present study were observed to exhibit a flehmen (see Table 4), offering support for Ewer's suggestion. Male domestic cats flehm more frequently than females (Hart, 1985); data from the present study demonstrate that in virtually all pairs observed, the male's rate of flehmen was higher than the female's (Figure 2d). The occurrence of a flehmen response also appears to be a good indicator of reproductive activity (Figure 2d).

Urine Marking. In felids, the most prominent scent-marking behavior is performed by spraying urine against vertical objects (Fiedler, 1955; Verberne, 1970; Schaller, 1972; Verberne and Leyhausen, 1976; Leyhausen, 1979). Some cats also scrape or scratch the substrate with their hind legs during/after urination (Kleiman and Eisenberg, 1973; Wemmer and Scow, 1977). These "scrapes" presumably serve to impregnate urine scent onto the hind feet of the cat as well as possibly functioning as a visual signal (Schaller, 1972;

Verberne and Leyhausen, 1976; Wemmer and Scow, 1977). Although urine is presumably used to mark a felid's territory, the urine spot itself is not a deterrent. Instead it allows for the temporal spacing and thus avoidance of confrontation (Hornocker, 1969; Schaller, 1972 Fox, 1974; de Boer, 1977).

Kleiman and Eisenberg (1973) state that both male and female felids spray, i.e., urinate on a vertical surface, but the behavior is much more common in males than females. Data from the present study support both these suppositions. Males from all species observed, and females from most species observed, urine marked, i.e., sprayed urine on a vertical surface (Table 4).

Males of most species sprayed urine at a higher rate than did females (Figure 2e). Notable exceptions were female servals. Total rate of all scent-marking behavior does not seem to be a good indicator of reproductive activity (Figure 2f).

In the present study, two behaviors were often seen in association with urine marking or spraying. Those behaviors are scraping with hind feet and "tail quiver." As discussed above scraping with hind feet may serve to impregnate urine scent on to the hind feet of the cat as well as possibly function as a visual signal. Tables 4 details in which species scraping with hind feet was observed during the present study.

A second behavior observed in the present study in association with urine marking is termed "tail quiver". When urine spraying, virtually all species observed raised their tails vertically while spraying. In some species, the terminal one-third of the tail sometimes twitched or quivered during the spraying. Table 4a and 4b detail in which species tail quivering while urine marking was observed during the present study. Wemmer and Scow (1977)

suggest that the tail is raised just prior to spraying in order to orient the direction and location of the spray. They further suggest that the quivering or twitching of the end of the tail may serve as a visual signal or may simply be an automatic manifestation of urine emission. Observations made during the present study cannot offer any additional insight into the function of this behavior. Even in those individuals who were observed to tail quiver, this behavior did not accompany every bout of spraying. The cats instead exhibited a tail quiver during sprays that appeared particularly "vehement" in execution.

In general, reproductively active felids appear to exhibit a higher rate of scent-marking behavior. However, no single marking behavior appeared to be a good indicator of reproductive activity. Rather, the relative change over time appears to be a better indicator of reproduction. Data to that effect will be presented later in this paper. Further, data will be presented indicating that the rate of scent marking by the male drops during the female's estrus, while the rate of scent marking by the female rises during estrus.

Social Behavior of Captive Small Felids

Cats communicate with one another via a combination of visual, auditory, and olfactory signals. Some aspects of olfactory communication have been discussed above, i.e., scent-marking behavior. Auditory communication was not addressed in the present study because many of the observations were made through glass barriers or in situations with substantial background noise and thus no systematic data were obtained on vocalizations. However, visual communication was addressed and measured with respect to selected social behaviors. Because the goal of the present

study was not a systematic evaluation of visual communication modes, but rather whether measurable changes in these behaviors might be indicative of reproductive activity, discussion of social behaviors will be brief.

Social behavior made up only 1-2% of the cats' time in captivity so the rates of occurrence were very low. Tables 5a (males) and 5b (female) present a listing of social behaviors observed in the present study with an indication of whether or not each of these behaviors was observed for a particular species. For ease of examination, data are represented as having been observed to occur, indicated by a plus (+) sign, or not to occur. These data are simply meant to serve as an overview of the occurrence of social behavior for these species of cats. As will be discussed later in this paper, the occurrence of social behavior was quite variable and changed over time. When graphed over time, patterns emerged.

Tables 5a and 5b suggest that a wide variety of small cats utilize similar broad behavioral categories with which to communicate. However, the details of each of these behavioral categories and their interaction with species-specific vocalizations are quite unique (see Leyhausen, 1979 for discussion of these differences).

Although it is not the intention of the present study to discuss in detail specific aspects of social behavior/visual communication in small felids, opportunities to view numerous agonistic interactions have prompted a brief discussion of the function of some of the more universal and conspicuous coat colors and markings on the fur of the small cats observed in the present study.

Table 5. Occurrences of Social Behaviors in Small Felids

a

Males	spit	hiss	growl	strike at	strike with paw	bite	mount	attempt mount	social head rub	social groom	anogenital sniff	social sniff	follow	displace	approach	chase	face off	lip quiver *	paw on chest *
Asian Cats																			
Pallas cat		+		+								+		+	+	+	+	+	
sand cat	+	+	+	+	+		+	+		+	+	+	+	+	+		+		
fishing cat		+		+	+						+	+	+		+		+		
Temminck's golden cat			+	+	+	+	+	+	+	+	+	+	+		+	+	+		
jungle cat		+	+	+			+	+		+	+	+	+	+	+	+			
rusty-spotted cat							+	+		+	+	+	+		+		+		
African Cats																			
serval		+	+							+	+	+	+	+	+		+		+
caracal		+	+	+			+			+	+	+	+	+	+				
black-footed cat	+	+	+										+		+		+		
South American Cats																			
Geoffroy's cat		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
jaguarundi		+	+							+	+	+	+	+	+	+	+		
ocelot				+		+	+	+	+	+	+	+	+		+		+		
Pampas cat	+	+			+		+	+	+	+	+	+			+				
European Cats																			
Scottish wildcat															+				
North American Cats																			
Canadian lynx					+						+			+					
World Wide Distribution																			
domestic cat		+		+	+	+	+	+		+	+	+	+	+	+	+	+		

* see text for description

b

Females	spit	hiss	growl	strike at	strike with paw	bite	lordosis	social head rub	social groom	anogenital sniff	social sniff	follow	displace	approach	chase	face off	lip quiver *	paw on chest *
Asian Cats																		
Pallas cat		+		+	+	+			+	+	+	+	+	+	+		+	
sand cat	+	+	+	+	+		+			+	+	+	+	+		+		
fishing cat		+			+	+				+	+	+	+	+	+	+		
Temminck's golden cat		+	+	+	+	+	+	+	+	+		+		+		+		
jungle cat			+	+	+				+	+	+	+		+	+			
rusty-spotted cat		+	+		+		+	+		+	+	+		+		+		
African Cats																		
serval		+	+	+	+	+		+	+	+	+	+	+	+	+	+		+
caracal		+	+	+	+	+	+	+	+	+	+	+	+	+	+			
black-footed cat	+	+	+	+												+		
South American Cats																		
Geoffroy's cat		+		+	+	+	+	+	+	+	+	+		+	+	+		
jaguarundi		+	+		+	+		+	+		+			+	+	+		
ocelot		+	+	+	+	+	+	+	+		+	+		+	+	+		
Pampas cat	+	+		+	+	+			+	+	+			+				
European Cats																		
Scottish wildcat**					+			+				+		+				
North American Cats																		
Canadian lynx		+							+	+				+				
World Wide Distribution																		
domestic cat																		

** hormonally implanted to prevent pregnancy

Markings on Pelage of Small Cats. Felids have the most varied coat patterns of any carnivore and although much of their coat pattern functions in thermoregulation and camouflage, other markings enhance communication (Ewer, 1973). The possible function of some of the more conspicuous markings will be discussed below.

The markings on the coats of these cats (especially on the face and tail), although overtly quite varied, contain several pervasive patterns. The backs of the ears in all species but one (jaguarundi) possessed a contrasting color and/ or marking, the most conspicuous being the white "eye spot" on the spotted cats (e.g., fishing cat, serval, black-footed cat, ocelot, and margay). Ewer (1973) suggests that these "eye spots" function to provide a visual cue for cubs when following their mother. From observations made in the present study, it appears that the contrasting color on the backs of the cats' ears function to emphasize a threat posture. During an agonistic interaction, a threatening cat rotates its ears laterally, while keeping them extended; the result is that the backs of the ears are highly visible to an individual facing that cat. Leyhausen termed this posture a "threat mask". (See photographs on p. 171 of Leyhausen, 1979). He proposed that "the proportion of the attacking mood is indicated by how much of the back of the ear is visible from the front" (p.195, Leyhausen, 1979). Conspicuous and/or contrasting markings on the backs of the ears appear to accentuate this threat posture (Fox, 1974; Leyhausen, 1979; pers. observ.).

Further, all species of cats observed in this study (except the jaguarundi) had contrasting rings and/or tip of the tail. Another aspect of agonistic interactions of cats involves the lateral thrashing of the tail. Such contrasting markings on the tail may function to exaggerate or accentuate this threat (Fox, 1974; Leyhausen, 1979; pers. observ.).

Reproductive Data for Captive Small Felids

Table 6 contains a compilation of reproductive data obtained as a result of the present study. The data presented in Table 6 contain only original data collected during the present study and are not a compilation of published information. Discussion of these data is presented below. Historical data were also collected on small cats at the seven zoos and used to determine if captive-born litters were produced seasonally. These data are presented in Figure 3 and are discussed in the text below.

Summary of Information on Small Cats Studied

A brief description of each the species observed during the course of the present study follows. For those cats in which breeding activity was observed, interactions are described in detail. Other reproductive parameters are discussed, especially in relationship with other information available on that species. Only those reproductive aspects for which the author had original data are compared to published information. Each of the species examined in the present study is also discussed with respect to its captive population size; and, where information was available, its level of inbreeding was evaluated. Inbreeding and its effects on small captive populations will be discussed in more detail in Part III of this dissertation. However, suffice it to say here that the deleterious effects of inbreeding on small captive populations have been well documented (e.g., Ballou and Ralls, 1982; Ralls and Ballou, 1982a, 1982b). Level of inbreeding is assessed by calculating an inbreeding coefficient (F), defined as the probability that two alleles present at a locus are identical by descent. The F value ranges from 0 (for non-bred individuals) to 1.0 (for totally homozygous individuals), and the degree of inbreeding is dependent upon how closely related the parents are (Ballou, 1983).

Table 6. Reproductive Data

	Scientific Name	Duration of [1] Mounts (min)	Length of [3] Estrus (days)	Length of Estrous Cycle (days) [4]	Gestation (days) [5]	Birth [6] Season
Asian Cats						
Pallas cat	*Felis manul*	-	-	-	-	yes
sand cat	*F. margarita*	8.83±2.13 (n=3)	5.25±0.75 (n=2)	46 (n=1)	66.5±0.50 (n=2)	no
fishing cat	*F. viverrina*	-	-	-	70 (n=1)	no
Temminck's golden ca	*F. temmincki*	-	6.00±0 (n=2)	39 (n=1)	-	no
jungle cat	*F. chaus*	2.50 (n=1)	-	-	63 (n=1)	-
rusty-spotted cat	*F. rubiginosus*	0.92±0.11 (n=8)	≥4 but < 6dys (n=1)	-	67.6±2.0 (n=4)	no
African Cats						
serval	*F. serval*	-	4 (n=1)	-	-	no
caracal	*F. caracal*	2.00±0.5 (n=3)	5 (n=1)	54 (n=1)	-	-
black-footed cat	*F. nigripes*	-	-	-	-	no?
South American Cats		[2]				
Geoffroy's cat	*F. geoffroyi*	1.14±0.25 (n=3)	2.50±0.50 (n=2)	20 (n=1)	71 (n=1)	no?
jaguarundi	*F. yagouarundi*	-	3.17±0.75 (n=6)	53.63±2.41 (n=8)	-	yes
ocelot	*F. pardalis*	1.50 (n=1)	4.63±0.63 (n=6)	25.11±4.33 (n=9)	83 (n=1)	no
margay	*F. wiedi*	-	4 (n=1)	-	84 (n=1)	no
Pampas cat	*F. colocolo*	-	-	-	-	no
European Cats						
Scottish wildcat	*F. sylvestris grampia*	-	-	-	-	yes
North American Cats						
Canadian lynx	*F.lynx canadensis*	1.50 (n=1)	-	-	-	-
Worldwide Distribution						
domestic cat	*F. catus*	2.64±0.32 (n=48)	5.13±0.24 (n=15)	15.10±0.70 (n=9)	62.9±0.74 (n=8)	yes

[1] mount with intromission; n= number of observations
[2] mounts observed but no apparent intromission
[3] period of interest by male &/or period of rubbing/rolling/ > vocalization by female
[4] measured from the first day mounting was observed during each of two consecutive estrous periods
[5] calculated from last day of observed mounts

Table 6. (continued) Reproductive Data

	Litter Size[7] (Mean ± S.E.)	Sex Ratio of Litter [8]	Age at [9] Maturity(wks)	Young Reared by Mother in Captivity?	2nd Generation Young Produced in Captivity?	Data based upon:
Asian Cats						
Pallas cat	3.57±0.53	7.13.5	F 57.43	yes	yes	7 litters to 5 pairs of 4.4 cats
sand cat	2.92±0 .21	18.22.33	M 67.67	yes	yes	25 litters to 6 pairs of 5.5 cats
fishing cat	2.22±0 .22	9.7.4	F 63.14	yes	yes	9 litters to 2 pair of 2.2 cats
Temminck's	1.11± 0.11	5.4.1		yes	yes	9 litters to 2 pairs of 2.1 cats
jungle cat	4 (1 litter)	0.0.4	-	yes	yes	I litter to I pair of 1.1 cats
rusty-spotted	1.60±0.25	3.1.4	F 124.6	yes	yes	5 litter to 2 pair of 2.2 cats
African Cats						
serval	2.30±0.21	13.5.5	-	yes	yes	10 litters to 4 pairs of 2.4 cats
caracal	1.50±0.50	2.0.1	-	yes		3 litters to 3 pairs of 2.3 cats
black-footed	1.71±0.18	5.5.2	F 50.43	yes	yes	9 litters to 4 pair of 3.4 cats
South American Cats						
Geoffroy's	2.31±0.13	14.7.7	-	yes	yes	14 litters to 3 pairs of 2.3 cats
jaguarundi	1.83±0.24	9.4.9	F 74.86	yes	yes	12 litters to 4 pairs of 4.3 cats
ocelot	1.67±0.21	16.13.8	F 133.85	yes	yes	23 litters to 8 pairs of 6.7 cats
margay	1.00±0	6.9.2	-	yes		17 litters to 3 pairs of 3.3 cats
Pampas cat	1.31±0.13	9.7.1	-	yes	yes	13 litters to 3 pairs of 3.2 cats
European Cats						
Scottish wild	2.50±0.22	9.8.8	-	yes	yes	10 litters to 3 pairs of 2.3 cats
North American Cats						
Canadian lynx	-	-	-	-	-	0 litters to 1 pair of 1.1 cats
Worldwide Distribution						
domestic cat	4.75 ± 0.25	16.18.4	F 42.00	yes	yes	8 litters to 8 pairs of 2.8 cats

[6] see Figure 3
[7] n= number of litters
[8] males . females . sex unknown
[9] females' date of birth to birth of 1st litter produced;males' date of birth to 1st litter sired

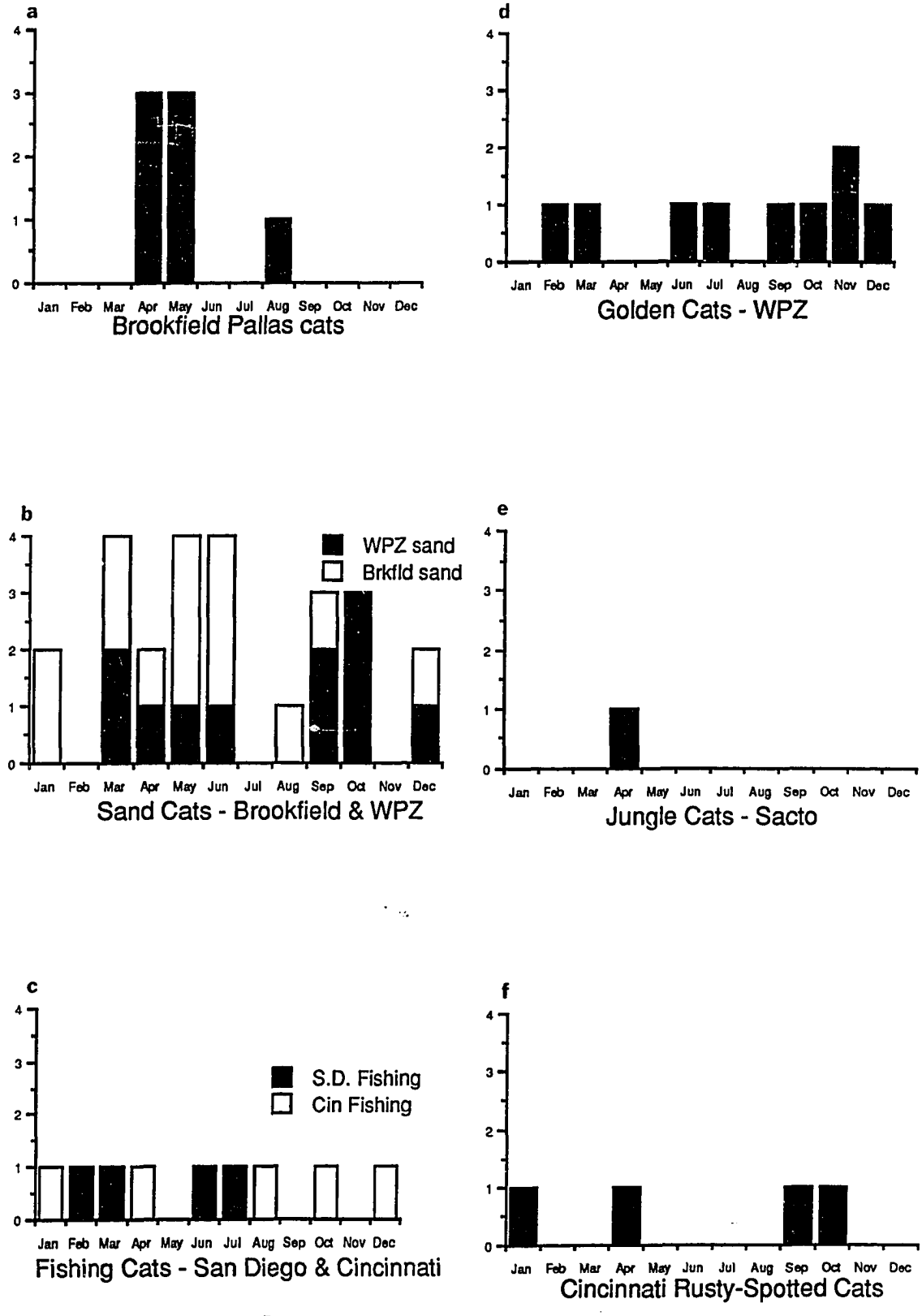


Figure 3. Seasonality of litters produced by small cats in captivity

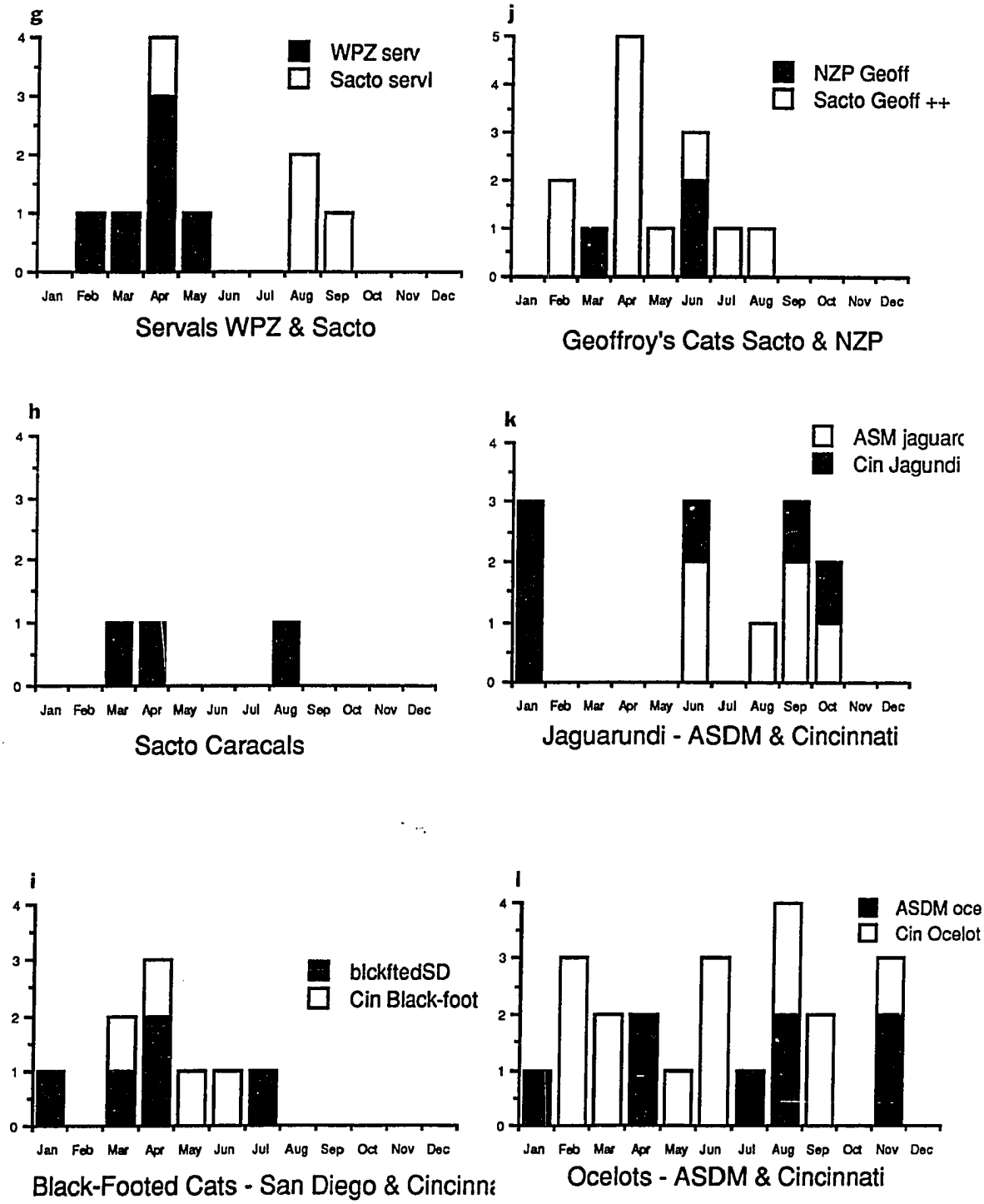


Figure 3. (cont) Seasonality of litters produced by small cats in captivity

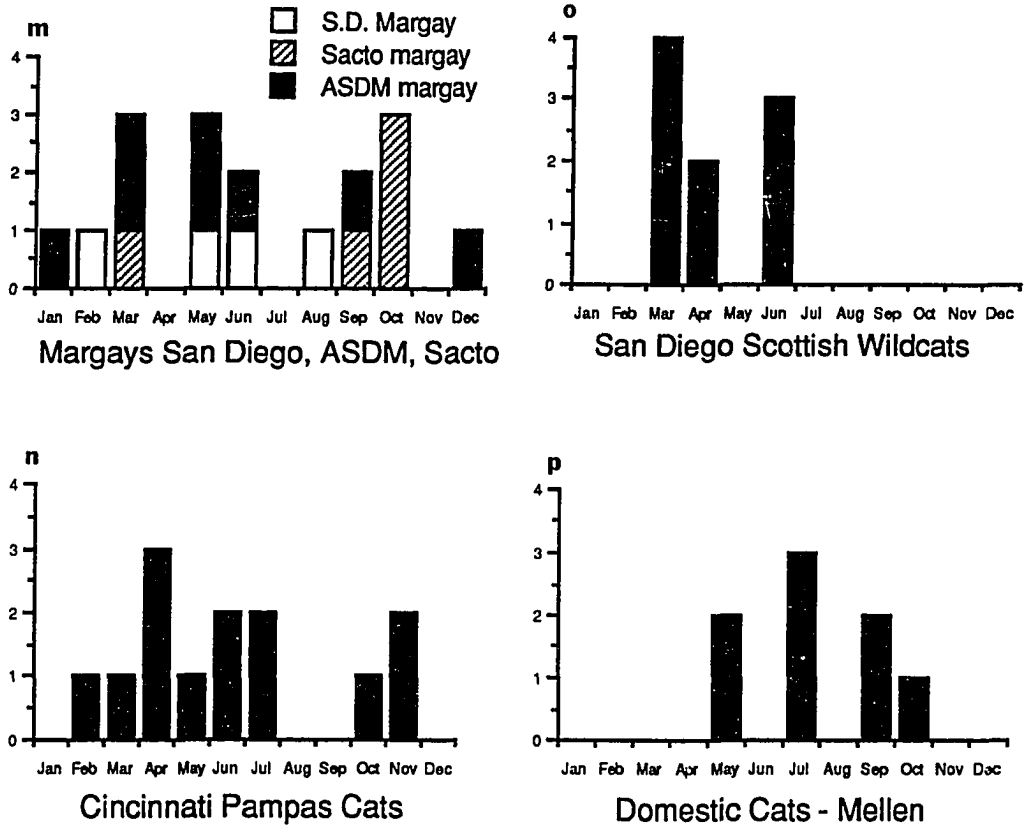


Figure 3. (cont) Seasonality of litters produced by small cats in captivity

Pallas Cats (*Felis manul*)

Pallas cats are found in the steppe and semidesert areas from the Caspian Sea to Kashmire, Mongolia, and central China, north to Inner Mongolia and east to Hopei (Honacki, Kinman, and Koeppl, 1982). They are slightly smaller (5 - 10 pounds) than a domestic cat with a stocky body, short legs, and a short, broad head with rounded laterally positioned ears. They have conspicuous eye stripes and a ringed tail. See Plate I. Some aspects of their markings resemble that of snow leopards (*Panthera uncia*) which are found possibly sympatrically with Pallas cats.

Several behaviors appear to be unique to Pallas cats. One was termed "lip quiver." This behavior involved orienting to a conspecific or a human, staring, and then raising the upper lip on one side of the muzzle and exposing the canine. The lip was rapidly raised and lowered. The duration of this behavior was usually about five seconds. Given the contexts under which this behavior was seen and from conversations with keepers, this behavior seems to be a threat. Another characteristic of Pallas cats was the cats' ability to move up the vertical component of their exhibit with little apparent effort. The exhibit in which the Pallas cats were observed in the present study was an accurate recreation of the steppes of the Himalayan Mountains. The Pallas cats did not overtly leap from ledge to ledge, but instead appeared to "flow" from perch to perch on stocky little legs.

The trio of cats in this study did not demonstrate any breeding activity during the time observed nor actually was there expectation that they would indeed show breeding. Pallas cats are reportedly seasonal breeders, with litters being produced in April and May (Seager & Demorest, 1986; Walker, 1983). In the present study, historical data showed that six of the seven litters produced occurred during April and May with the seventh litter produced in

Plate I
Upper Left: Pallas Cat (*Felis manul*) - Photo by J. Mellen. Upper Right: Sand Cat (*Felis margarita*) - Photo by J. Mellen. Center Left: Fishing Cat (*Felis viverrina*) - Photo by M. Gutierrez. Center Right: Temminck's Golden Cat (*Felis temminicki*) - Photo by S. Ford. Bottom Left: Jungle Cat (*Felis chaus*) - Photo by C. Lofton. Bottom Right: Rusty-spotted Cat (*Felis rubiginosus*) - Photo by J. Mellen.

August (Figure 3a) supporting the conjecture regarding seasonal breeding in this species. Litter size is reported to be five or six (Seager & Demorest, 1986; Walker, 1983). The data from the present study produced a mean litter size of 3.57 (Table 6).

The current status of the captive population is quite bleak; ISIS lists 12 individuals in captivity (Table 7). Virtually all the Pallas cats produced in North America are the offspring of two wild-caught individuals, possibly siblings. There is currently only one pair of Pallas cats in a breeding situation anywhere in North America. This pair is related (half-sibs) and probably past reproductive age.

Pakistan Sand Cat (*Felis margarita sheffeli*)

The sand cat's original range includes the deserts of Morocco, Senegal, Algeria, Pakistan, Niger, Egypt, S.E. Arabia, Iran (Honacki, et al., 1982). All of the sand cats in this study are of the subspecies, *sheffeli*, from Pakistan. The sand cat is one of the smallest felids (about 5 pounds). It is a sandy color and characterized by large ears located somewhat laterally on the skull, a broad face with faint eye stripes eminating laterally from the eyes, and black tipped tail with faint rings proximal to the black tip; the backs of the ears are tipped with black. See Plate I. The fur between the pads of the feet is long, presumably to protect the feet from the heat of the sand and to provide traction in the sand.

Hemmer (1977) states that the behavior of sand cats is remarkably similar to that of domestic cats except for its vocalizations. Results of the present study support both those comparisons. Hemmer referred to a vocalization of sand cats as being similar to "barking" as if from a small dog. This barking vocalization was emitted by both the male and female sand cat in this study when they were newly introduced .

Table 7. Census of Small cats (*Felis*) in Captivity from Shoemaker, 1988*

Common Name	Scientific Name	No. of Specimens	Status
cougar	*F. concolor*	194	
serval	***F. serval***	**169**	
bobcat	*F. rufus*	156	
lynx	***F. lynx***	**110**	
caracal	***F. caracal***	**92**	
ocelot	***F. pardalis***	**76**	E **
margay	***F. wiedi***	**58**	E
Geoffroy's cat	***F. geoffroyi***	**35**	
fishing cat	***F. viverrina***	**33**	
jaguarundi	***F. yagouaroundi***	**32**	
black-footed cat	***F. nigripes***	**31**	E
jungle cat	***F. chaus***	**29**	
leopard cat	*F. bengalensis*	27	E
Temminck's golden cat	***F. temmincki***	**22**	E
Pallas cat	***F. manul***	**12**	
rusty-spotted cat	***F. rubiginosus***	**12**	
pampas cat	***F. colocolo***	**10**	
Pakistan sand cat	***F. margarita sheffeli***	**9**	E
European wildcat	***F. silvestris***	**8**	
African wildcat	*F. libyca*	6	
marbled cat	*F. marmorata*	4	E
Florida panther	*F. concolor coryi*	2	E
jaguarundi	(endangered subspecies only)	2	E
flat-head cat	*F. planiceps*	1	E
Mexican bobcat	*F. r. escuinapae*	1	E

*data are from ISIS (International Species Inventory System) current as of 30 June 1988

** E = endangered and thus regulated by the U.S. Endangered Species Act

those species in **bold** print were examined in this study

Of the four different observation sets for sand cats in this study, only one pair produced offspring within one year of the respective observation periods. Figures 4a, 4b, 4c, and 4d demonstrate that pronounced behavioral changes occurred during the days surrounding copulation in that pair. The pair was observed to copulate during Weeks 3 and 9 of the observation set (indicated by arrows pointing to those weeks in the Figures). The male's rate of scent-marking dropped during the weeks of actual copulation (Figure 4a). The female sand cat exhibited a dramatic increase in both cheek rubbing and urine marking during those same two periods (Figure 4b). In fact, the only time this particular female was observed to urine mark was in association with the two periods of breeding activity that occurred during the 10 weeks of observation. This is in contrast to remarks by Bennett and Mellen (1983) who studied the same pair of sand cats and reported no overt signs of estrus. Both the male and the female were observed to exhibit a flehmen response after sniffing an object or another cat. This also is in contrast to that reported by Bennett and Mellen (1983) who said flehmen was not observed. Figure 4d demonstrates the male's "interest" in the female both during the weeks of actual copulation as well as during a considerable period preceding and following these weeks. Figure 4d demonstrates that just prior to and following actual receptivity, the female responded aggressively to the male's "interest."

A description of a copulatory sequence in a pair of captive sand cats is as follows:

10:10 - 10:30AM Female moved around the enclosure cheek-rubbing logs and rocks at a high rate (about 1 time per minute). The male occasionally followed the female and on two occasions, struck at her with his front paw.

10:33AM Male sniffed Female's back and then vocalized ("barking").

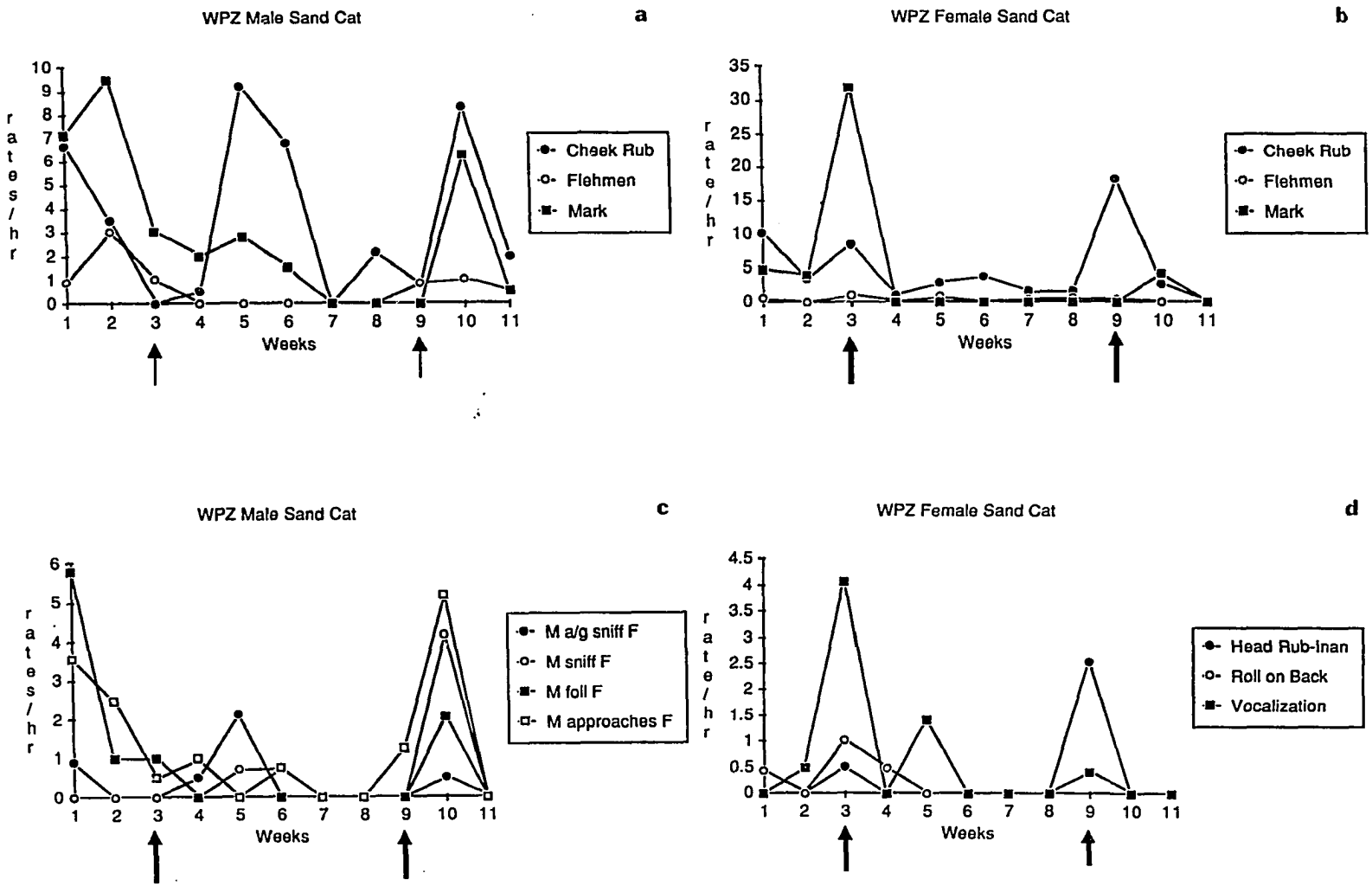


Figure 4. Rates of selected behaviors exhibited by a pair of reproductively active sand cats. Arrows indicate those weeks in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g sniff = Anogenital Sniffing; foll = Following; Head Rub-Inan = Head rubbing (inanimate)).

10:37AM Male essentially "pounced" from a rock 2-3 feet above the Female and immediately grasped her by the nape of the neck and then mounted, first straddling with his front feet and then hind feet. The Male was not oriented properly, there was no apparent intromission and the mount lasted about 15 seconds.

10:38-10:39AM Female cheek rubbed against a log 13 times and head rubbed against that same log three times. She also rolled on her back.

10:39AM Male mounted the Female a second time with a nape bite. Female assumed a lordosis posture; Male still nape-biting and still mounting female in proper orientation.

10:41AM Female began to tread with her hind feet

10:42AM Male no longer nape-biting Female although he was still mounting and appeared to be properly oriented.

10:44AM Male resumed nape bite

10:47AM Male let go of the Female's nape and then leapt backwards off the Female (actual duration of this mount: 7.5 minutes)

10:47AM Female reared and struck the male 5-10 times with her front paws; the Male reared up on his haunches and struck back at the female. They then began a "face off." The Male was twitching his tail. Face off lasted until 10:55. Each time the Male appeared to try to move away from the Female, she struck at him with her front paws.

10:56AM The Male moved away from the Female (about two body lengths) but continued to watch the Female. The Female groomed her genitals for about 60 seconds.

Hemmer (1977) provides information as to mean litter size and sex ratio of *F. m. sheffeli* . However, he used some information from the sand cats at the Brookfield Zoo and so it is not possible to separate his results from data collected from the Brookfield Zoo data during the present study. He suggested that sand cats are seasonally polyestrous (deduced from captive data) and further stated that Heptner and Sludskij (1972) report breeding in the spring

for wild sand cats from Transcaspia. This is contrary to the results in the present study in which litters were produced throughout the year (Figure 3b). In the present study, a mean gestation of 66.5 days was calculated (Table 6). This is somewhat longer than the 61 day average determined by Hemmer (1977).

The current status of the captive population is extremely bleak (Table 7). As of 28 August 1988 there were 21 living specimens of *F. m. sheffeli* in captivity worldwide, 9 in North American zoos and none in European zoos. Almost one-third of the entire captive population has an inbreeding coefficient of 0.250 or 0.406. These inbred animals are all the descendants of one wild caught pair, possibly siblings. Only three of the sand cats in North America have an inbreeding coefficient of zero (K. Sausman, unpublished studbook). Many of these captive individuals seem particularly susceptible to respiratory diseases, which are sometimes fatal. This chronic problem may be due to housing conditions or ultimately to inbreeding depression. Since this sub-species may be extinct in the wild, the sand cats in captivity today may well represent living museum specimens.

Fishing Cat (*Felis viverrina*)

The fishing cat is found in the wetter, marshy areas of India, Sri Lanka, Vietnam, Sumatra, Java, and Bali (Honacki, et al., 1982). It is a heavy, stocky, spotted cat weighing about 25 pounds with white spots on the backs of its ears and rings on its tail. It has a relatively short tail and is characterized by semi-retractile claws and webbing between its toes. See Plate I.

Neither of the pairs of fishing cats in which direct behavioral observations were made exhibited any reproductive behavior nor had either pair produced offspring six months after observations were terminated. The fishing cats observed in this study exhibited a high rate of head rubbing

inanimate objects, "sharpening" claws, and flehmen response relative to other species observed (Figure 2), especially in light of the fact that neither pair demonstrated any sexual activity. Several zoos routinely provided minnows or goldfish for their fishing cats. All of the cats observed were quite adept at capturing and killing the fish.

Historical data were available on reproductive parameters from two pairs of fishing cats. From archival data collected in the present study, a 70-day gestation was estimated from keeper reports on one birth (Table 6). This is substantially longer than that of 63 days reported on a pair observed at the Philadelphia Zoo (Ulmer, 1968). Since actual copulation was observed in Ulmer's study, it would seem more reliable than the gestation length reported in the present study. Data from the present study show that at least in North American zoos, fishing cats produce young year round (Figure 3c). The two litters born at the Philadelphia Zoo (Ulmer, 1968) each contained two kittens. This is in agreement with the data collected in the present study in which the average litter size was 2.2. Ulmer (1968) further reports that the estrous female approached the male, head rubbed against him, and exhibited a lordosis posture prior to mounting; this is in contrast to information obtained in this study in which keepers had not observed overt estrous behavior in their breeding females.

The captive population of fishing cats in North American and European zoos is currently 33 individuals (Table 7). Most are related to stock originally bred at the Rotterdam Zoo and the population is probably inbred.

Temminck's Golden Cat (*Felis temmincki*)

Temminck's golden cat inhabits the wooded areas of Nepal, southwestern China, Sumatra, and Thailand (Honacki, et al., 1982). The golden cat is one of the largest of the *Felis* , weighing about 25-30 pounds. It

is lithe and sinewy in appearance. It is a rusty color with eye stripes and the ventral aspect of the tail is conspicuously white; the backs of its ears each have a black"eye" spot. See Plate I.

During the course of this study, the pair of golden cats showed signs of breeding activity during Week 1 and again during Weeks 7-8. There was a very pronounced change in both how they spent their time (measured by percentage of time spent in proximity (Figure 5a)) and in rates of behaviors (Figures 5b, 5c, 5d, and 5e).

The male golden cat's rates of scent-marking behavior declined somewhat during Week 2 (Figure 5b), but did not show the pronounced drops seen in the male sand cat (previously discussed). The female golden cat did show a dramatic increase in scent-marking during Weeks 2 and 7-8. Her rates of neck rubbing and head rubbing inanimate objects were also very high during these periods of estrus (Figure 5c). This pattern is similar to that described previously for the female sand cat. The male's rates of social behaviors increased substantially during Weeks 2 and 7-8 (Figure 5d), especially his rates of approaching and following the female.

Just prior to both breeding periods, the female had blood in her urine. Whether this is indeed a sign of impending estrus, simply coincidental, and/or unique to this female remains to be determined. The female observed in this study showed very pronounced signs of estrus. She repeatedly approached the male, head rubbed against him, adopted a lordosis posture in front of him (Figure 5e), and on several occasions appeared to try to crawl underneath him.

Only one mount was actually observed by the author during the formal observations over the 10 weeks. The mount did not appear to include

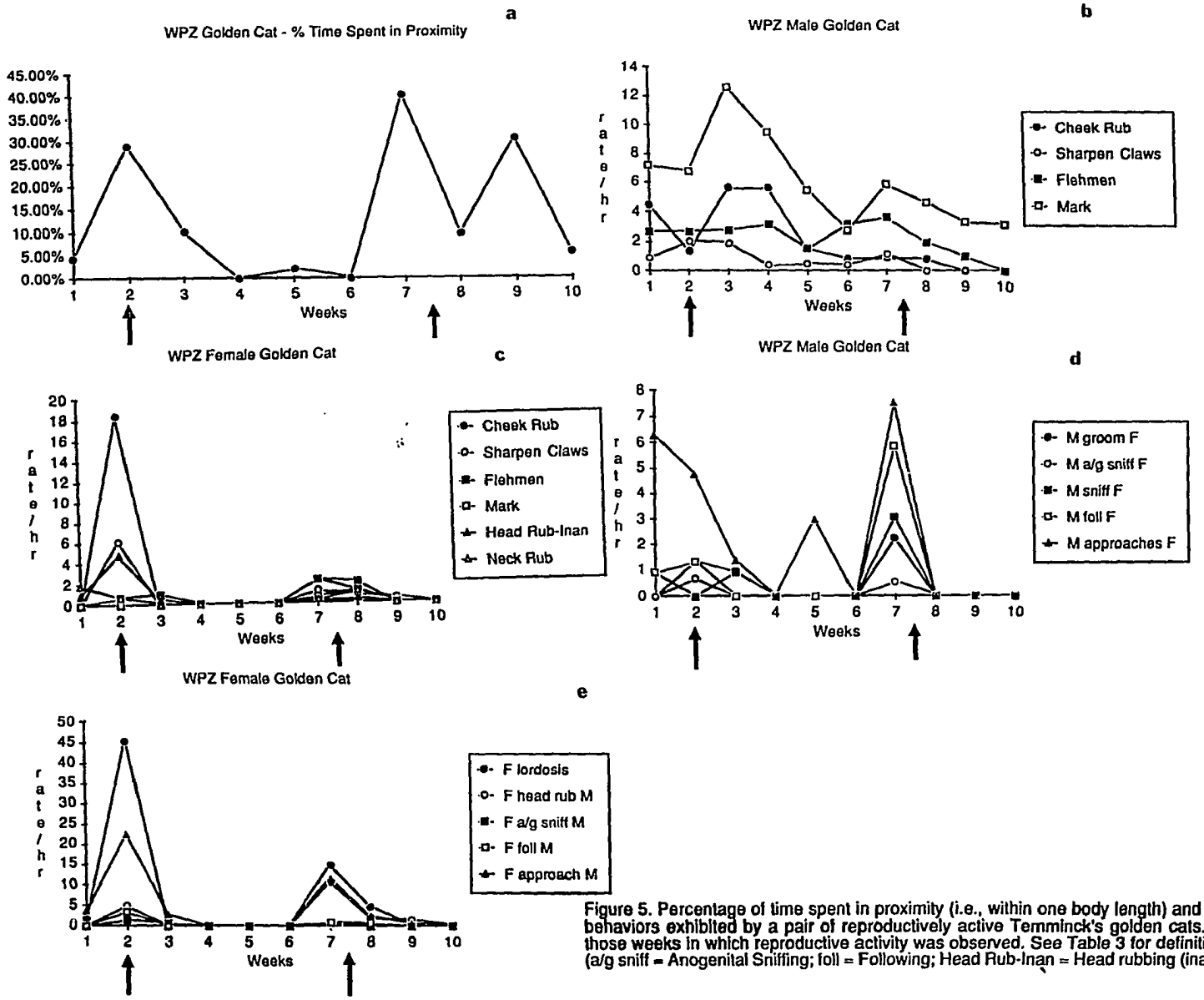


Figure 5. Percentage of time spent in proximity (i.e., within one body length) and rates of selected behaviors exhibited by a pair of reproductively active Temminck's golden cats. Arrows indicate those weeks in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g sniff = Anogenital Sniffing; foll = Following; Head Rub-Inan = Head rubbing (inanimate)).

intromission. (Other mounts were observed by other Animal Management personnel.)

Female approached Male and adopted a lordosis posture with tail deflected to one side.

Male sniffed Female's back and then grasped her neck (nape-bite) while standing over Female. When Male began pelvic thrusting, he let go of her nape. Male thrust for about 5 seconds and then dismounted.

Male walked a few paces away and then returned to again mount Female. He did not nape-bite, but did pelvic-thrust. This second mount lasted about 15 seconds and did not appear to include intromission/ejaculation.

Entire sequence lasted 33 seconds.

The male's almost "casual" response to the female was in strong contrast to the cautious approach and deliberate pounce seen in the breeding male sand cat. The female golden cat did not conceive during either of the estrous periods during this study, but she did produce a kitten four months after the formal observations were terminated.

It has been suggested that in the wild these cats are not seasonal breeders (Nowak and Paradiso, 1983). The female in the present study produced litters throughout the year (Figure 3d). All ten of her litters contained a single kitten (Table 6). Barnett (1972) reports a litter consisting of a single male and Louwman and van Oyen (1968) report two litters each containing a single kitten. Two other litters have been documented as each containing two kittens, but neither litter survived (P. Andrews, pers. comm.). Seager and Demorest (1986) report a range of 1 to 3 kittens.

Louwman and van Oyen (1968) mention that on one occasion the male was left with the female and kitten and was tolerant of the kitten, suggesting that males may be safely left with pregnant females. The male observed in the

present study killed kittens born unexpectedly on more than one occasion. Therefore, it seems prudent to remove males when pregnancy is suspected.

Louwman and van Oyen (1968) described a female as being "very nervous" with her kitten. In contrast, the female observed in the present study was relatively calm when caring for her kittens. She sometimes paced while carrying a kitten, but she successfully raised most of her litters.

As with other species of small cats, the captive population is very small. ISIS lists 22 specimens (Table 7), but communications with listed holders of North American institutions suggest this number to be overestimated. As of December, 1988, there are only two breeding pairs of Temminck's golden cats in North America, one of which was part of the present study; the other pair includes a male offspring of this study's Portland pair (pers. obs.). It is apparent that for future captive propagation to continue, additional animals are needed.

Jungle Cat (*Felis chaus*)

The jungle cat is found in a wide range of habitats including the woodlands, grasslands, and cultivated areas of India, Thailand, Vietnam, Sri Lanka, and the Tibet and Szechwan, Yunnan areas of China (Honacki, et al., 1982). The jungle cat is somewhat larger than a domestic cat, weighing 15 to 20 pounds. It is reddish gray in color with faint eye stripes. The backs of the ears are black with an indistinct white "eye spot"; the ears have small pencils of black hairs at the tips. The tip of the tail is black and the middle of the tail has faint black rings. See Plate I.

The pair of jungle cats observed in this study was observed to copulate during the second week of the study; 63 days following this observed copulation, the female gave birth to a litter of four kittens. The behavioral indicators of estrus in this pair of jungle cats were less pronounced than in

other reproductively active pairs observed in the present study (Figures 6a, 6b, 6c, and 6d). The female showed virtually no behavioral signs of estrus (Figures 6b and 6d), but there was a more pronounced change in the male's behavior (Figures 6a and 6c). During the days immediately prior to the observed copulation, the male's rate of vocalization went up and he was described by keepers as "intently watching" the female, moving and following the female each time she moved.

Copulation was observed by two students assisting in data collection. The following description of the copulatory behavior is from their notes:

Prior to the mount, both male and female sniffed each other's anogenital region, and the Male repeatedly followed the Female, both vocalized repeatedly. Male cheek-rubbed and exhibited numerous flehmen responses after sniffing a heavily marked area in the corner of the exhibit. Female was "crouched" (possibly in lordosis) on the floor of the exhibit in the heavily marked corner area. The Male approached from behind and assumed a nape bite, Female assumed a pronounced lordosis and the Male began to step with his hind feet, rubbing against the Female's haunches while stepping.

Female's tail was deflected to one side and her hind quarters were elevated.

Approximately two and a half minutes after the Male assumed the nape bite, the Female vocalized loudly (presumably a "copulatory cry"). (The Male continued to grasp the Female's nape throughout the mount and let go only as he was rapidly dismounting.)

The Female immediately turned and growled at the Male.

The Male remained in close proximity, but appeared "wary" of the Female.

The Female rolled on her back "many times" and then groomed her genitals.

Following this mount, the Male again followed the Female, vocalized repeatedly, and sniffed the anogenital region of the Female.

This copulatory sequence is virtually identical to that observed for domestic cats (pers. obs.).

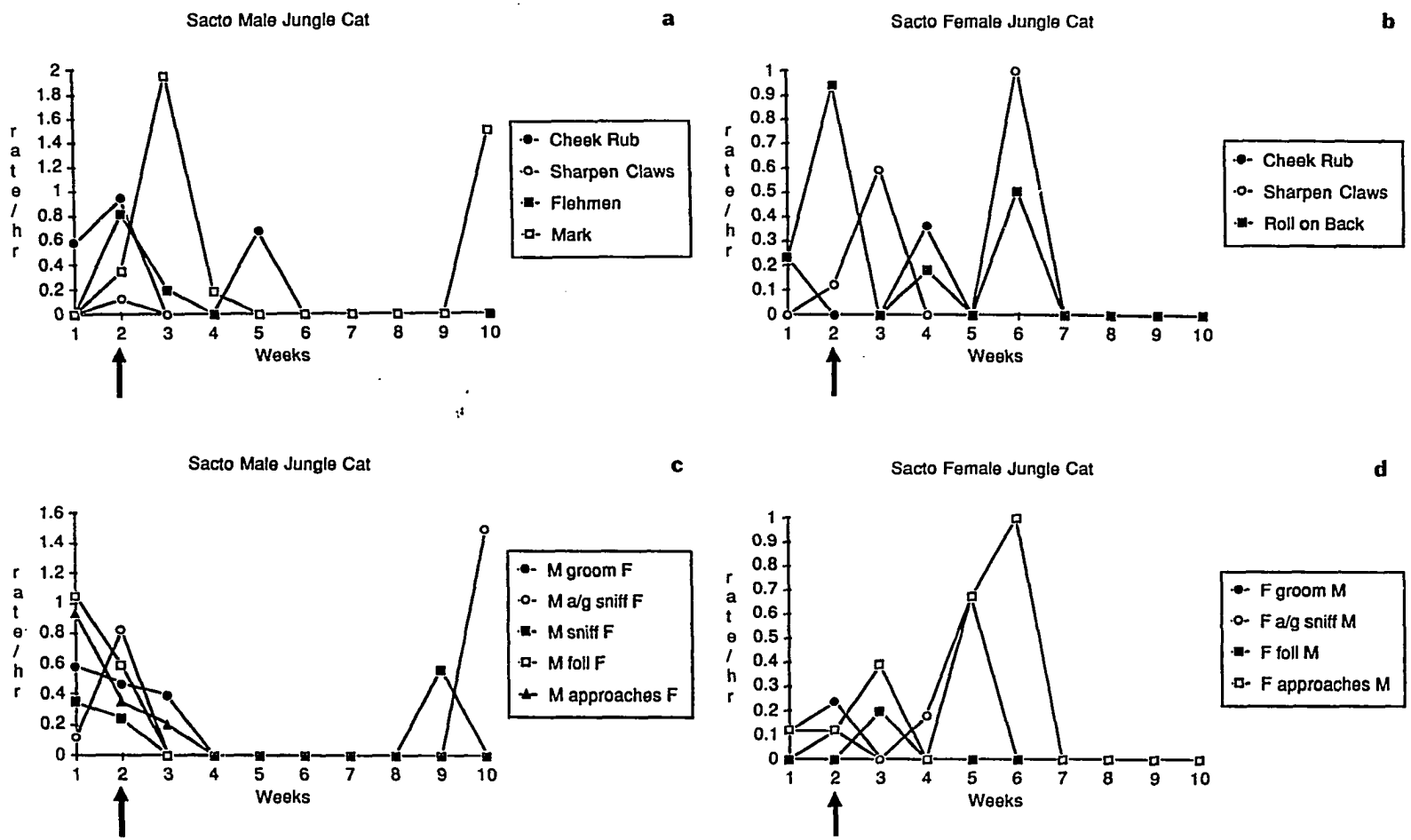


Figure 6. Rates of selected behaviors exhibited by a pair of reproductively active jungle cats. Arrow indicate that week in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g sniff = Anogenital Sniffing; foll = Following).

A gestation of 66 days and a litter size of three to five young were reported in several references (Hemmer, 1979; Walker, 1983; Seager and Demorest, 1986), but the original source of this information is unclear. At any rate, the data collected from the present study of a 63-day gestation and a litter of four kittens are in agreement with this information (Table 6). The April birth of the litter is within the range of the spring breeding season suggested by Guggisberg (1975) (Figure 3e).

ISIS lists 29 jungle cats (Table 7). Origins, relatedness, and level of inbreeding of this population are unknown.

Rusty-Spotted Cats (*Felis rubiginosus*)

The tiny rusty-spotted cat is the smallest member of the cat family. It is rusty-reddish in color with brown spots on its dorsum. Its ventrum is white with a few black spots. The tips of its ears and tail are black. See Plate I. It is known to inhabit both scrub, dry grasslands and humid mountain forests (Nowak and Paradiso, 1983) of India and Sri Lanka (Honacki, et al., 1982).

Rusty-spotted cats were studied on a short-term basis (two weeks). The situation in which these animals were housed provided an ideal situation in which to study the pair's behavior. The male and female were housed separately in adjacent cages and were given access to each other only during observation periods. During the second week of study the pair was observed to copulate over a four-day period. Unfortunately, the pair was not observed over the week-end and so it can be suggested that the estrous period is at least four days in length and no longer than six days in length (as no behavioral signs of estrus were observed on the previous Friday) (Table 6).

The following sequence occurred over a 10-minute period and is representative of the copulatory behavior observed in this pair:

Male sniffed, flehmed, sniffed an area in Female's cage.

Male approached Female four times, groomed her once, sniffed her anogenital region four times and sniffed her head once.

Male followed Female and approached her when she stopped.

Male sniffed, flehmed, sniffed area in Female's cage.

Female approached Male and sniffed his anogenital region.

Male followed Female and sniffed her anogenital region.

Male approached and mounted Female first by biting her nape area, then straddling her first with his front feet and then his hind feet. Female adopted a lordosis posture with hind end elevated and tail deflected to one side. Male "pelvic thrusted." Fifty seconds after the nape bite, Female emitted a low growl (presumably a "copulatory cry"), Male backed slowly away from Female.

Female groomed her anogenital region and then rolled on her back five times.

Male then groomed his anogenital region.

The female sometimes seemed to place herself in the path of the male and assumed a lordosis posture, sometimes treading with her hind feet while in that posture. This behavior appeared very similar to the apparently solicitous behavior of the female Temminck's golden cat.

Figures 7a, 7b, 7c, and 7d (graphed daily as opposed to weekly as in previous figures) show a dramatic change in the behavior of the pair during the second week. Virtually all social behaviors occurred during the four days of October 24-27 (Figures 7c and 7d) and most of the behaviors associated with scent-marking are limited to those days (Figures 7a and 7b). This dramatic shift may in part be due to the cats being more acclimated to the presence of the observer by the second week.

A total of 20 mounts was observed over four days for an average of 7.64 mounts/hour. It appeared that intromission occurred during eight of the mounts. Mean duration of mounts in which intromission was presumed was

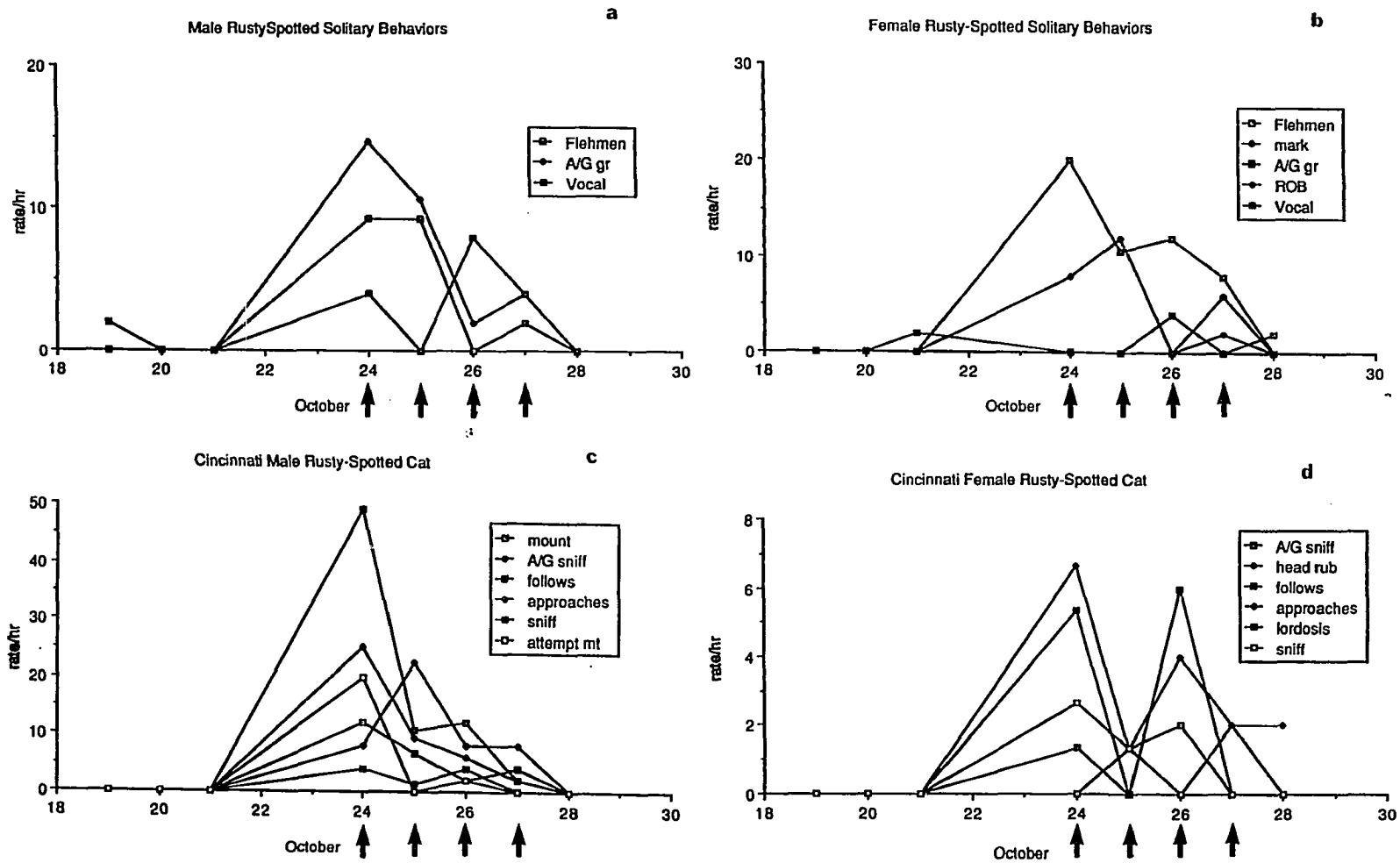


Figure 7. Rates of selected behaviors exhibited by a pair of reproductively active rusty-spotted cats. Data are graphed daily. Arrows indicate those days in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g gr = Anogenital Grooming; Vocal = vocalizations; ROB = Rolling on Back; a/g sniff = Anogenital Sniffing; foll = Following; attempt mt = Attempted Mount).

0.92 minutes ± 0.11 S.E. while mounts where intromission did not appear to take place lasted 0.62 minutes ± 0.10 S.E.. This very short duration may be due to the extreme predation pressure these very tiny cats are presumably under in the wild. Weigel (1972) states that, in the wild, young are born in the spring; however, data from the present study do not support this (see Figure 3f).

ISIS lists 12 individuals held in zoos (see Table 7). However, there appears to be only one female currently in North American zoos. Again, more individuals are necessary for maintenance of a captive population.

Serval (*Felis serval*)

The serval is found in the grasslands and scrub of much of Africa (Honacki, et al., 1982). It is a larger *Felis*, weighing 25 to 30 pounds. Its long legs and neck give this spotted cat a distinctive appearance. The backs of its large ears possess distinctive black and white markings and its relatively short tail has black rings on it. See Plate II.

Next to the cougar (*F. concolor*), the serval is the most commonly exhibited species of small cat in zoos (Table 7) and breeds readily in captivity (Shoemaker, 1988). Ironically, only one (from the Sacramento Zoo) of four pairs observed in this study had reproduced and that pair exhibited no discernable reproductive behavior during the period it was observed.

One female (from WPZ) appeared to show signs of estrus during Week 8 of the observation set (Figures 8a, 8b, 8c, and 8d), but no copulations were observed. Indeed, this female vehemently rebuffed approaches by the male (Figures 8c and 8d). This week (Week 8) was characterized by a very high rate of urine marking by both the male (Figure 8a) and the female (30.22 times per hour) (Figure 8b). Kingdon (1977) provides a detailed description of the behavior of an estrous female serval and reported that estrous behavior

Plate II
Upper Left: Serval (*Felis serval*) - Photo by J. Mellen. Upper Right: Caracal (*Felis caracal*) - Photo by J. Mellen. Center Left: melanistic Geoffroy's Cat (*Felis goeffroyi*) - Photo by J. Mellen. Center Right: Black-footed Cat (*Felis nigripes*) - Photo by J. Mellen. Bottom Left: Ocelot (*Felis pardalis*) - Photo by J. Mellen. Bottom Right: Jaguarundi (*Felis yagouarundi*) - Photo by J. Mellen.

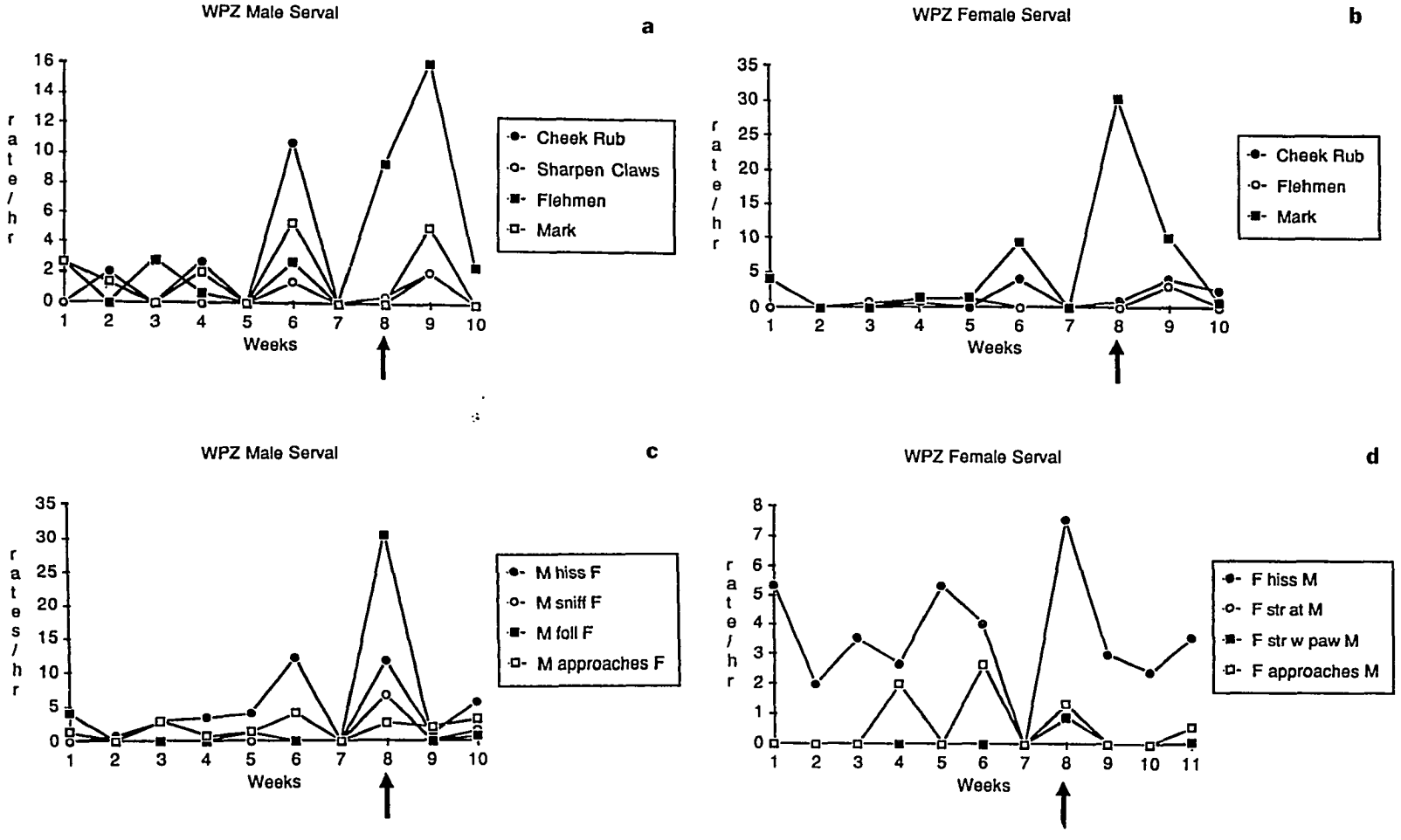


Figure 8. Rates of selected behaviors exhibited by a pair of servals. Arrow indicate that week in which reproductive activity was suspected. See Table 3 for definitions of behaviors (foll = Following; str at = Strike at; str w paw = Strike with Paw).

includes a high rate of urine spraying. All the females in the present study were observed to urinate in their mate's face.

During agonistic interactions observed during the course of the present study, three pairs of serval were seen to display the following: one individual placed its paw on the chest of the second cat, while the second cat repeatedly "bobbed" its head up and down, sometimes biting at the raised paw of the first cat. Leyhausen (1979) described and illustrated this interaction in detail. He termed the raised-paw behavior a "paw prod."

Wackernagal (1968) reports the duration of estrus as one day (based on three females), noting that it also may last for three to four days. The female that was presumed to be in estrus in the present study (suggested by an increase in scent-marking behavior and a sudden and pronounced interest in the female by the male) exhibited these behaviors over a four-day period (Table 6). It would be interesting to determine if the shorter estrous period is associated with those females that copulated as studies on domestic cats have shown that the duration of estrus is substantially shorter in queens that bred (Schmidt et al., 1983).

Figure 3g details the dates of captive births from the present study. Births occurred from February through May and August through September. By comparison, Wackernagal (1968) reports data from 20 births at the Basel Zoo. Combining these data with those of the present study, births have been recorded in captivity during all months except June and July with a peak during the months of March, April, and May.

Mean litter size calculated from data collected during the present study is 2.31 with a sex ratio of 13.5.5 based on 10 litters (Table 6). This compares nicely with data from Wackernagal (1968) who reports a mean litter size of 2.35 with a sex ratio of 24.22.1 based on 20 litters.

As stated above, servals are commonly kept and bred in zoos (Table 7). Origins, relatedness, and level of inbreeding of this population are unknown.

Caracal (*Felis caracal*)

Caracals inhabit the woodlands, savannahs, and acacia scrub of the subsaharan regions of Africa, India, and Egypt (Guggisberg, 1975; Honacki, et al., 1982). They are about the same size as the serval, but heavier in appearance. Their most distinguishing features involve the markings on the face and the ears. This golden-colored cat has distinctive black stripes which extend from the lower eyelid margin down and medially to the tip of the nose. The large ears are fringed with long tufts of hair (2-3 cm) and the backs of the ears are black. See Plate II.

Caracals are also commonly kept in zoos, surpassed only by cougar, lynx, bobcat, and serval (Table 7); they breed readily in captivity. In the present study, two different pairs of caracals were observed. One pair (G & C) had been recently introduced and exhibited no discernable signs of reproductive behavior during the observation periods. The female of this pair did, however, produce a litter one year after these observations were made.

The second pair (L & R) was observed breeding during Weeks 4 and 12 of the observation period (see Figures 9a, 9b, 9c, and 9d); these two copulations were observed by two different undergraduate assistants. Both described the breeding behavior as "casual." Copulatory sequence is as follows:

Male approached Female and both sniffed one another.

Male grasped the Female's nape and the Female crouched, but did not elevate her hind quarters (i.e., no apparent lordosis) and then the Male straddled the Female with both his front feet and hind feet.

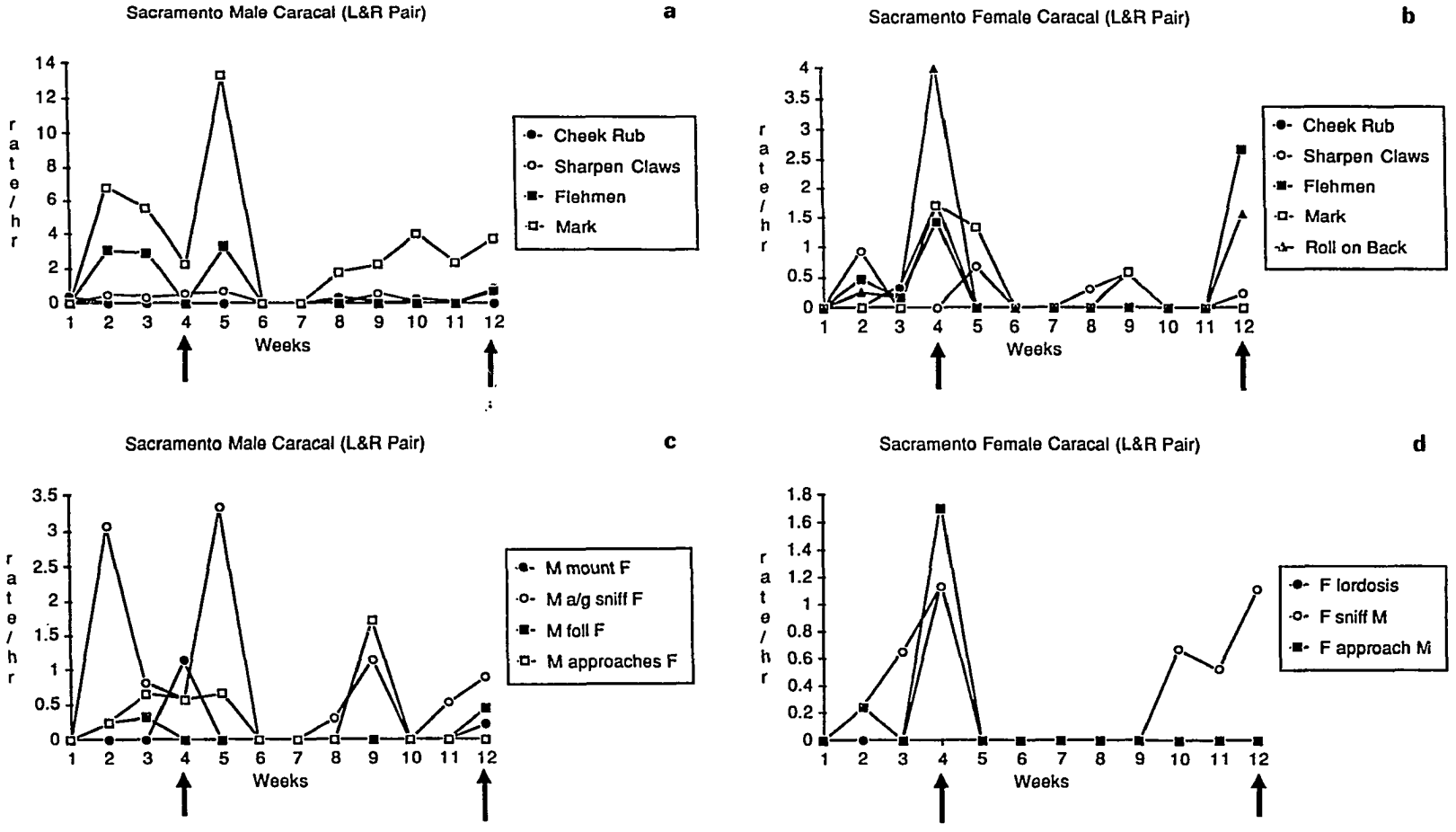


Figure 9. Rates of selected behaviors exhibited by a pair of reproductively active caracals. Arrows indicate those weeks in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g sniff = Anogenital Sniffing; foll = Following).

Male began pelvic thrusting and at that point the Female assumed a lordosis posture (i.e., elevated her hind quarters and moved her tail to one side).

After "a few thrusts, the Female just walked away - no aggressive sign toward Male.

[Female] rolled on her back many times and then groomed her genitals.

Male watched calmly.

Then they approached each other and social groomed each other a lot"

(notes from M. Wood's data sheets, 16 May 1985). This description is very similar to that of Bernard and Stuart (1987) which is as follows: "The copulation sequence was always initiated by the female assuming a lordotic position, the male would then approach, mount quickly and disengage rapidly after (presumed) ejaculation. This sequence was followed by self-grooming (by both male and female) in all 12 observed copulations, and on two occasions, aggressive behaviour towards the male" p. 178. Both Gowda (1967) and Law and Boyle (1981) describe the female "growling" during the mount (presumably a "copulatory cry"); otherwise their descriptions of the copulatory sequence were similar to those described above.

The female in the present study was also observed to visually orient towards the male, crouch, and elevate her hind quarters, i.e., adopt a lordosis posture (Figure 9d) . She then rolled on her back. This behavior was not immediately associated with any mounting behavior. This is similar to what has been described above for the female golden cat and rusty-spotted cat. As with some of the other cats observed, the rate of marking behavior declined in the male and increased in the female during the two weeks in which breeding occurred (Figures 9a and 9b).

Several species of small cats possess ear tufts or pencil hairs (lynx, bobcat, jungle cat, Indian desert cat (*F. silvestris ornata*)), but the ear tufts on caracals are the longest. In fact, in the two pairs observed in this study, the ear

tufts of the males were substantially longer than those of the females. The function of these tufts has not been determined. One suggested function of ear tufts is to facilitate the location of sounds, acting like "antennas." It is claimed that when the tufts are cut off (at least in lynx) it decreases their ability to hear and locate sound sources (Weigel, 1972). While this is certainly an interesting theory, it appears to remain untested. These tufts do appear to function to accentuate certain facial expressions. In fact, Kingdon described the ears of the caracal to have evolved "into highly mobile and extraordinarily decorative signalling structures....The long tufts on the tips serve to emphasize the linear direction of the ear" (Kingdon, 1977, p. 331). During aggressive interactions observed in the present study, a threatening caracal oriented towards another and with ears erect, rotated the ears so that the backs of the ears "faced" forward. Tufts on the ears may accentuate this posture. Kleiman and Eisenberg (1973) also describe "ear flicking" in caracals accentuated by the tufts.

The most detailed research to date on the reproductive biology of caracals (Bernard and Stuart, 1987) provides the following information: duration of mounts averaged 3.8 minutes (range = 1.5 - 8 minutes); duration of estrus was 4.5 days (Range = 3 - 6 days); the estrous cycle was 14 days; the average gestation was 79 days; births occurred throughout the year with a pronounced peak in summer; average litter size was 2.2; the youngest male to successfully fertilize a female was 12.5 months old and the youngest female to conceive was 14 months old. The data collected during the present study fall within the ranges of the data presented by Bernard and Stuart (1987). See Table 6 and Figure 3h.

Caracals are commonly kept and bred in zoos (Table 7). Origins, relatedness, and level of inbreeding in this population are unknown.

Black-Footed Cat (*Felis nigripes*)

The black-footed cat is one of the smallest of the felids and is approximately the same size and configuration as the sand cat (but with smaller ears). See Plate II. It is found in the dry savannah areas of South Africa, Namibia, and Botswana (Honacki, et al., 1982). It is a small spotted cat whose plantar surface of the hind legs are black (thus, a black-footed cat). It has lateral eye strips and rings on the end of its tail. Guggisberg (1975) lists the black-footed cat as the smallest felid species. However, from observations during the present study, it would seem that the rusty-spotted cat is substantially smaller in appearance than the black-footed cat.

In the present study, black-footed cats were studied only on a short-term basis: a female and her kitten, a young adult sibling pair, and a newly introduced adult pair were each observed for two weeks. No reproductive behavior was observed in the newly introduced pair, indeed they virtually did not interact at all.

Two behaviors that appeared to be characteristic of black-footed cats was an ear posture and the cats' mode of stalking. The ear posture involved a lateral extension of the ears into an "airplane" posture. Although certainly all species of cat observed extended their ears laterally in a similar posture (see also Leyhausen, 1979, p. 195; Nowak and Paradiso, 1983, p. 1067), the black-footed cats' adoption of this posture was characterized by being particularly conspicuous. They seemed to adopt this posture during mildly aggressive interactions with conspecifics or when a keeper enters their enclosure. With regard to their stalking behavior, on several occasions the author observed a female stalking a large bird (jungle fowl) located just outside of her enclosure. The stalking phase of the hunting sequence involved the female flattening her body against the substrate, much more so

than observed in other small cats stalking. When cautiously moving closer to the bird, the female moved from behind one small boulder to another in an almost "serpentine" manner, appearing to almost "flow" from rock to rock. She also exhibited the "teeth chattering" sometimes observed in hunting cats. The size, body shape, and some mannerisms of black-footed cats are reminiscent of sand cats.

Leyhausen and Tonkin (1966) report births in April and May; Schürer (1988) reports that 90% of all litters were produced between February and August. If the data from Leyhausen and Tonkin (1966) and Schürer (1988) are combined with data from the present study (Figure 3i), there is a strong suggestion of birth seasonality. In the wild births occur in November or December (Visser, 1977). Average litter size reported by Leyhausen and Tonkin (1966) was 1.67 with a sex ratio of 2.3.0. Based on 50 litters born at the Wuppertal Zoo, average litter size was 1.94 with a sex ratio of 50.38.9 (Schürer, 1988). Similar data were presented in the present study (Table 6). Schürer (1988) reports that a female in his collection produced her first litter at 44 weeks of age; in the present study a female produced her first litter at 50 weeks of age.

ISIS lists 31 black-footed cats in zoos (Table 7). With the exception of several recently imported individuals from South Africa, virtually all of the black-footed cats in captivity originated from animals bred at the Wuppertal Zoo. Some of the animals in North America have a fairly high inbreeding coefficient (0.3125) and this may be a contributing factor in the chronic respiratory problems and kidney disease seen in some specimens.

Geoffroy's Cat (*Felis geoffroyi*)

The Geoffroy's cat is a small spotted cat from the scrubby woodlands and open bush country of Bolivia, Argentina, Uruguay, and Brazil (Honacki, et

al., 1982). The Geoffroy's cat has conspicuous eye stripes, white "eye" spots on the backs of its ears, and a ringed tail. See Plate II.

In the present study, three pairs of Geoffroy's cats were observed. Two pairs showed no reproductive activity: one female gave birth soon after the observation period ended and so was pregnant during that period (and in fact, the observation set was terminated early because the male was separated from the female as a precaution for impending parturition); the second pair still has not, to date, reproduced.

Mounting was observed in the third pair during Weeks 1 and 3 of the study (Figures 10a, 10b, 10c, and 10d). However, the male appeared to attempt mounts (see attempted mounts in Figure 10c) throughout the observation period. Except during Weeks 1 and 3 when the female adopted a lordosis posture during mounts (Figure 10d), she rolled on her side or back when mounted or threatened the male and/or ran away. There was a sharp rise in the female's rate of marking, especially during Week 3 (Figure 10b) and a slight decline in the male's marking during that same week (Figure 10a). This same pattern has been described for other reproductively active pairs of cats in the present study.

Although mounts were observed in the present study, at no time did it appear that intromission occurred. Absent during the observed mounting sequences were: any discernable "copulatory cry", vehement throwing of the male off her back, or exaggerated/ repeated rolling on back after a mount. Although this pair had produced offspring in the past, no kittens were produced within four months of these observations. Kachuba's (1977) description of copulation notes a lack of a lordosis posture in the female. In contrast to the pair observed in the present study, Kachuba's pair did produce a litter. He too reported no discernable "copulatory cry", vehement throwing of

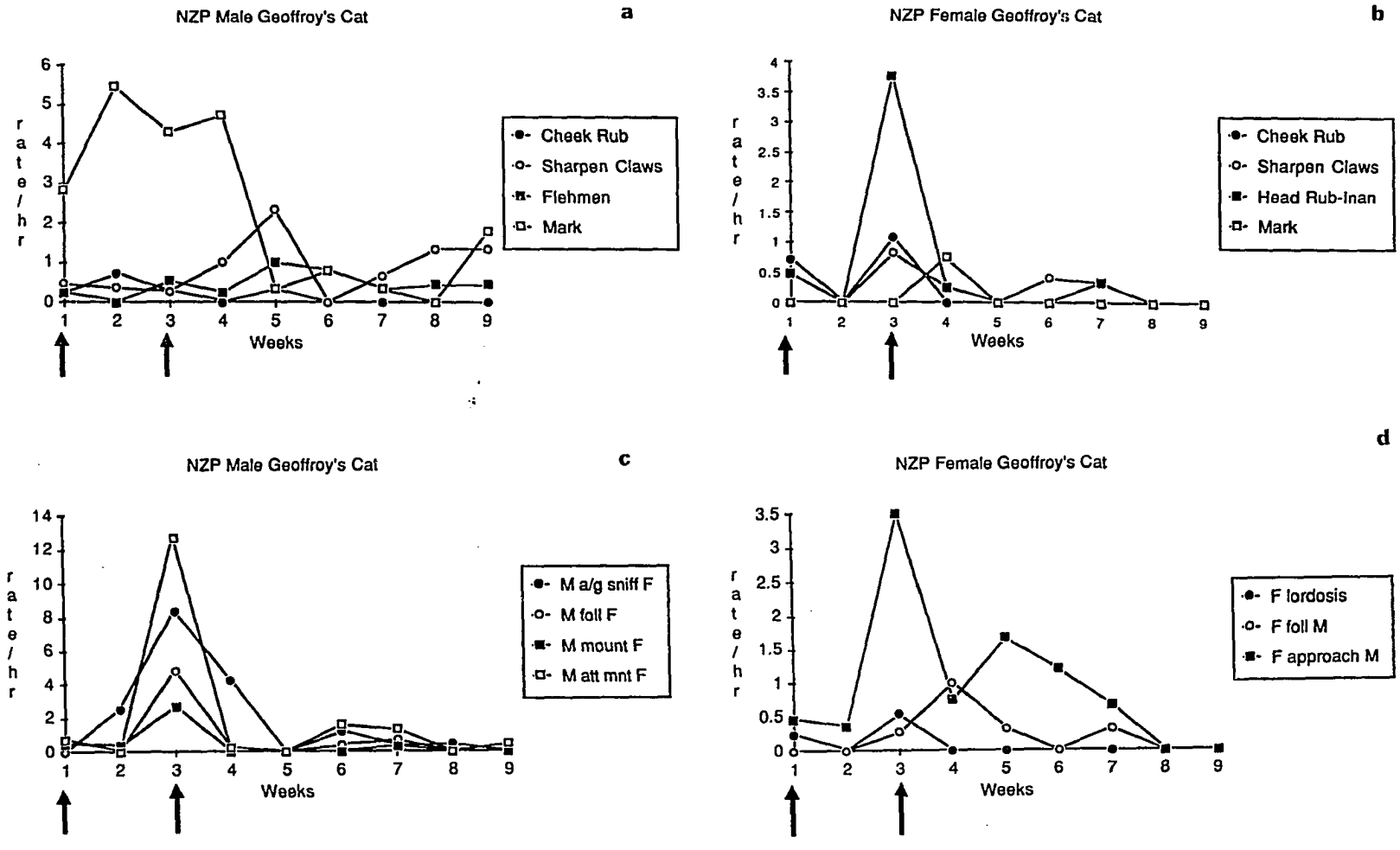


Figure 10. Rates of selected behaviors exhibited by a pair of reproductively active Geoffroy's cats. Arrows indicate that week in which reproductive activity was observed. See Table 3 for definitions of behaviors (Head Rub-Inan = Head rubbing (inanimate); a/g sniff = Anogenital Sniffing; foll = Following).

the male off her back, nor exaggerated/ repeated rolling on back after a mount. Whether he saw these behaviors or not is unclear.

Data from the present study suggest an estrus of two to three days (mean = 2.50) (Table 6) whereas Anderson's data (1977) suggest a mean of 4.29 (based on seven heats). Anderson's data (1977) also present an average gestation of 65.3; this is substantially shorter than the 75-76 day gestation described by Scheffel and Hemmer (1975). However, Anderson's data are based on calculating gestation from mean date of the female's receptive period and this may account for the lower figure. Data from the present study (one observation) show a gestation of 71 days.

Mean litter size from data collected during the present study was 2.31 with a sex ratio of 14.7.7, in good agreement with Anderson's average of 2.6 kittens per litter and 8.5.5 sex ratio (Table 6). Kachuba (1977) observed two mounts in his study of Geoffroy's cats. One mount lasted one minute, the second two minutes. This is in agreement with the data collected during the present study in which mounts lasted on average, 1.14 minutes. Hemmer (1979) reports a gestation of 74-76 days while Seager and Demorest (1986) report a gestation of 71 days. Data from the present study, based on only one observation, produced a gestation of 71 days. Ximenez (1975) reports births in the wild during December and May in Uruguay; data from the present study show litters born February through August with nearly a third of the litters born in the month of April (see Figure 3j). However, by adding data from nine litters born at the Memphis Zoo (Anderson, 1977), captive data show births in all months except January, September, and November.

ISIS shows 35 Geoffroy's cats in zoos (see Table 7). Virtually all of these animals are related to a very prolific pair at the Sacramento Zoo (G. Foreman, pers. comm.).

Jaguarundi (*Felis yagouarundi*)

Jaguarundis are the least "cat-like" in appearance of any member of the Felidae. Their common name in German means "weasel-cat" (Guggisberg, 1975) and indeed with their elongated body, short legs, and short rounded ears, they resemble a mustelid more than a felid. They have no contrasting marks and range in color from a grizzled gray to rusty red. Jaguarundis are found in mesquite and chaparral habitats as well as near water from the southern United States to Brazil and Peru (Honacki, et al., 1982) (Plate II).

In this study, jaguarundis were studied only on a short-term basis: one pair exhibited reproductive activity at the beginning of the two-week period; a second pair was observed on a short-term basis, but no reproductive activity was observed. During the last two days of observing this second pair, the resident female was replaced by a new female. Descriptions of that introductory period are presented below.

With regard to the first pair observed, Figures 11a, 11b, 11c, and 11d, illustrate that the male showed a great deal of "interest" in the female (Figures 11a and 11b) on January 26 and that the female was most aggressive towards the male on that day (Figure 11c). Further, the male spent January 26 in close proximity to the female (Figure 11d). On that day, whenever the female moved, the male immediately followed her. This particular male had sired offspring with other females; the female had, to date, not reproduced.

The jaguarundis observed in the present study were never seen to mark, i.e. to urinate, on a raised vertical surface. Given the stature of these weasel-like animals, this is not surprising. However, it is the only species of cat observed that did not mark on a vertical surface. Instead, the primary marking behavior appeared to be scraping with the hind feet. This was done

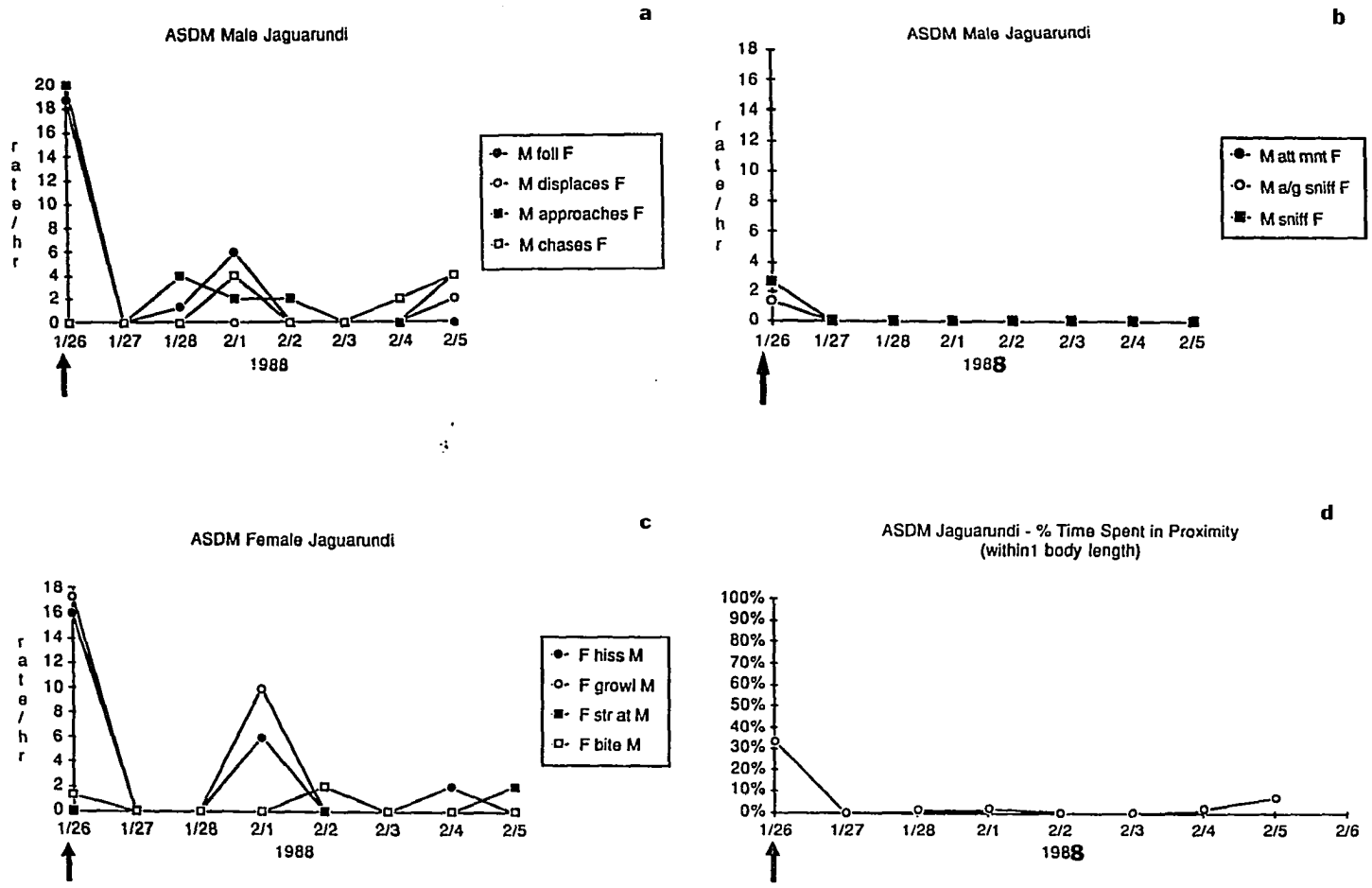


Figure 11. Rates of selected behaviors exhibited by a pair of jaguarundi and percentage of time spent in proximity (i.e., within one body length) . Arrow indicate the day in which reproductive activity was observed. See Table 3 for definitions of behaviors (attempt mt = Attempted Mount; a/g sniff = Anogenital Sniffing; str at = Strike at).

both with and without simultaneous urination. Marking behavior has been described elsewhere for this species (Hulley, 1976).

Below is a description of the introduction of a five-year old male who had sired six litters with other females to an 11-month old female. The female had been given sole access to the enclosure for two days prior to the introduction:

Male entered enclosure and sniffed many areas within it; female retreated to an upper branch of a tree.

Female came down from tree and chased the male around the enclosure (5-10 laps).

Both faced off, stared at one another and scraped the substrate with their hind feet; there were also some exchanges of hissing.

Male continued to scrape with his hind feet, sometimes while orienting to the female, sometimes quite possibly out of her view.

Female continued to hiss at the male and did more scraping with her hind feet.

Male approached several times to about one and a half body lengths and rolled on his back and neck rubbed the substrate repeatedly; female watched the male and occasionally hissed at him.

Male alternated between approaching the female to about one and a half body lengths, neck rubbing or rolling on his back, and returning to a small log where he scraped with his hind feet and urinated.

Female approached male several times and hissed at him; he hissed in return.

Female retreated up a tree and male continued to move around the area sniffing.

Female came down tree and chased male around the exhibit again, catching him several times, clawing and biting him.

Both eventually moved to separate areas of the exhibit; the male watched the female, the female occasionally neck rubbed the glass front of the enclosure.

Based on observations made throughout the present study on both reproductively successful and unsuccessful male cats, the behavior of the male jaguarundi described above appears to be characteristic of a "good breeding male." Reproductively successful males seemed to tolerate a great deal of aggression from females, seldom responding with a high level of aggression in return. Implications of this behavior are discussed in the Summary and Conclusions.

Weigel (1972) reports a gestation of 63 - 70 days with litters of two to four; he reports that litters are born twice per year in March and August, but that jaguarundis may not be seasonal breeders in the tropics. Hulley gives average gestation at 73.33 with an average litter size of 2.33 (data from three litters). In the present study, no data were available on gestation in jaguarundis, but births occurred in January, June, and August through October (Figure 3k); litter size averaged 1.83 (Table 6).

ISIS lists 34 jaguarundis in zoos (Table 7). Origins, relatedness, and level of inbreeding of this population are unknown.

Ocelot (*Felis pardalis*)

The ocelot is a relatively large member of the genus *Felis*, weighing 25 to 35 pounds. It is a spotted cat with eye stripes, conspicuous white "eye" spots on the backs of its ears, and rings on the end of its tail. See Plate II. It is found from the southern United States to Brazil, Paraguay, Argentina, and Peru (Honacki, et al., 1982).

Two pairs of ocelots were each observed on a short-term basis. The first pair had been copulating the week prior to the initiation of observations; early data reflect numerous approaches by the male with the female responding aggressively. As the observation set progressed, the pair seemed

to "settle in" to simply resting together. Towards the end of the observation set, social interactions mostly involved social grooming.

The second pair was placed together during the first day of observation. (The male had previously been removed for treatment of a minor injury.) Prior to introduction, the female had been showing strong signs of estrus: vocalizing, rubbing, and rolling; her vulval area was also swollen. The pair exhibited numerous behaviors associated with reproduction throughout most of the two weeks in which they were observed (Figures 12a, 12b, 12c, and 12d). On the fourth and fifth day of observation (October 20 and 21), the male attempted numerous mounts; on the sixth and eighth day after reintroduction, the male mounted the female (Figure 12c). Both exhibited a high rate of scent-marking behavior throughout the study period (Figures 12a and 12b).

The copulatory behavior of this pair of ocelots can also be described as "casual," although this pair may be exceptionally well suited to one another in that they have, to date, produced 11 litters together. Certainly, caution must be taken in describing the reproductive behavior of only one pair. Eaton (1977) describes high levels of aggression during courtship in some pairs in his study.

One copulatory sequence in the pair observed in the present study is as follows:

Male simply got up and walked over to the female, straddling her first with his front legs, then his hind, grasped her nape, and began pelvic thrusting.

Female assumed a lordosis posture.

Female growled (presumably a "copulatory cry") and male walked away.

Female neck rubbed and then groomed her genitals.

Duration was 1.5 minutes.

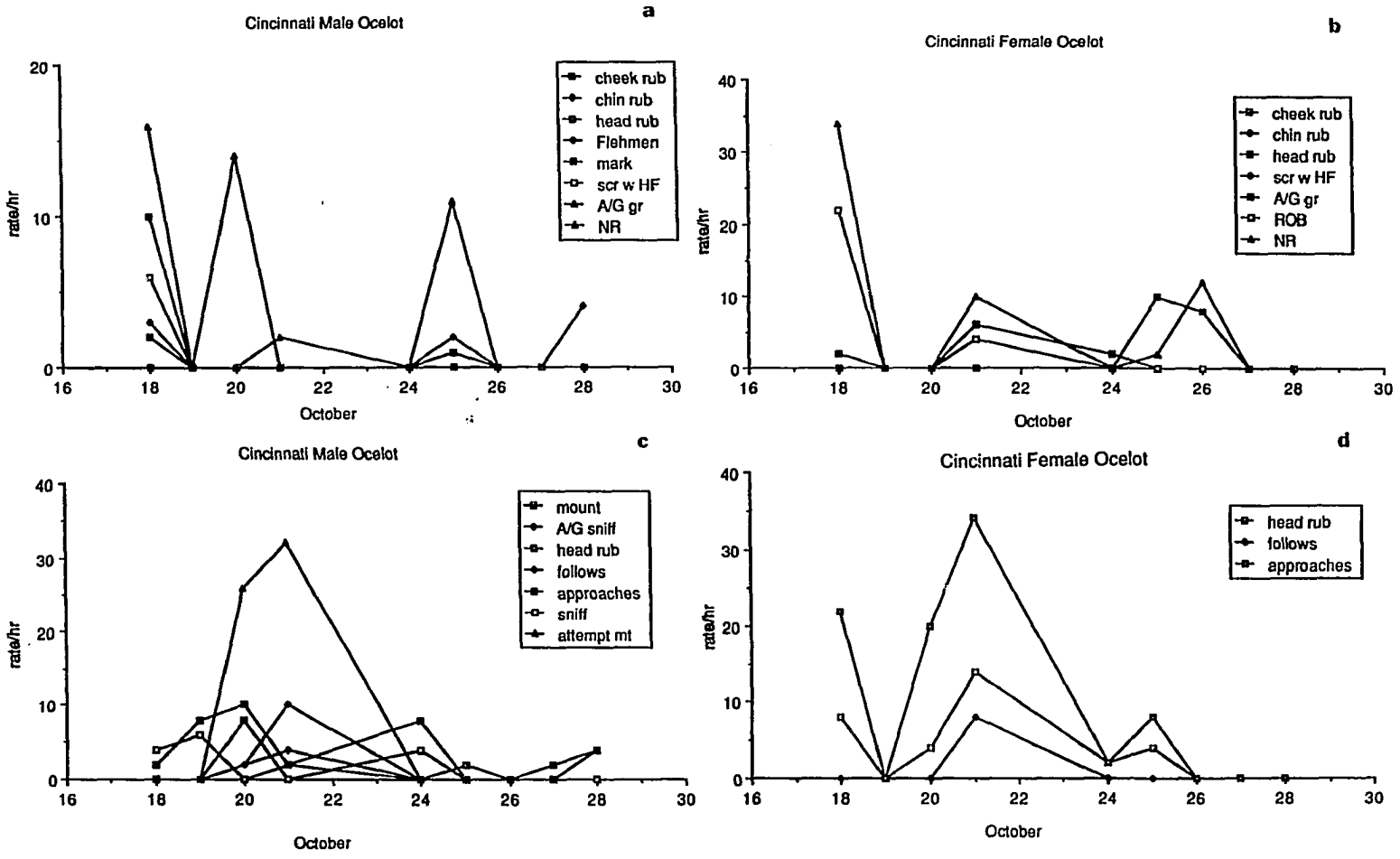


Figure 12. Rates of selected behaviors exhibited by a pair of reproductively active ocelots. See Table 3 and text for definitions of behaviors (scr w HF = scraping with hind feet; A/G gr = Anogenital grooming; NR = neck rubbing; ROB = Rolling on Back; a/g sniff = Anogenital Sniffing; attempt mt = attempted mount; head rub = Social Head Rubbing).

The female was observed to head rub both inanimate objects and the male, roll on her back, and adopt a lordosis posture while in close proximity to the male (Figure 12b, 12d). Of all the species observed during the course of the present study, the ocelot, by far, exhibited the most pronounced signs of estrus.

Eaton (1977) compiled data on captive ocelots from a number of zoos and private breeders. He found an average length of estrus to be 5.35 days, average estrous cycle to be from 15 days to six weeks, an average gestation to be 79.7 days, suggested birth peaks in March, May, and September-October, and an average litter size of 1.33, and a sex ratio of 18.12.1. The youngest female to give birth in Eaton's study (1977) was 2.5 years (130 weeks). With the exception of the suggested birth peaks, all of the data compiled in the present study are similar to the data presented by Eaton (1977) (Table 6). Data from the present study (Figure 3 I) show births in all months except October and December. No peaks were apparent.

There are 76 ocelots listed in ISIS; this species ranks sixth with regard to representation in the ISIS population just behind caracals (Table 7). Origins, relatedness, and level of inbreeding of this population are unknown.

Margay (*Felis wiedi*)

The margay in many respects resembles a smaller version of an ocelot. The margay weighs between 7 and 15 pounds, has a longer tail, and is more "delicate" in appearance than the ocelot. See Plate III. Its range, too, is similar to that of the ocelot: from the southern United States to Brazil, Paraguay, Argentina, and Peru (Honacki, et al., 1982). The margay is an arboreal hunter whereas the ocelot is terrestrial (Guggisberg, 1975).

No behavioral observations were made on margays in this study although they were represented at four of the institutions where data were

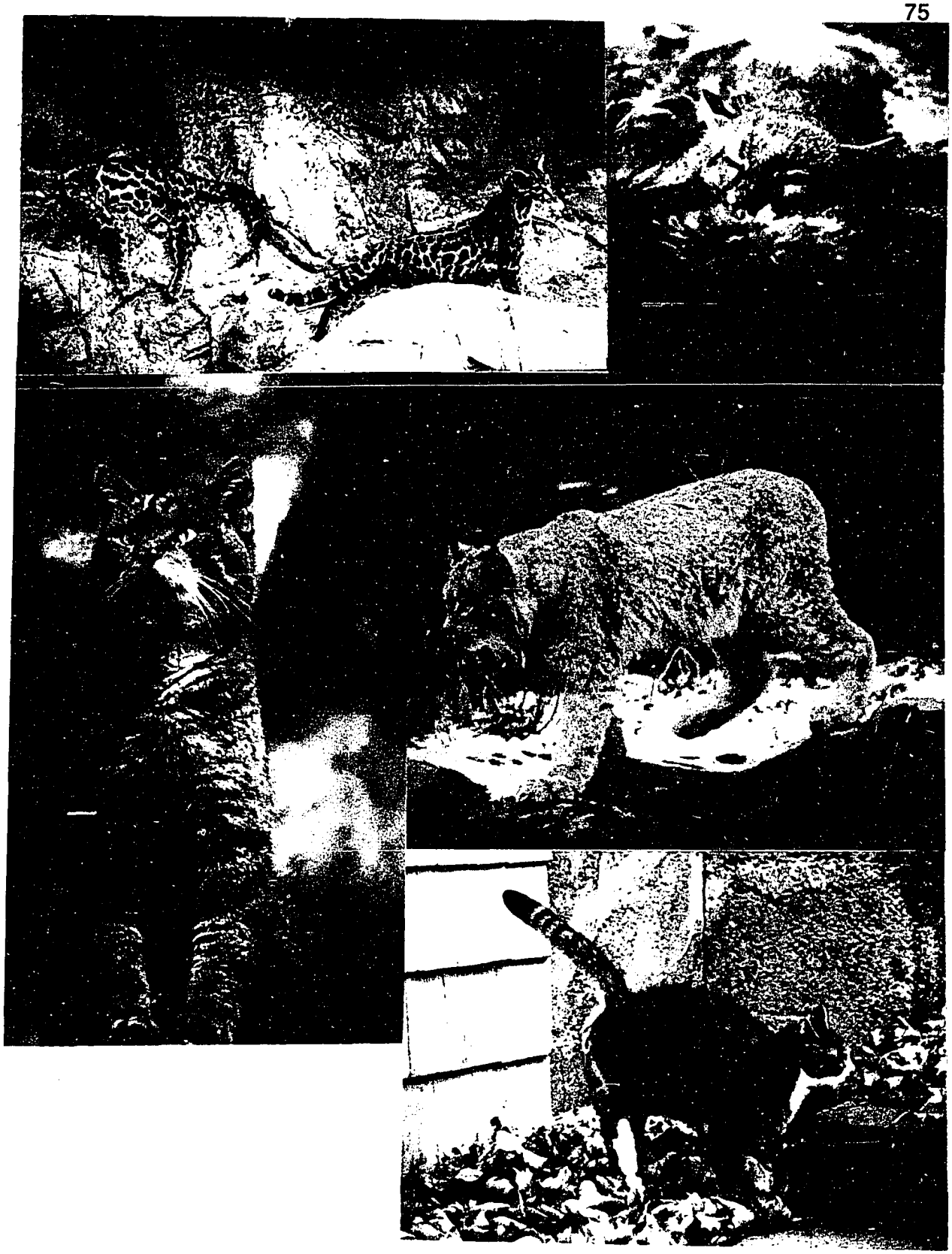


Plate III
Upper Left: Margay (*Felis wiedi*) - Photo by W. Spencer. Upper Right: Pampas Cat (*Felis colocolo*) - Photo by J. Mellen. Center Left: Scottish Wildcat (*Felis slyvestris grampia*) - Photo by J. Mellen. Center Right: Canadian Lynx (*Felis lynx canadensis*) - Photo by L. Master. Bottom: Domestic Cat (*Felis catus*) - Photo by J. Mellen.

collected. In each instance, females were pregnant, lactating, or not currently paired with a male. Historical reproductive data were available from three zoos (Table 6).

Seager and Demorest (1986) reported estrus length of 7 to 10 days and a gestation of 83 to 84 days. Petersen (1977) reported an average number of days in estrus at 10.13. In this study, length of estrus was only documented once and the duration was only four days, substantially shorter than those reported above. A gestation length of 84 days, is however, in agreement with the above data (see Table 6 for details). No birth peak was apparent (Figure 3m). Weigel (1972) states that there is probably no birth peak in the wild. He further says that litters are usually one to two kittens. In data collected for the present study using data from 17 litters, all litters consisted of a single kitten.

There are 58 margays listed in ISIS; this species ranks seventh with regard to representation in the ISIS population just behind ocelots (Table 7). Origins, relatedness, and level of inbreeding of this population are unknown.

Pampas Cat (*Felis colocolo*)

The Pampas cat inhabits the open grasslands of Equador, Peru, Brazil, and Bolivia, Chile, Argentina, and Uruguay (Honacki, et al., 1982). This cat is about the same size as a domestic cat and in many respects resembles a long-haired, delicate boned, domestic cat. It is quite variable in color (from yellowish to gray-brown). It has conspicuous eye stripes, the backs of the ears are black, and it has a ringed tail. See Plate III.

Two pairs of Pampas cats were observed on a short-term basis (two weeks). One pair showed no reproductive activity during the observation period. The second pair showed some breeding behavior during the first two days (October 18 and 19) of the study (Figure 13).

On Day 1 of the observations, the male of this second pair was seen to briefly and repeatedly mount the female at a rate of 24 times per hour and 30 times per hour on Day 2. All mounts were less than 10 seconds in duration. The mounts included a nape bite, straddling with both front and hind legs, plus pelvic thrusting. In all instances the female rolled on her side when mounted, tried to move away from the male, or bit him. On several occasions the male dragged the female a short distance by the nape. The repeated mounting behavior had a stereotypic component to it in its intensity, frequency, and

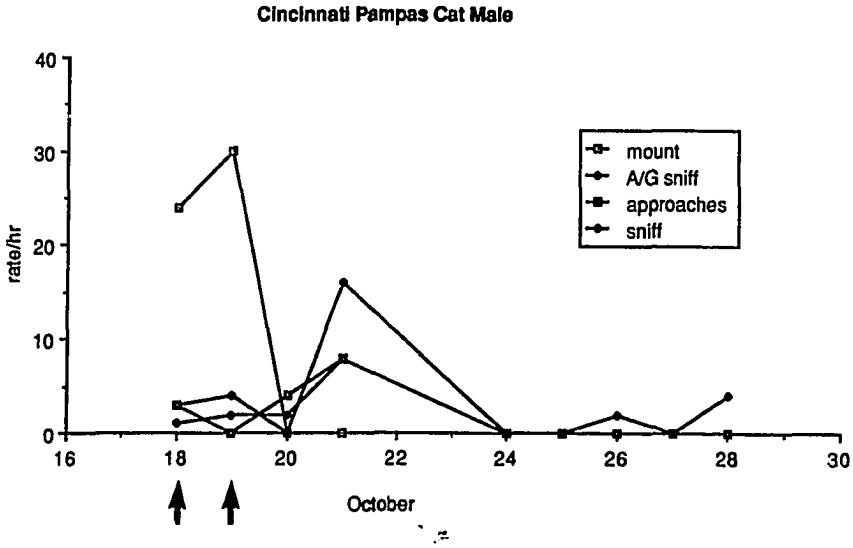


Figure 13. Rates of selected behaviors exhibited by a pair of reproductively active Pampas cats. Arrows indicate those days in which reproductive activity was observed. See Table 3 for definitions of behaviors (a/g sniff = Anogenital Sniffing).

predictability. It almost appeared like the male was pacing over the female, stopping briefly to "pelvic thrust. "

The female may have been at the end of an estrus. She had given birth 13 days prior to the onset of observation (one did not survive and the other was being raised in the zoo's nursery). Mounting behavior was not observed after the first two days and the pair did not interact a great deal subsequent to that time (Figure 13).

Nowak and Paradiso (1983) report litter size as being from one to three kittens. In the present study, the average litter size was 1.31 (Table 6). Given the dates of captive births, there is no strong suggestion of seasonality (Figure 3n).

ISIS lists 10 Pampas cats (Table 7). From data collected during this study, it appears that all individuals in North America, with one exception, are the offspring of one pair that are possibly siblings.

Scottish Wildcat (*Felis silvestris grampia*)

The Scottish wildcats are widely distributed throughout Scotland, seeming to prefer the woodland areas . This cat is the same size as a domestic cat (about 10 pounds) and, indeed, is thought to be closely related to the ancestors of the domestic cat (Guggisberg, 1975). To quote many zoo visitors, "it looks just like a regular [domestic] cat" with an orange-gray coat. See Plate III.

A trio of Scottish wildcats was observed on a short-term basis (two weeks). However, the two females had received hormonal implants to prevent conception, so no reproductive activity was observed. However, historical data were available to discern some information about reproduction in this subspecies. Average litter size was 2.50 with a sex ratio of 9.8.8; births seemed to be seasonal (Table 6 and Figure 3 o).

No other data on Scottish wildcats were found. However, there were data on the European wildcat (*F. s. silvestris*). Average litter sizes were reported to be 4.19 (Meyer-Holzapfel, 1968) and 3.13 with a sex ratio of 17.22 (Volf, 1968) and 109.110 (Conde and Schauenberg, 1969). Births of *F. s. silvestris* appear to be confined to the months of March through August (Meyer-Holzapfel, 1968; Volf, 1968; Conde and Schauenberg, 1969); this is similar to those recorded for *F. s. grampia* in the present study (Figure 3 o).

However, the average litter size reported for *F. s. silvestris* appears to be larger than that of *F. s. grampia* documented in the present study.

The three Scottish wildcats observed in the present study are the only individuals listed in ISIS (Table 7). All are related.

Canadian Lynx (*Felis lynx canadensis*)

The Canadian lynx inhabits the old-growth forest with dense undergrowth and windfalls of Canada, Alaska, and some of the very northern regions of mainland United States (Tumlison, 1987). The Canadian lynx is the largest of the *Felis* species observed in the present study. Its weight ranges from 40 to 50 pounds and is characterized by long, sturdy legs, disproportionately large feet, a short tail, and ear tufts (Guggisberg, 1975). The coat color is variable, but is often a gray color, sometimes having spots. The short tail is tipped black and the tufted ears have conspicuous eye spots. Canadian lynx also possess a characteristic facial ruff. See Plate III

The pair in this study was observed to copulate five days prior to the onset of observations. No other reproductive behavior was observed and the pair did not produce offspring for at least two years after observations were made.

Canadian lynx are widely held in zoos. ISIS lists 60 individuals (Table 7). Contrary to what might be indicated from data collected in the present study, this subspecies breeds quite well in captivity. Origins, relatedness, and level of inbreeding of this population are unknown, but many specimens are obtained through donations of confiscated wildborn animals (Shoemaker, 1988).

Domestic Cat (*Felis catus*)

The domestic cat is found throughout the world. Its average weight is about 10 pounds and the most common or "wild-type" coat color is a tiger-

striped tabby pattern (Wright and Walters, 1980). The tabby pattern includes conspicuous eye stripes and a ringed and black-tipped tail; the backs of the ears are a contrasting color and further fringed by yet another color. See Plate III.

Data presented here are from a colony maintained by the author for a related study (see Part II). Data are presented for the purpose of comparisons to other felids (Table 6 and Figure 3p).

In this study (Part II of this dissertation), the average duration of mounts was 2.64 minutes, considerably longer than the 1.42 and 1.52 respectively described by Michael (1961) and Whalen (1963). This difference was likely due to the early rearing experience of the females (see Part II of this dissertation). Length of estrus in the present study was 5.13 days. This is similar to the 5.4 days described by Schmidt et al., (1983). In the present study, the average length of an estrous cycle was 15.10 days (Table 6); this is somewhat longer than the 8-day average described by Schille, Lundstron, and Stabenfeldt (1979), although they report a range of 3 to 15 days. Feldman and Nelson (1987) suggest that queens may fail to show behavioral signs of estrus, although physiologically cycling. Average gestation in the present study (62.9 days) was similar to the 64.2 days described by Schmidt et al., (1983). The domestic cats in the present study showed pronounced seasonality (May through October) with respect to births (see Figure 3p). This is in agreement with Liberg (1983). Mean litter size in the present study was 4.75, somewhat larger than the 4.0 mean litter size reported by Hurni (1981), with a sex ratio of 100:89 somewhat lower than the 100:95 reported by Schmidt et al., (1983). Age at maturity was 42 weeks for the cats in the present study. This is the lowest of any species for which data were collected in the

present study, offering some support for the supposition that domestic cats have the fastest developmental rate of any felid (Hemmer, 1979).

Copulatory Behavior

The copulatory behavior of small cats appears to be very similar among all species observed. Their copulatory pattern has been described as one with "no lock, no intra-vaginal thrusting, ejaculation on a single insertion, and multiple ejaculations" (Dewsbury, 1972; Lanier and Dewsbury, 1976).

The typical sequence is as follows: the male approaches the female, grasps her by the nape, mounts by straddling the female first with the front feet and then the hind feet. The female responds to the nape bite by adopting a lordosis posture, i.e., elevating her hind quarters, and moving her tail to one side; the female sometimes also treads with her hind feet. The male sometimes at this point begins stepping with his hind feet, often rubbing against the female's flanks while doing so. This may function to induce the female to adjust or to exaggerate her lordosis posture. The male then begins pelvic thrusting. (Lanier and Dewsbury (1976) term this behavior as "extra-vaginal pelvic thrusting" and believe it to function in detecting the vaginal orifice.) In the present study, pelvic thrusting typically lasted one to five minutes. Intromission is apparently signalled by a "copulatory cry" by the female; this "cry" is typically a low, barely audible growl. About five to ten seconds after the female emits this vocalization, she throws the male off her back, often threatens the male, and begins vehemently rolling on her back. Rolling on the back typically lasts five to thirty seconds. Both the male and the female usually then groom their own anogenital regions. Although numerous mounts were observed in the present study, only in those mounts in which a "copulatory cry" and rolling by the female were observed was it assumed that intromission occurred.

Summary and Conclusions

Behavioral Observations as a Tool

Results from this study demonstrate that an accurate reproductive profile can be produced via systematic behavioral observations. More specifically, measurable differences in behaviors associated with copulation were consistently detected in reproductively successful pairs of cats. Further, these behavioral data provide information on the compatibility of a pair, providing additional information for the captive management of small cats. The best indicators of estrous behavior appear to be the examination of selected scent-marking and changes in social behaviors over time. Neither percentage of time spent in proximity nor percentage of time spent in various behaviors proved a good indicator of impending estrus.

Other methods have been used to detect behavioral estrus in captive felids. Keepers typically record the presence or absence of sexual behavior *ad libitum* (Altmann, 1974) as part of their daily routine. However, careful review of keeper records at a variety of zoos suggests that keepers often do not observe or necessarily record the occurrence of reproductive activity of their animals. (This was determined by counting backwards the approximate gestation length from the birth of kittens and examining keeper records around the time of conception.) This is not meant as a criticism of these care-takers, but rather as an explanation. The behavior of the cats often changes dramatically in the presence of keepers, even to the point of cats curtailing reproductive activity in the presence of their keepers. The issue is simply raised to point out that more careful observations than via keeper records may be necessary for an accurate assessment of reproductive activity.

Another commonly used method of detecting behavioral estrus is the determination of an additive "sexual score" (see, e.g., Kleiman, 1974; Schmidt et al. 1979,1988; Seal et al., 1987). This has proven to be a reliable method for assessing the presence or absence of estrus, especially in singly housed female cats. However, when pairs of animals are to be examined, a more complex data collection method, such as the one used in the present study, yields a great deal more information. A similar additive sexual scoring system was used by the author to assess copulatory behavior and reproductive success of differentially reared female domestic cats paired with experienced male cats. This additive sexual behavior score method proved not to be a valid measure of relative reproductive success.

In the present study, the most reliable indicator of estrus and/or reproductive activity was a change in the relative rates of some behaviors. Neither the *ad libitum* nor the additive sexual behavior score method are particularly good at detecting these relative changes over time. Further, the two categories of behavior most indicative of reproductive activity were scent-marking behavior and social behavior yet cats spent less than five percent of their time, on average, engaged in those behaviors. Thus, *ad libitum* observations, especially, would tend to miss these activities.

Yet another advantage to systematic behavioral observations is the acquisition of a substantial increase in our knowledge of reproductive parameters in this group of animals. Virtually all the information available on length of estrus, gestation, birth season, litter size, age at maturity, etc. to date have come from brief reports on one or few animals. These sources then are referenced and re-referenced. Comments like "female is very nervous with kittens" or "male remained with the kittens and appeared to contribute to their

care" begin as single incidents, but soon evolve into a characteristic of that species.

Behavioral Characteristics of Reproductively Successful Small Cats

The single most pronounced and pervasive characteristic of reproductively successful pairs of small cats observed in the present study is a male's extremely high tolerance for aggression directed toward him by the female. A successful male avidly monitors a female by sniffing her anogenital region and her scent marks. He watches, pursues, and persists in his approaches when the female is in estrus. When the female directs hisses, spits, strikes with her paw, and/or bites at a reproductively successful male, he typically moves just out of her reach, but continues to stay in close proximity and seldom does more than hiss back at the female. A reproductively successful male often cheek rubs and/or neck rubs while orienting towards a female, especially towards a newly introduced or reintroduced female.

Characteristics of reproductively successful females were less distinct. Certainly, successful females were characterized by allowing the male to mount, but until a male successfully did so, it was difficult to predict an outcome. Females that were extremely aggressive, yet showed obvious signs of estrus (like neck rubbing, rolling on back) were particularly enigmatic. At the other extreme, a number of the females observed in the present study, e.g., golden cat, rusty-spotted cat, the Cincinnati ocelot, showed pronounced proceptive behavior, approaching and following of their respective mates.

Behavioral observations such as the type made in the present study can shed light on whether 1) the female is cycling and 2) whether both members of the pair or just one member may be contributing to reproductive failure. However, absence of <u>any</u> reproductive activity is difficult to assess.

Reproductive success may also be influenced by the early rearing experience of the cats, by management protocols at the individual institutions, and/or by the the deleterious effects of inbreeding on these small captive populations. Part II of this dissertation examined the influence of early rearing experience on subsequent sexual behavior. In Part III of this dissertation, a discussion of management (husbandry) protocols and an assessment of captive populations are presented with regard to small cats in captivity.

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Part II. 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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Abstract. The importance of early rearing experience on subsequent sexual behavior in mammals has long been recognized. However, with the exception of some of the studies on primates, research has focused almost exclusively on males. The purpose of this study was to systematically examine the effects of human-rearing on female domestic cats (*Felis catus*) as it relates to successful copulation. Three groups of female domestic cats were reared under three different conditions and then paired at sexual maturity with sexually experienced males. Cats in Condition 1 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 her 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. Implications of rearing techniques for small exotic cats in a zoo setting are discussed.

INTRODUCTION

It is the general, although certainly not pervasive opinion, among zoo professionals that maternal rearing of animals is preferable to human- (hand) raising (Kleiman, 1975; Eaton, 1977a, 1984; Brambell & Jones, 1977; Meier, 1986). Most feel that handling by humans early in development may have an adverse effect on subsequent adult behavior. In the last 15 years, much conjecture about optimal rearing conditions has been made concerning one group of exotic animals - 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 Velander, 1977). Cats that are raised by humans are thought to become sexually imprinted on humans (Hediger, 1950, 1955; Klinghammer, 1973; Eaton, 1974, 1977a; Freeman, 1977a; Leyhausen, 1979). It is speculated that human-raised exotic felids may 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). Adult human-raised females that abandon or cannibalize their litters, may do so in response to genetically deficient kittens. Eaton (1984), in a survey of zoos, tried to collect data comparing breeding success of felid mothers that were maternally- or human-raised, but found that zoos tended to provide information only related to successful breeding. In addition, zoo records often do not include the conditions under which adult cats were raised (pers. obs.). Thus, it does not appear that the effects of human-raising on subsequent reproductive success can be determined from zoological records. Alternative approaches must therefore be considered.

The Influence of Early Rearing Experience on Subsequent Adult Sexual Behavior: A Review

Lorenz's classic studies in greylag geese were the first to detail the phenomenon of sexual imprinting (1935/1970). However, the first convincing experimental evidence in non-primate mammals that individual experience influences adult sexual behavior was presented by Valenstein, Riss, and Young (1955), Valenstein and Goy (1957), Riss, Valenstein, Sinks, and Young (1955),and Valenstein and Young (1955). They found that social isolation of male guinea pigs adversely affected mating behavior as adults. The males appeared to show interest in estrous females but were unable to orient correctly to achieve mounting.

Similar studies of male domestic rats resulted in conflicting conclusions. Some (e.g., Beach, 1942, 1958; Kagan and Beach, 1953) found no difference in sexual behavior of isolate-reared vs group-reared male rats; others (e.g, Zimbardo, 1958) found that social isolation impaired the sexual behavior of male rats. These differing results appear to be due to inconsistencies in the ages at which the rats were first isolated, i.e., older rats may have acquired experience important for adult sexual behavior prior to separation (Larsson, 1978).

Duffy and Hendricks (1973) examined sexual behavior of male and female rats raised in social isolation. This was one of the few studies that systematically examined both sexes in non-primate mammals. Both male and female rats that had been socially isolated showed a reduction in male sexual behavior as compared to normally raised controls. (Females were ovariectomized at weaning and later treated with androgens and estrogen/progesterone.) Isolate-reared females showed appropriate female sexual behavior after receiving replacement estrogens. The authors

concluded that male sexual behavior is essentially a social response and requires exposure to appropriate social stimuli during critical periods of development; conversely, the sexual behavior of females is thought to be a response to physiological states not dependent upon early social experience.

Wodzicka-Tomaszewska, Kilgour, and Ryan (1981) and Chenoweth (1981) reviewed the effects of varying types of early social deprivation in domestic livestock on subsequent male sexual behavior. Again, the effects of early rearing conditions are inconsistent. For example, rams raised in social isolation copulated normally (Zenchak and Anderson, 1980), while socially isolated boars showed reduced courtship and mating abilities (Hemsworth, Beilharz, and Galloway, 1977; Hemsworth, 1980).

Signoret (1970) examined the effects of social deprivation on female pigs. He raised gilts (young female pigs) in social isolation, then measured sexual and maternal behavior and found no deficiencies in the sexual/maternal behavior of these isolate-reared females. Signoret suggested an innate basis for the patterns of female sexual behavior in sows. His is one of the few studies conducted on female domestic livestock species.

Beach (1968) examined the effects of varying amounts of social isolation in male dogs. One group was raised in total isolation from conspecifics, a second group was allowed 15 minutes of daily contact with males and females, and a third group was raised continuously with females. The isolated group showed deficient sexual behavior while the group allowed only 15 minutes of contact with conspecifics showed normal sexual behavior (as did the group-raised males).

Early work on captive primates suggested the importance of early social experience on adult sexual behavior (e.g., Bingham, 1928; Yerkes and Elder, 1936; and later Harlow, 1965). Mason (1960) was the first to report the

effects of rearing conditions on subsequent sexual behavior of rhesus monkeys. He compared wild-caught males and females to laboratory-born monkeys separated from their mothers early in life. The lab-raised males showed deficiencies in most aspects of copulatory behavior, e.g., incorrect orientation, lack of foot clasp. The lab-raised females exhibited a presentation posture which was less stereotyped and less accommodating than that of wild-caught females. His results demonstrated that early experience is more important in males than in females.

Additional studies examined the long-term effects of early social deprivation in primates. Inept sexual behavior and exaggerated and inappropriate aggression persisted well into adulthood (Mitchell, Raymond, Ruppenthal, and Harlow, 1966). Again, although neither male nor female rhesus exhibited normal sexual behavior, the males seemed more debilitated by early social deprivation than did females (Harlow, 1965; Mitchell, 1979). Thus, early isolation rearing appears to have a lasting effect on subsequent sexual behavior in non-human primates. Further, the above research demonstrates that isolation is more debilitating to males than to females.

Sexual Behavior in Domestic Cats

Much of the early work on the sexual behavior of cats focused upon the associated neural (e.g.,Beach, Zitrin, and Jaynes, 1955, 1956; Zitrin, Jaynes, and Beach, 1956) and hormonal (e.g.,Harris, Michael, and Scott, 1958) mechanisms. Although Beach et al. (1955, 1956) and Zitrin et al. (1956) presented some descriptions of sexual behavior, the most intensive behavioral studies done in the 1950's were conducted by Rosenblatt and Aronson (1958 a, b). They allowed groups of male domestic cats varying degrees of sexual experience, castrated them, and then examined the decline in sexual behavior. Males raised in isolation from an early age failed to

display any but the most preliminary aspects of sexual behavior when they reached puberty (Rosenblatt, 1968). In contrast, even in the absence of male hormones, the sexually experienced males continued to show sexual behavior long after castration. These data were among the first to demonstrate that in at least one species, male sexual behavior is, to a degree, independent of hormonal control.

Michael (1961) examined the effects of spaying on the subsequent sexual behavior of sexually experienced female cats. He found no vestige of an estrous response nor did matings occur after spaying. Even those females ovariectomized at peak estrus did not show estrous behavior upon recovery from anesthesia and re-testing 24 hours later. Whalen (1963a) focused on the interaction between a particular male and a particular female cat. He found that the total sexual behavior of the pair is a function of the particular individuals within the pair and the sexual state of both individuals at any given time.

The Effects of Early Rearing Experience on Subsequent Adult Behavior: Domestic Cats

A number of other studies have reported that domestic cats raised in social isolation exhibited inappropriate social behavior when placed with conspecifics (Weiss, 1952; Kuo, 1960; Baerends-van Roon and Baerends, 1979). Weiss (1952) isolated two kittens from all conspecifics beginning at one week of age. In subsequent tests when confronted with conspecifics, these cats always attempted to escape. Kuo (1960) raised kittens with rats (and in the absence of conspecifics); these cats not only failed to kill rats later in life, but also showed exaggerated aggression toward other cats. Baerends-van Roon and Baerends (1979) isolated two female kittens from all conspecifics after seven weeks with their mothers. When a conspecific was

later placed in the same cage with one of these isolate-reared cats, the isolate would repeatedly bite at parts of the cage. In a larger enclosure, the isolate fled to a corner. When these cats came into estrus, they vocalized and rolled in typical fashion, but when approached by a male, they withdrew, hissed and scratched. Copulation with the isolate-reared females did occur at peak estrus, " . . . and only with a very patient sire; but immediately after copulation fierce agonistic behavior resumed" p. 83; 1979. The two females subsequently killed and ate all the kittens in their first litter. Of these two females, one continued to kill and eat her next four litters; the second female successfully raised a second and third litter.

In contrast, Kling, Kovach, and Tucker (1969) found that isolate-rearing of kittens had no effect on the maturation of play or aggression. The results of these studies are conflicting and may be due to different methodologies. For example, differences existed in the age at which the kittens were first isolated, and in the total amount of time the cats were isolated. Sample sizes were small in some instances.

Seitz's work (1959) examined the age of separation from mother and subsequent adult behavior in domestic cats. He raised kittens in social isolation after separating them from their mother and littermates at two, six, and twelve weeks of age. When the cats reached adulthood (at nine months), their behavior was compared in a series of tests measuring activity during exercise period, emergence from home cage, response to an unfamiliar enclosure, response to intense sound/light, response to food frustration and a feeding competition situation, and acquisition of a learned response. The results of this study showed no sex differences among the three treatment groups for the behaviors examined. The group of cats which had been removed from their mothers at two weeks of age were the most disturbed by

novel environments and situations. This group displayed the most fearful and aggressive behaviors toward other cats and humans and showed the most physical aggression during feeding competition. Interestingly, this group also developed an asthma-like condition for which there was apparently no medical cause. The group isolated at 12 weeks of age exhibited more vocal aggression toward conspecifics than did the other two groups.

The early social environment was found to influence play behavior in domestic cats. Social play was found to differ with the presence or absence of a littermate (Koepke and Pribram, 1971; Guyot, Cross, Bennett, 1980a; Mendle, 1988) and with the gender of the littermates (Caro, 1981b). In fact, play behavior in domestic cats has been intensively studied (e.g., West, 1974; Barrett and Bateson, 1978; Bateson and Young, 1981; Caro, 1981b). Specifically, predatory play, social play, object play, and locomotory play have been examined. At 4-6 weeks, kittens first show social play which is gradually replaced by object play (high at 8 weeks) (Barrett & Bateson, 1978; Caro, 1981; Martin & Bateson, 1985). None of the studies perused made any mention of sexual play, e.g., play mounting, except that Kling, Kovach, & Tucker (1969) saw some elements of sexual behavior (mounting and neck grip) as early as four months of age and West (1975) observed a decline in social play coinciding with independence from the mother (at 20 weeks of age) and an increasing interest in sexual activity on the part of the males.

In strong contrast to both the pervasive opinion of zoo professionals and the implications of the experiments described above, private breeders of exotic felids generally feel that human-raising is preferred over exclusive maternal raising of kittens (e.g., Quillen, 1981). Private breeders usually remove kittens from the mother at two weeks or, if the mother is tractable, the

kittens are simply handled a great deal from birth and left with the mother (Rosemond, CA, pers. comm.). The success rate of these private breeders appears to be superior to that of many zoos. Further, private breeders claim that their human-raised animals are calmer, show fewer stereotypic behaviors, breed willingly, and the females care for their offspring.

A definite need exists for the resolution of questions regarding optimal rearing conditions for exotic cats. Unfortunately, historical information on early rearing conditions for captive felids, whether in a zoo setting or maintained by private breeders, is for the most part unavailable. One alternative to the archival approach used by Eaton (1984) and Dvornich(1984) is an experimental approach using domestic cats as a model. In this study, domestic kittens were raised under the various conditions typically occurring in zoos, i.e., human-raised alone, human-raised with a sibling, and maternally-raised with a sibling. At maturity, these females were systematically paired with experienced males and their behaviors recorded.

Domestic Cats: A Behavioral Model for Small Exotic Felids

Domestic cats have been used as a model for a great deal of research on the reproductive physiology of exotic felids (e.g., Seager, 1976; Seager and Demorest, 1978; Platz et al., 1978; Wildt et al., 1980; Wildt et al., 1981; Wildt et al., 1983; Shille, Wing, Lasley, and Banks, 1984). Further, the courtship patterns of numerous species of felids have been described as virtually identical to or very similar to those of domestic cats (e.g., Cooper, 1942; Leyhausen, 1965, 1979; Ewer, 1973; Kleiman and Eisenberg, 1973; Mehrer, 1975; Lanier and Dewsbury, 1976; Eaton, 1978; Part I of this dissertation). The development of domestic cats is also similar to other felids, both physically (Hemmer, 1976, 1979) and behaviorally (Fagen, 1981; O'Connor and Freeman, 1982).

Although the similarities of domestic cats to wild felids is emphasized above, the influence of the domestication process on *Felis catus* must be addressed. Most of the behavioral studies and descriptions of domestic cats state that the domestication process has affected the behavior very little (e.g., Fox, 1974; Todd, 1978; Liberg, 1980, 1981; Clutton-Brock, 1981; Wolski, 1982; Izawa, 1983). The ability of almost any domestic cat to revert to a feral existence suggests little change. However, domestic cats are different in that females produce more litters per year and larger litters than those of any other *Felis* species (Weigel, 1972); age of first walking is also earlier than for other felids (Hemmer, 1976, 1979). The major behavioral distinction between wild *Felis* and domestic cats is the potential for greater sociality in domestic cats (Todd, 1978; Clutton-Brock, 1981; Fagen, 1981; Macdonald et al., 1986; Natoli, 1983, 1985). The degree of sociality exhibited by an individual seems to be dependent upon the quality of the habitat and population density (Dards, 1983). The potential sociality in other felid species may be underestimated. For example, social aggregations have been observed in jungle cats (*F.chaus*) and lynx (*Lynx lynx*) (Lindemann, 1955).

Domestic cats appear to be the result of natural selection (see Price, 1984) within captive populations. Unlike other domesticated species, domestic cats typically have not been artificially selected for particular morphological or behavioral traits by humans (Kling, Kovach, and Tucker, 1969; Todd, 1978); the process of domestication for this species has been more passive than active (Wolski, 1982). (The obvious exception is the recent development of particular cat breeds.) Thus, although *Felis catus* is presumed to be the first animal to be domesticated by humans (F. Simoons, pers. comm.), it may be one of the least affected by the domestication process (Reed, 1980). Its role in association with humans has simply been to remain

in proximity to humans and exploit the rodent population and human refuse (Todd, 1978; Wolski, 1982). Larger litters, rapid maturation rate, and increased sociality might simply be the result of natural selection having acted upon this species (Todd, 1978).

Together, these data suggest that the similarities between the domestic and wild small felids outweigh the differences and that domestics represent an accurate model for the experimental examination of reproductive failure in captive exotic felids, especially since exotic felids in captivity may well be in the initial stages of domestication (Hediger, 1954; Fox, 1968) as Price (1984) defines the process. In this study, domestic cats were used to systematically study the effects of early rearing experience on subsequent sexual behavior.

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 obtained by contacting employees and volunteers at the Washington Park Zoo in Portland, Oregon, U.S.A. Individuals willing to aid in this study were asked to contact the author if they had a pregnant *non*-purebred cat of average size. Owners of pregnant cats were asked to notify the author immediately after the birth of their cats' kittens. Two female kittens were removed from each mother at 48-hours 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, because of the altricial nature of the kittens, had had minimal interaction with conspecifics. A total of 15 kittens was 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. A total of eight kittens was 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 (much to the chagrin of the author) was mis-sexed and at 154 days of age was separated from *his* sibling. Thus, a total of 21 female cats, 7 in each of three groups, was 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. The toms were fed canned Science Diet®. Each of the two males was separately housed in "breeding" enclosures each measuring 3.05m x 1.83m x 2.44m, made of wood supports and chicken wire. Each breeding enclosure contained two wooden den boxes each measuring 0.61m x 0.305m x0.305m 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.

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 x 0.915m x 1.22m. Each cage contained two perching shelves, one to two branches, a litter pan, food and water dishes, a variety of small cat toys, and a heated den box measuring 0.61m x 0.305m x0.305m. These cages, as well as those of the males, were located in an outdoor, off-exhibit area at the Washington Park Zoo in Portland, Oregon. At sexual maturity, i.e., once estrous behavior was noted in those females in Conditions 2 and 3, all 21 female cats were individually housed in the 1.22 m x 0.915m x 1.22m plywood and hardware cloth enclosures.

One of four caretakers, including the author, checked the experimental cats daily for signs of estrus, i.e., lordosis posture, tail deflection to one side, treading with hind feet, vocalizations, cheek rubbing, rolling, and increased "friendly" behavior. In addition to checking for estrous behavior, the caretaker fed and watered each cat, monitored the health of the animal, and cleaned the litter pan. 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 kittens - Conditions 1 and 2

A total of 15 kittens was randomly assigned to Condition 1 or 2. Kittens assigned to Condition 1 were raised by humans beginning at two days of age and had no physical contact with conspecifics until sexual 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 eleven months of age from kidney failure; the death of this individual occurred after her sister came into estrus for the first time.

With the exception of four kittens, all of the rearing of the kittens assigned to Conditions 1 and 2 was done by the author. Two additional caretakers raised two kittens each, two from Condition 1 and two from Condition 2 for the first three weeks post-partum and then returned them to the author for subsequent care. The kittens in Conditions 1 and 2 remained in the author's home until twelve 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.

Kittens were weighed daily for the first 40 days of life. Each was bottle-fed Borden's Kitten Milk Replacement (KMR)®, gradually weaned onto Purina Kitten Chow ®, and then eventually switched to a combination of dry Purina cat chow® and Kal-Kan® canned food. Some cats showed an intolerance to the Purina cat chow® and Kal-Kan® canned food combination and were fed canned Science Diet®.

Maternally-raised kittens - Condition 3

As described above, four female barn cats each raised two female kittens (actually a total of seven female kittens, as one was mis-sexed). Human interaction with the mothers and kittens was 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, although auditory and olfactory contact occurred. Beginning on Day 9, each kitten was weighed once a week for five weeks.

The maternally-raised kittens were weaned onto a combination of dry Purina cat chow® and Kal-Kan® canned food. Some cats showed an intolerance to the Purina cat chow® and Kal-Kan® canned food combination and were fed canned Science Diet®.

The weights of the individuals in the three groups were compared using a Kruskall-Wallis test to determine if any differences between human-raised and maternally-raised kittens existed that might have an effect on subsequent behavior.

Experimental Design

Sexual maturity in these domestic cats 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. This four-day period falls between the average length of estrus, 7.5 days, for domestic cats (Feldman & Nelson, 1987). Two males were used in this study 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 four days, the female was placed in the male's area (the breeding pen) either for 30 minutes, until three copulations had occurred, or until the session was discontinued if the author felt that injury to one of the animals was imminent. 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.

The frequency of a variety of behaviors associated with reproductive behavior in felids was recorded. These are listed and defined in Table I.

Table 1. All occurrences of some behaviors

Behavior	Description
Social sniffing	cat sniffs any region other than the anogenital region of another cat
Follow/Chase	one cat rapidly follows within one body length for a distance of at least two body lengths
Social grooming	one individual licking, chewing, and/or cleaning the fur of another cat
Approach	one cat approaches the other within one body length
Social head rubbing	"forehead" of one cat rubbed against another cat
Anogenital sniffing	cat sniffs the anogenital region of another cat
Lordosis	female elevates hind quarters while resting most of her weight of her forepaws and chest
Treading	while in a lordosis posture, female "steps" in place with her hind feet
Tail to Side	while in a lordosis posture, female deflects her tail laterally away from her 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 his hind feet, usually rubbing the sides of the female with his hind feet
"pelvic" thrusting*	while mounting, male makes searching/thrusting movements with his pelvic region contacting the anogenital region of the female
Intromission	intromission was 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	as implied
Anogenital self-grooming	cat grooms its own genitals for a least four seconds
Cheek rubbing	cheek of cat rubbed against an inanimate object
Neck rubbing	cat vigorously rubbed or scraped 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	cat orients to another cat and emits a hissing vocalization
Growl vocalization	cat orients to another cat and emits a growl
Strike at	cat strikes at another with its paw, but no contact is made
Arch Threat	"Halloween" cat posture, i.e., with arched back
Strike with paw	cat strikes another with its paw
Biting	as implied

*Using Dewsbury's classification (1972), domestic cats do not pelvic thrust. The behavior, instead, appears to be a "searching" motion and occurs prior to intromission

Analysis of Results

A Kruskal-Wallis test (Conover, 1980) was used to determine if there were any statistically significant differences among the weights of the three groups of cats when they were kittens. Comparisons of weights were made for Days 9, 15, 22, 29, and 36 of the kittens' lives.

A chi-square-goodness-of-fit test (Conover, 1980) was used to determine if there was a significant difference among the three groups in terms of the total number of females that copulated during the experimental pairings.

The frequency of all behaviors recorded were converted to average rates per hour for each of the 21 subjects. Of these behaviors, selected ones were tested using a Kruskal-Wallis test (Conover, 1980) to determine statistical significance among the three groups; appropriate post-hoc tests (Conover, 1980) were used in those instances where statistical significance occurred. All behaviors were not tested in this manner because, given a maximum p value of 0.05, if all behaviors were tested, by chance some behaviors might prove to be statistically different.

Each estrous female was alternately placed with two males for four days. A chi-square goodness-of-fit (Conover, 1980) was used to determine if there was a significant difference in the relative reproductive success of the two males. Both the total number of females bred by each male and total number of intromissions were compared.

A single-factor analysis of variance test was used to determine if there was a significant difference in the duration of mounts among the three groups of females. A Tukey-Kramer method of multiple comparisons was used to determine which of the three groups differed from one another (Neter, Wasserman, and Kutner, 1985).

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. These differences approached significance ($\underline{X}^2$=4.96, df=2, $\underline{p}$=0.084).

Physical Measurements of the Females

Maternally-raised with sib kittens tended to be heavier than hand-reared kittens on Days 9, 15, and 22 while the reverse was true on Days 29 and 36. (See Figure 1.) These differences were not significant.

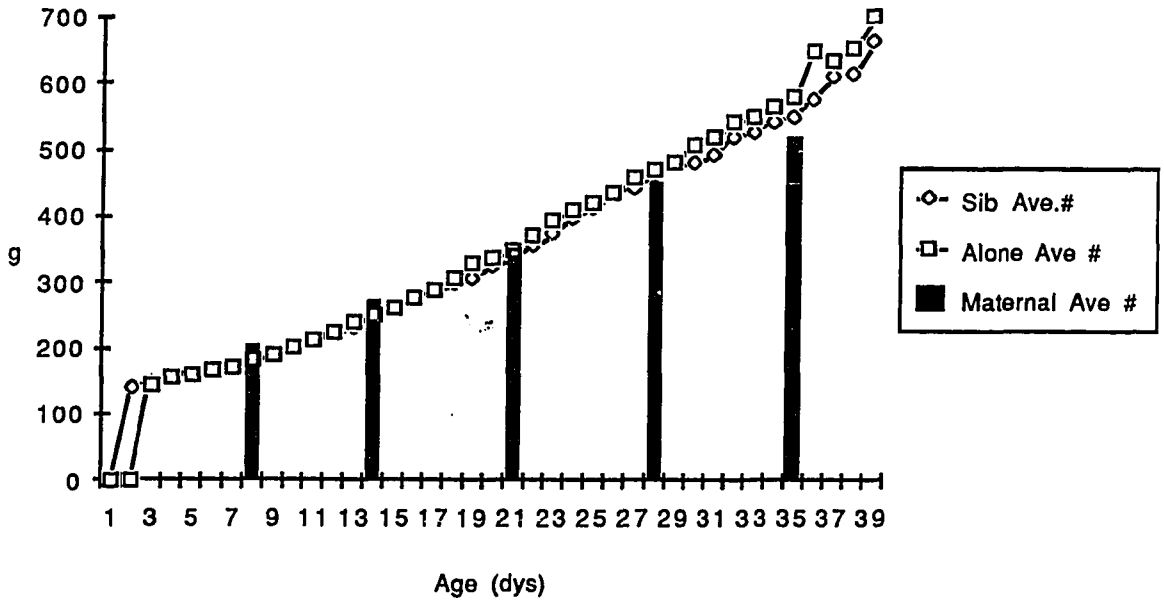

Figure 1. Comparison of weights of the three groups of kittens

Another physical assessment was made at the end of the study. To ensure there were no physical, i.e., pathological, reasons for failure to

copulate, the gross morphology of the ovaries and uteri were examined for all females upon completion of the study. No abnormalities or pathologies were apparent in any of the cats. Thus, differential breeding success between the groups of females was probably not due to any overt dysfunction of the reproductive system.

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 ($\underline{X}^2$=0.1037, df=1, $\underline{p}$>0.250) nor the total number of intromissions achieved ($\underline{X}^2$=0.08, df=1, $\underline{p}$>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 intromitted only 26 and 24 times respectively - perhaps an example of "intromittent" reinforcement.

Comparisons of Rates of Behavior Among the Three Groups

Table II presents the average rates of behaviors for each group of females; Table III presents the average rates of behaviors exhibited by the two males while paired with the females in each particular group. All behaviors

Table II. Mean Rates of Behavior per Hour (± Standard Error) for Behaviors Exhibited by Females in Different Treatements *

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

* only those behaviors in **bold** print were tested for signficiance

* *Kruskal-Wallis Test (Conover, 1980) (df = 2, N = 21)

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

* only those behaviors in **bold** print were tested for signficiance

* *Kruskal-Wallis Test (Conover, 1980) (df = 2, N = 21)

associated with copulation were highest in the maternally-raised with sib group of females. Two behaviors associated with copulation, rolling on back and neck rubbing, were tested and found to be statistically higher in the maternally-raised with sib group (see Table II). With the exception of one 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 II). 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 copulated (as measured by the number of intromissions) significantly more often than did the females which were human-raised alone (see Tables II and III). In addition to the average rate of intromission, Table III shows that the males approached, followed, and sniffed the ano-genital 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 III) . 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 response were practically identical for the males in response to all three groups of females (Table III).

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 five minutes seldom resulted in intromission. Figure 2 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. A mount lasting 20 seconds was the shortest mount (in duration) that resulted in an intromission.

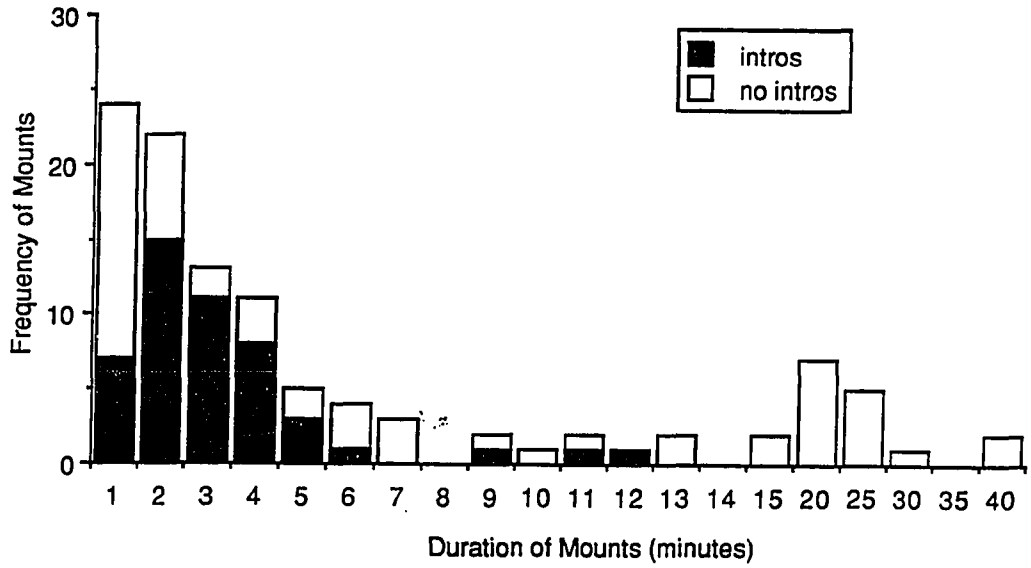

Figure 2. Duration of mounts. Note that the X-axis is divided into 1 minute segments until 15, then increases at 5 minute intervals. Figure is based on 48 mounts in which there was intromission and on 59 mounts in which there was not intromission.

The duration of mounts was also assessed in terms of the average length of mounts by 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 3.

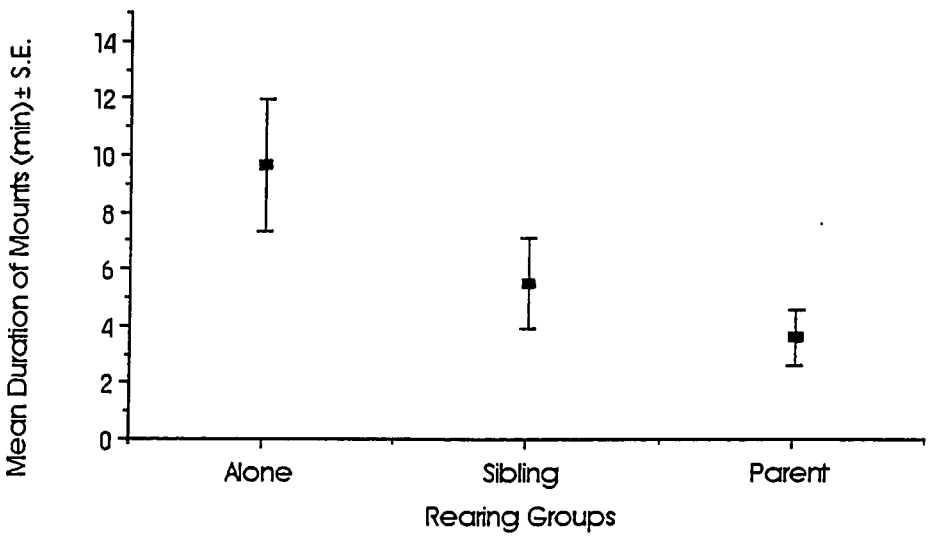

Figure 3. Mean duration of mounts ± S.E. for three groups of females

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., intromission. However, in situations in which the females were overtly "cooperating" with a male during a mount, i.e., in lordosis posture with tail deflected and treading, no difference could be discerned in

the positions/postures of females who successfully copulated as compared to 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 male, 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 of the individuals were extremely aggressive. They usually responded aggressively (biting, scratching, growling) to almost any type of direct 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 gloves in order to safely reach 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, 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 II) 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.

Maternal Behavior

Originally, it was the intention of this experiment to also assess the maternal behavior of the females in each of the three groups. This aspect was terminated when only one of the cats conceived in each of the two human-raised groups. Since no statistical assessment was possible, this aspect was not pursued because the single female that conceived in the human-raised alone group proved to be an adequate mother. She gave birth to a litter of three kittens. On Day 2 of the kittens' lives, a caretaker found one of the kittens outside of the nest box and placed the kitten back with the other two.

All three kittens survived to maturity without any other intervention. The only female to conceive in the human-raised with sib group gave birth to a litter of five kittens. She appeared to be an extremely attentive mother and all five of her kittens survived to maturity.

Since it was decided not to systematically assess maternal behavior of these cats, most of the females in the maternally-raised with sib group were spayed immediately after the estrous period in which they copulated. However, several of the females in this group were allowed to give birth. The following anecdote is presented to illustrate the potential for cross-fostering of exotic kittens to lactating domestic cats.

One of the females, Scooter, lost her litter. A second female, Mary, gave birth to a litter of five kittens four days later. The day after Mary's kittens were born, she was allowed the opportunity to voluntarily leave her home cage, which she did readily. Scooter was then given the opportunity to enter Mary's cage, which she did readily. Scooter immediately entered the den box and laid down next to the kittens. When Mary returned to her cage, she curled up with her kittens and Scooter, without any aggression towards Scooter. For the next four days, the females were alternated with the litter, until it was determined that Scooter had enough milk to successfully raise the kittens. At that time she was left permanently with her foster litter. She raised all five kittens to maturity. It should be noted that Mary and Scooter shared adjacent cages and although visual contact between the two was restricted, it seems likely that a certain amount of familiarity was possible via olfaction and/or audition. Also, these females had different (and unrelated) mothers, but were sired by the same male.

DISCUSSION

Physical Effects of Early Rearing Conditions

Weights of the three groups of females were measured from birth through weaning. The mother-raised group was heavier in weight during the first three weeks of life, but the two hand-rasied groups were heavier at four and five weeks of age. These results are in agreement with other comparisons of human-raised vs. maternally-raised kittens (Kling, Kovach, and Tucker;1969). It should be noted that both human-raised groups were weaned onto solid food by 29 days of age while the maternally-raised kittens were still nursing (and showed no interest in solid food until well after weighing was discontinued at 40 days). It has often been said that whenever possible, it is advantageous to allow the mother to raise the kittens because they are healthier. At least with this measure (weight), human-raised kittens did not differ substantially from those raised by their mother.

Effects of Early Rearing Experience on Subsequent Adult Behavior

Studies in which early rearing experience was varied 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; Konrad and Bagshaw, 1970), 2) males raised alone showed a reduced ability to copulate (Rosenblatt, 1965), and, 3) kittens raised only with a surrogate "brooder" were termed "hypergregarious" by Guyot et al. (1980a, b).

In this study, the human-raised alone group (Condition I) 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 and van roon 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 (1975) 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" p. 172. The general descriptions of the "personalities" of the cats parallel those of Seitz (1959) who separated kittens from conspecifics at two weeks of age.

With regard to the human-raised with sibling group (Condition II), 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 are unclear as to the level at which the

presence of a sibling compensated for the lack of a mother, but certainly are at odds 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 subsequent reproductive success, 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 Harlow's lab (Harlow and Harlow, 1962; Chamove, Rosenblum, and Harlow, 1973). These monkeys were much better socially adjusted than individuals raised alone, but nevertheless their social behavior was substantially debilitated as compared to more normally reared monkeys. Peer-reared female Rhesus, as adults, showed impaired sexual behavior, e.g., an inadequate support pattern when mounted. Further, Goldfoot (1977) felt 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 they 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 which 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. Another possible outcome of interactions

with mothers is that kittens learn not to be afraid of conspecifics larger than themselves. (In my 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 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 was paired with a reproductively successful male at the Sacramento Zoo. The female's response to the male's attempts at copulation were similar to those described for the domestic cats raised under the same conditions in the present study. The pair later successfully copulated when moved to a new enclosure (pers. observ.). Certainly, the human-raised with sibling cats (Condition 2) in this study seemed better able to adjust to their environment than the human-raised alone group and so at least in this regard human-raising with a sibling would seem preferential to human-raising in the absence of all conspecifics. Whether this rearing technique results in improved reproductive success remains to be seen.

As Guyot et al. (1980b) pointed out, it is still unclear as to whether this kind of atypical social behavior was due to the absence of the mother, absence of the littermates, or both. These researchers further believe that the development of social play was affected by isolation and that social play is necessary for appropriate adult social behavior (but see Martin, 1984; and Martin and Caro, 1985). Whether because of lack of social play or an inability to accurately perceive the communication modes of conspecifics, isolate-reared animals seem to behave inappropriately in social situations, especially in agonistic ones (Mason, 1960; Sackett, 1974; Meaney and Stewart, 1985).

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 this study, the human-raised alone females (Condition I) were hyperaggressive in their behavior towards males. It may well be that the males' lack of reproductive success with the human-raised alone females was due to an inability to even approach and contact, i.e., begin to mount, because the females responded so aggressively to any movement by the male. Mating in felids is thought to be "dangerous" to both parties because cats possess the ability to seriously injure one another and because aggressive tendencies must be overcome during courtship (Wemmer and Scow, 1977).Baerends and van roon 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 stated that the effects are more debilitating to the male than to the female (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). 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 this study suggest that early rearing experience may also influence subtle differences in the lordosis posture of female domestic cats which were in essence, isolate reared. The average duration of mounts for the two human-raised groups was over five minutes and yet most successful mounts (with intromission) were less than five minutes in length. These findings are suggestive of some subtle differences in the postures of the two human-raised groups. So, even if the male is successful in overcoming the higher level of aggression shown by these females, he may still be unable to successfully complete a mount because of slight postural abnormalities. The data do suggest that early rearing experience of females may influence the ability to achieve or maintain sexual postures that result in successful copulation (Beach, 1976).

Rosenblatt & Aronson (1958b) suggest that "...the effects of past experience influence the readiness with which males respond to the receptive female. In addition, they enable the male to develop a repertoire of general social behavior, which is modified and adapted in adulthood to form an integrated mating pattern" p. 287. Rosenblatt (1968) later reiterated that the disturbance in sexual behavior is of a deeper nature than the observed difficulties in orientation might first suggest and is associated with broader difficulties in social responsiveness. Data from this study suggest the same holds true for female domestic cats. It has been said that sexual receptivity in the female cat is strictly dependent upon the presence of ovarian hormones (e.g., Michael, 1961). However, data from this study as well as those of Whalen (1963b), suggest that although the presence of increased levels of estrogen are *necessary*, they may not be *sufficient* for successful copulation.

Courtship Behavior of the Domestic Cat

The courtship sequence has been described in domestic cats by many researchers (e.g., Rosenblatt and Aronson, 1958a,b; Whalen, 1963a; Michael, 1961; Leyhausen, 1979). Further, Scott (1970) presented drawings of some aspects of the courtship sequence. In subsequent review articles concerning reproduction in domestic cats, Rosenblatt and Aronson's descriptive table is most often cited, sometimes supplemented with Scott's diagrams (e.g., Rosenblatt and Schneirla, 1962; Kling, Kovach, and Tucker, 1969; Voith, 1980; Christiansen, 1984; Feldman & Nelson, 1987). In this study, the actual copulatory pattern observed was similar, but not identical to that described by Rosenblatt and Aronson (1958a,b). Rosenblatt and Aronson's (1958a,b) descriptive table has distinct advantages over paragraphs of text; however, they list some behaviors which have not been reported by others and thus should be reassessed,especially in light of its previous use. During the pre-copulatory or courtship phase, Rosenblatt and Aronson (1958b) and Leyhausen (1979) report the male giving a "mating call" or "chirping." This vocalization was not heard in the two males used in this study, Whalen (1963a) reports its presence sometimes, and Michael (1961) does not include it in his description. Neither were any of the initial courtship behaviors (crouches, rubs nose and mouth, rolls, vocalizes, treads) described by Rosenblatt and Aronson (1958a,b) observed in any of the females in this study. However, crouching, rolling, treading and vocalizing were described by Whalen (1963a), Michael (1961), and Leyhausen (1979) as behaviors associated with precopulatory behaviors in the cats they studied.

During the copulatory sequence, "forepaw rubbing" was not observed during the present study as described by Rosenblatt and Aronson (1958b) except in one instance when a female kept moving forward while being mounted. In this situation, the male exhibited what could have been described as "forepaw rubbing", but in actuality, it appeared more like he was simply walking forward to maintain his mount on the female. None of the mounted females in this study appeared to "bend [her] hind end". During the post copulatory reactions, neither "rubbing nose and mouth" nor "pawing male" were observed in the females.

Two additional behaviors in the females which were associated with copulatory behavior in this study were neck rubbing and cheek rubbing. Neck rubbing by the females, in many respects, appeared to be an exaggeration of cheek rubbing. Rolling on back seemed in some respects to be an exaggeration of the behavior, neck rubbing. Rolling on back was seen in two contexts: one was the vehement rolling immediately after copulation; and, a second was a "milder" or less exaggerated form of the behavior that seemed to be a continuation of the cheek rubbing - neck rubbing - rolling on back continuum. This less exaggerated rolling, as well as neck and cheek rubbing, seemed to function as general indicators of estrus. During data collection, the two types of rolling were not differentiated. The two males cheek rubbed at a high rate, in association with approaches, and while apparently orienting to the females.

Also in the pre-copulatory phase, the females in this study usually did not adopt a lordosis posture or tread prior to being mounted. This is more characteristic of naive queens as Whalen (1963b) described them. Leyhausen's descriptions (1979) of reproductive behavior provide more detail on the courtship (pre-copulatory) phase of reproduction. His are descriptions

of cats in a less controlled situation and in fact he is somewhat critical of the controlled laboratory environment and the use of exogenous hormones in other studies (Rosenblatt and Aronson, 1958a,b; Whalen, 1963a; Michael, 1961). In the present study, males did a great deal of cheek rubbing, neck rubbing, and rolling while orienting toward a female. These appeared to be amicable behaviors and are in good agreement with Leyhausen's suggestion (1979) that they are part of the precopulatory or courtship phase. Females frequently sniffed areas where males typically cheek rubbed. In one instance, a male sniffed the area where a female had just cheek rubbed. He then flehmed, cheek rubbed and chin rubbed that same spot. Verberne and de Boer (1976) very elegantly demonstrated that males respond differentially and preferentially to the cheek rubbings of estrous females. With regard to the absence of pre-copulatory behaviors in laboratory pairings, experienced males and females may habituate to the setting and to each other, forgoing many of the aspects of courtship.

Further, males exhibited "sharpening" of claws in what subjectively could be termed "frustrating" or "ambivalent" situations where a male repeatedly and vigorously was threatened by a female. Females were never seen to sniff the areas where males "sharpened" their claws, but they did sharpen their claws over areas where males had previously done so. Neck rubbing was also seen in apparent response to an odor. Three females (all from the sibling raised group) neck rubbed on areas where a male had urine marked. This response appears similar to the catnip response described by Palen and Goddard(1966).

I would propose the following modification of Rosenblatt and Aronson's table (1958b) which incorporate the descriptions of Michael, (1961), Whalen (1963a), Leyhausen (1979) and the present study. (See Table IV.)

Table IV. Copulatory Behavior of Domestic Cats (from Rosenblatt and Aronson, 1958 a,b)*

Time	Male	Female
	Pre-Copulatory Behaviors	
	orients towards	lordosis
10 sec. to	**follows**	treads
5 min.	**circles**	**rolls**
	approaches	**cheek rubs**
	sniffs ano-genital area	**neck rubs**
	cheek rubs	*vocalizes*
	neck rubs	
	Copulation	
	takes nape bite	**crouches, i.e., lordosis**
	mounts with front legs	
	mounts with hind legs	
1 to 3	**steps with hind legs**	**treads with hind legs**
min.	**pelvic thrust**	**swings tail to one side**
	penile erection	
	pelvic lunge	**vaginal dilation**
	intromission	**copulatory cry**
5 to 10	**ejaculation**	**pulls forward**
sec.	**penis withdrawn**	**turns & threatens male**
	Post-Copulatory Behaviors	
M less than	**sits near female**	**rolls on back**
1 min.	**licks genitals**	**licks genitals**
F about	**watches female**	
5 min.		

* those behaviors in **bold** print were observed in this study

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 this study, then suggest that early rearing experience has a strong influence on subsequent adult sexual behavior and that human-raised alone females are less likely to successfully breed than controls raised with both mother and sibling.

How do private breeders of exotic cats who typically remove kittens from their mothers at two weeks or less, end up with docile, friendly breeding individuals (c.f. Quillen, 1981)? It may be that development is well buffered against variations in early experience. This concept, termed "equifinality"(Bateson, 1976), asserts that an organism can reach the same steady state in development from different initial conditions and in different ways. Thus, the same behavioral end, in this case, the ability of females to successfully copulate, may be attained by way of a variety of different developmental routes. In other words, given an experiential environment, above some threshold, different developmental routes can lead to the same developmental end point, e.g., successful reproduction. Similarly, the attainment of adult predatory skills in domestic cats also appears to be achievable via a number of different routes (Martin and Caro, 1985; Martin, 1984).

The results of this study suggest that the developmental endpoint, successful copulation, could not be reached by animals from the human-raised alone group. Thus, this rearing condition would appear to provide an environment below the developmental threshold necessary for eventual reproductive success and is 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 to rise above a minimum threshold so that mature individuals will successfully reproduce? This is especially important in members of Felidae because alternate techniques to natural breeding, e.g., artificial insemination, embryo transfer, have not been consistently successful in any exotic species.

The second experimental condition in this study was intended to simulate another common rearing condition in zoos - human-raising of littermates together. The human-raised with sibling group in this study was intended to approximate this condition and to test whether the presence of a peer would substantially compensate for more normal rearing conditions. Further, in a zoo setting, if a single exotic kitten had to be human-raised, a domestic cat foster sibling could provide the necessary environment to move the exotic kittens above the threshold and toward reproductive success. 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 can not 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 (beyond conspecifics) must be examined as possible facilitators to reproductive success. What can be added to the environment of human-raised animals to supplement their development?

Presence or absence of sibling or mother are not the only variables which may influence ultimate reproductive success. As was pointed out by a nursery zookeeper (Shaeffer-Cooper, pers. comm.), the two human raised groups differed in one major way from the typical human-raising style (at least at the Washington Park Zoo). Human-raised exotic cats at the Washington Park Zoo receive a great deal of handling by numerous nursery volunteers during their development. These volunteers hold the kittens and later play with the developing kittens using toys. Single kittens, i.e., human-raised alone, are played with more often than are kittens with siblings, i.e., human-raised with a sibling. In the experimental situation of the present study, a total

of four caretakers cleaned and fed the study animals, but did not spend a great deal of time playing with them.

Thus, I am suggesting that a more varied environment might compensate for the lack of conspecifics. Nursery rearing conditions at the Washington Park Zoo appear to be similar to those provided by private breeders of exotic cats. (Unfortunately, data do not exist on the subsequent reproductive success of the human-raised exotics from the Washington Park Zoo.)

This "richer" environment may provide the inertia to bring the human-raised animal above the threshold necessary for successful reproduction. Using Waddington's analogy (1957) of the "epigenetic landscape", the environment must be sufficiently rich to at least place the "ball", i.e., the developing individual, at the top of the hill. Alternate rearing strategies, i.e., the particular valley through which the developing ball descends, may produce a successfully reproducing adult if they provide the necessary and sufficient social environment.

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Part III. Implications for Management of Small Cats in Captivity

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Natural History of Felids

As with all animals, to understand captive management, it is first necessary to review the natural history of the group (Eisenberg and Kleiman, 1977). All cats, large and small, are characterized by a highly specialized body plan with little gross variation except with regard to size. They all have large eyes, short muzzle, smooth round and wide skulls, and "weapons" of considerable proportion (Fagen, 1981). In the wild, most species of cat hunt in heavy cover, do not live in groups (except for females with dependent offspring), and live in relatively low densities; the lion and cheetah are obvious exceptions (Kleiman and Eisenberg, 1973). Each species has refined and adapted to its own niche. For example, fishing cats and jaguarundis have evolved to utilize a semi-aquatic niche; sand cats inhabit desert regions; an arboreal niche is utilized by the margay and the marbled cat; lion and cheetah utilize the open grasslands. Unique to the smaller cats is the fact that these small predators are also potential prey to a variety of larger predators.

In strong contrast to the heavy cover, solitary social structure, and low density of the environment in which small cats have evolved, the captive environment typically provides little or no cover, cats are routinely housed in pairs, and they are often maintained in close proximity to both other species of small cats (and thus presumably at a high density) and large cats (which they may perceive as potential predators). Whereas the primary activity of cats in the wild is hunting, cats in captivity (both large and small) are usually fed once per day.

Further, zoos, in many instances have attempted to fit the animal to the captive environment, as opposed to creating an environment that optimally fits the animals' requirements. By doing so, managers of these populations, may be artificially selecting for those individuals as founders of captive populations that are somehow "pre-adapted" to the captive environment (see Price, 1984). For example, if dozens of servals were acquired from the wild, but only those individuals that somehow were genetically predisposed to acclimating to the traditional zoo enclosure reproduced, those servals are then the founders for captive populations. Such strong selection on an already small population further reduces the maintenance of genetic diversity.

It is suggested here that small cats, at both the individual and population level, should be managed in such a way as to more closely mimic their original wild environment. These changes in management may facilitate their propagation and well-being in a captive setting.

Management of Small Cats in Captivity

From an evaluation of the results obtained in this dissertation, the following management protocols for small cats evolved. These suggested protocols represent a direct application of results obtained and suppositions acquired during the course of this research. The captive management of any population necessitates input at two levels: 1) at the level of the individual (husbandry protocol), and, 2) at the level of the population (population management).

Suggested Husbandry Protocol for Small Cats

The following husbandry protocol for small cats is suggested. Most of these recommendations are not new. See, for example, Leyhausen (1961), Hediger (1965), Foster, (1978), and Fowler (1986).

1) **Males and females should be housed singly and given access to each other for an hour or so each day.** During that hour, their behavior should be monitored for reproductive activity. Exceptions are those pairs that show a positive pair bond. It is suggested that these highly compatible pairs be maintained together (but still monitored daily). Appendix II contains a simple checksheet, instruction sheet, and definitions of behaviors for the study of reproductive behavior in captive small felids. The checksheets can be used by keepers, docents, or students to monitor the reproductive activity of the cats. See also Kleiman (1974).

2) **Each cat should always have a hiding place in which to retreat.** For cats on view to the public, clever placement of heating pads can often encourage them to rest on view, but the cats should always have a retreat area as an alternative. If cats use the retreat box as a latrine, the addition of a litter box or a second retreat box, may be alternatives.

3) **Cats should be individually fed at least twice per day and never fasted.** The pattern of feeding once per day with a fast day each week appears to be a transference of a husbandry technique used for large cats; while this pattern is similar to the feeding schedule of large cats in the wild, it is substantially different than the hunting/feeding pattern of small cats that feed on much smaller meals, e.g., small birds, rodents, several times per day. The prepared feline diet fed by most zoos in North America should be re-evaluated. Many of these commercial diets contain significant amounts of two compounds that are known to act as weak estrogens (Setchell, et al., 1987), excessive levels of Vitamin A (Dierenfeld, 1988), and insufficient levels of the essential amino acid, taurine (Burton, Gillespie, Rogers, and Morris, 1988; Dierenfeld, 1988). Freshly killed or frozen chicks and mice, beef bones, and live fish or crickets should be offered as a supplement to any prepared diet.

4) **Cats kept off-exhibit and/or in relatively small enclosures should be provided with several perching shelves and limbs or planks to serve as arboreal "skyways."** Many enclosures do not allow the cats to utilize the vertical component of the cage; addition of such shelves and branches would effectively increase the usable space for the cat.

5) **Cats should never be human-raised alone.** Whenever possible, kittens should remain with their mothers. If kittens are neglected by the mother, they should be raised together, with domestic kittens, and/or by a non-human surrogate mother in a rich and varied environment. The reasons for these suggested alternatives are presented in detail in Part II of this dissertation as well as in Mellen (1988).

6) **Whenever possible, kittens should be checked, weighed and "socialized" by their human caretakers on a daily or near daily basis.** In this way, health of the animal can be monitored and kittens can learn not to fear their human caretakers. This is not to suggest that kittens should be human-raised or made into pets. Instead, the goal is to produce kittens that are cared for by their mother, yet show substantially reduced fear towards the humans that, by the very nature of the captive environment, are an integral part of the cats' existence. Socialization is discussed below.

Socialization. Human socialization is defined as the development of an animal-human relationship (Foster, 1978) and in many respects is similar to Hediger's use of the term "tameness" (1950) which he describes as an animal whose flight distance has been reduced to zero. Socialization is characterized by daily human-animal interaction above and beyond routine cleaning, feeding, and weighing. It includes stroking the animal, playing with it and is usually initiated when the animal is young and presumably within the animal's socialization period. In captive snow leopards, attempts to socialize a 12-week

old cub were unsuccessful whereas littermates of that cub were successfully socialized when interactions began at six and a half weeks (Foster, 1978).

The purpose of the socialization process is to minimize the stresses of captivity by removing the animals' fear of humans while at the same time providing the cats with an enriched environment to facilitate normal behavioral development. Adult snow leopards that had been socialized as cubs adjusted well to new enclosures after transfer to another zoo, bred, successfully reared offspring (O'Connor and Freeman, 1982; Freeman and Hutchins, 1978; Foster, 1978) and, were calmer around human caretakers than non-socialized snow leopards (C. Lewis, pers. comm.).

It should be emphasized that successful socialization does not produce animals that are sexually imprinted on humans. (See Klinghammer (1973), Hediger, (1965) and Bateson (1978).) Instead, the purpose of socialization is to reduce the fearful response to human caretakers. A major component of the captive environment is the human caretaker. If a cat is fearful of that caretaker, it may negatively influence the general well-being of the animal and possibly affect its reproductive potential.

Thus, it is proposed here to substantially increase the amount of human contact with maternally-raised cats and to substantially decrease the amount of human contact with nursery-raised cats. The goal is to produce animals that are neither overly fearful of their human caretakers nor sexually imprinted on them.

Captive Populations of Small Cats

The recommended effective population size for a self-sustaining captive population with minimal loss of genetic diversity is 100 individuals (Foose, 1983). All but four of the species of small cats currently listed in ISIS fall below that number; over half of the *Felis* species kept in captivity contain less than 35 individuals (see Table 1). With numbers this small, these captive populations are destined for extinction. The potential for acquiring more individuals into the captive breeding population is confounded by the fact that most of these cats are endangered species. Legally (and morally) this means that wild-caught animals cannot be exported from the country of origin.

This information presents a bleak picture. In effect, the work presented in this dissertation may be a documentation of the extinction of a group of animals in captivity. Seidensticker (1987) described "bearing witness" to the extinction of two subspecies of wild tigers. Some of the factors contributing to the tigers' extinction were habitat loss, World War II, starvation and disease, and civil unrest. These factors are much more dramatic than the one that seems to have contributed to the decline of small cat populations in captivity: benign neglect.

Most specimens of small cats present in zoos today were acquired in an unplanned manner. Confiscated animals as well as cats from the private sector were given to zoos, or animals were acquired from dealers. In all cases, the exact region from which these animals came is almost never known (Shoemaker, 1988).

Table 1. Census of Small cats (*Felis*) in Captivity from Shoemaker, 1988*

Common Name	Scientific Name	No. of Specimens	Status
cougar	*F. concolor*	194	
serval	***F. serval***	**169**	
bobcat	*F. rufus*	156	
lynx	***F. lynx***	**110**	
caracal	***F. caracal***	**92**	
ocelot	***F. pardalis***	**76**	**E***
margay	***F. wiedi***	**58**	**E**
Geoffroy's cat	***F. geoffroyi***	**35**	
fishing cat	***F. viverrina***	**33**	
jaguarundi	***F. yagouaroundi***	**32**	
black-footed cat	***F. nigripes***	**31**	**E**
jungle cat	***F. chaus***	**29**	
leopard cat	*F. bengalensis*	27	E
Temminck's golden cat	***F. temmincki***	**22**	**E**
Pallas cat	***F. manul***	**12**	
rusty-spotted cat	***F. rubiginosus***	**12**	
pampas cat	***F. colocolo***	**10**	
Pakistan sand cat	***F. margarita sheffeli***	**9**	**E**
European wildcat	***F. silvestris***	**8**	
African wildcat	*F. libyca*	6	
marbled cat	*F. marmorata*	4	E
Florida panther	*F. concolor coryi*	2	E
jaguarundi	(endangered subspecies only)	2	E
flat-head cat	*F. planiceps*	1	E
Mexican bobcat	*F. r. escuinapae*	1	E

*data are from ISIS (International Species Inventory System) current as of 30 June 1988
** E = endangered and thus regulated by the U.S. Endangered Species Act
those species in **bold** print were examined in this study

What then is the solution? The following management protocol for populations of small cats is suggested:

1) A Zoo organization, The American Association of Zoological Parks and Aquariums, should organize a small cat interest group, The purpose of this group would be to:

a) determine the genealogies of all species of small cats listed in the International Species Inventory System. This has already been accomplished for several species: Geoffroy's cats (G. Foreman, pers. comm.), Pakistan sand cats (K. Sausman, pers. comm.), and black-footed cats (U. Schürer, pers. comm.).

b) *coordinate efforts to maximize outbreeding in existing populations.*

2) **Efforts should be made to facilitate breeding and research facilities in countries of origin.** Organizations with a special interest in small cats, e.g., the International Society for Endangered Cats, Inc. should implement such a system. These facilities would greatly increase knowledge of these species. Captive-bred animals surplus to any local reintroduction program could become sources for captive populations. This new zoo "stock" could be properly managed, by sub-species, to maximize outbreeding. The zoo stock then could become a viable, self-sustaining population, capable of providing genetic material to/for dwindling wild populations.

3) **Zoos should maintain a wider variety of small cat species.** A need exists for a more equitable distribution of the species exhibited. Currently only 25% (233) of all small cats listed in ISIS are endangered; the other 898 cats are common, non-endangered species (Shoemaker, 1988). By replacing the more common bobcat, caracal, or lynx with rarer species, zoos can provide more "rooms in the Ark" (Soulé, Gilpin, Conway, and Foose, 1986) for these critically endangered cats.

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Appendix I. Instructions for Making Behavioral Observations on Captive Pairs of Small Cats

I. When to Observe

The cats should be observed at approximately the same time each day. Because the interest here is in detecting reproductive activity, time of day when the cats are likely to be active is the best choice. If the cats are moved off exhibit for cleaning and/or feeding, the best time to observe is likely to be immediately after they are returned to their enclosure.

II. What to Observe

Below is a listing of behaviors found to be indicative of reproductive behavior. These behaviors are defined and reference is made to other sources where these behaviors are illustrated by line drawings and/or photographs:

Table 1. Ethogram for Observing Reproductive Behavior in Captive Pairs of *Felis*

Behavior	Description
Solitary Behaviors - Record for both the male and the female	
Cheek rubbing	cheek of cat rubbed against an inanimate object [Wright & Walters, 1980, p. 124; Hart & Hart, 1985, p. 135; Freeman, 1983, p. 19]
"Sharpening" claws	claws of front paws are used to scratch some surface (usually wood) [Wright & Walters, 1980, p. 124; Hart & Hart, 1985, p. 135]
Flehmen	open mouth grimace following the sniffing of an object or another cat [Wright & Walters, 1980, p. 112; Hart & Hart, 1985, p. 167; Freeman, 1983, p. 20]

Urine marking	urinating on vertical surface, tail is usually held straight up and sometimes the distal one-third of the tail is vibrated or appears to quiver; behavior sometimes includes scraping substrate with hind feet [Wright & Walters, 1980, p. 124; Hart & Hart, 1985, p. 135; Freeman, 1983, p. 18]
Vocalization	vocalization which appears to be a non-directed "calling"

Social Behaviors - Record for both the male and the female

Hiss/Growl	cat orients to another cat and emits a hissing/growling noise
Strike with paw	cat strikes another with its paw
Anogenital sniffing	cat sniffs the anogenital region of another [Freeman, 1983, p. 15]
Following	cat follows within two body lengths other cat for a distance of at least two body lengths
Approaching	cat directly approaches another cat (within one body length) and the cat approached does not move away

Reproductive Behavior - Record for the male

Mounting	male dorso-ventral mounts female, straddling her with both front feet and hind feet, and sometimes stepping with hind feet [Wright & Walters, 1980, p. 130-131; Hart & Hart, 1985, p. 167-168]
Nape Bite	male grasps back of female's neck (nape) with his teeth; the male may or may not be simultaneously mounting the female [Wright & Walters, 1980, p. 130; Hart & Hart, 1985, p. 167-168]
"Pelvic" thrusting	while mounting, the male repeatedly thrusts his genital region in the vicinity of the female's genital region [Wright & Walters, 1980, p. 130-131; Hart & Hart, 1985, p. 167-168]
Anogenital (A/G) grooming after mount	self-grooming of the anogenital region - scored only if it occurs within three minutes after a mount [Wright & Walters, 1980, p.131; Hart & Hart, 1985, p.168]

Reproductive Behavior - Record for the female	
Lordosis	female lowers her forequarters while elevating her hindquarters; this posture can occur in conjunction with mounting or the female may simply exhibit this behavior without any direct contact by the male [Wright & Walters, 1980, p. 130-131; Hart & Hart, 1985, p. 167-169]
Tail to one side	while the female is exhibiting a lordosis posture, her tail is moved laterally, exposing her anogenital region[Wright & Walters, 1980, p. 130; Hart & Hart, 1985, p. 167]
Threaten after mount	the female threatens the male (hisses, growls, strikes at with her paw, strikes male with her paw) within 30 seconds of being mounted [Wright & Walters, 1980, p.131]
Rolls on back after mount	the female rolls on her back within 30 seconds of being mounted[Hart & Hart, 1985, p. 169]
Anogenital (A/G) grooming after mount	self-grooming of the anogenital region - scored only if it occurs within three minutes after a mount [Wright & Walters, 1980, p.131; Hart & Hart, 1985, p.168]

In addition to the behaviors listed and defined in Table 1, notes can be made describing the general activities of the pair.

III. How to Observe

There are many sampling methods that can be utilized to systematically record the behavior of animals. These various methods are described elsewhere (e.g., Altmann, 1974; Lehner, 1979; Mellen, Hage, Carlson, and Pfeiffer, 1982; Martin and Bateson, 1986; Crockett, in press). The specific sampling method described here for the study of small cats is termed **one/zero** or **checklist** . It is one of the simplest sampling methods to use and affords a high level of inter-observer reliability.

Figure 1 is a data sheet that can be used for collecting behavioral data for pairs of small cats. Below are instructions on how to use this data sheet. Using an audible timer set for a 30-second interval, the observer simply scores whether or not the male and the female were observed to exhibit any of the listed behaviors within that 30-second interval. Each behavior exhibited by the male and the female during that 30-second interval is checked off. At the end of each 30-second interval (signalled by the audible timer), the observer moves to the next column on the checksheet and again checks off those behaviors exhibited by the male and female, if they occur. In any given 30-second interval all of the behaviors could be exhibited by a cat, some of the behaviors could be exhibited by a cat, or none of the behaviors could be exhibited (and thus none of the cells representing that interval would be checked). Regardless of how many times a behavior occurs within each 30-second interval, that behavior is simply checked off as having occurred. For example, a male may cheek rub 13 times within a particular 30-second interval; for that interval, cheek rubbing is simply checked, indicating that at some point within the interval the male was observed to have cheek rubbed. This sampling method is termed "one/zero" for that reason. Regardless of the true frequency, i.e., how many times the cat actually cheek rubbed within the interval, the behavior is given a score of "one" (or checked off) if it occurred, or given a score of "zero" (or not checked off) if it did not occur. At the end of the observation period (usually 60 minutes), the total number of check marks are totalled for both the male and the female. These totals represent the total number of intervals in which the various behaviors occurred. Figure 2 is a sample data sheet and illustrates how data are collected. Note that instead of a check mark, an "M" for male and an "F" for female were used. These symbols were used instead of check marks to make tallying the data easier.

NAME _____ DATE _____ TIME _____ PAGE ____

1/0 Data Collection Method				1				2				3				4				5				6	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Cheek Rub																										
Sharpen Claws																										
Flehmen																										
Urine Mark																										
Vocalize																										
Hiss/Growl																										
Strike with Paw																										
Anogenital Sniff																										
Follows																										
Approaches																										
Mounts																										
nape bite																										
"pelvic" thrust																										
A/G groom after mount																										
lordosis																										
tail to one side																										
threaten after mount																										
roll on back after mount																										
A/G groom after mount																										

Figure 1. Blank data sheet to be used for observations on small cats in captivity

Mellen, WPZ

			7				8				9				10			Total	Total
M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F			Male	Female
																Cheek Rub			
																Sharpen Claws			
																Flehmen			
																Urine Mark			
																Vocalize			
																Hiss/Growl			
																Strike with Paw			
																Anogenital Sniff			
																Follows			
																Approaches			
																Mounts			———
																nape bite			———
																"pelvic" thrust			———
																A/G groom after mount			———
																lordosis	———		
																tail to one side	———		
																threaten after mount	———		
																roll on back after mount	———		
																A/G groom after mount	———		

Figure 1. (cont) Blank data sheet to be used for observations on small cats in captivity

NAME Mellen DATE 16 Oct 88 TIME 9:45 AM PAGE 1

1/0 Data Collection Method				1				2			3			4				5			6		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Cheek Rub										F				F										
Sharpen Claws								F																
Flehmen																								
Urine Mark																								
Vocalize																								
Hiss/Growl																								
Strike with Paw																								
Anogenital Sniff																								
Follows																								
Approaches																								
Mounts																								
nape bite																								
"pelvic" thrust																								
A/G groom after mount																								
lordosis										F				F				F						
tail to one side																								
threaten after mount																								
roll on back after mount																								
A/G groom after mount																								

Notes: F head rubs leg F head rubs M

Figure 2. Completed data sheet illustrating how data are collected, tallied, and converted to proportions

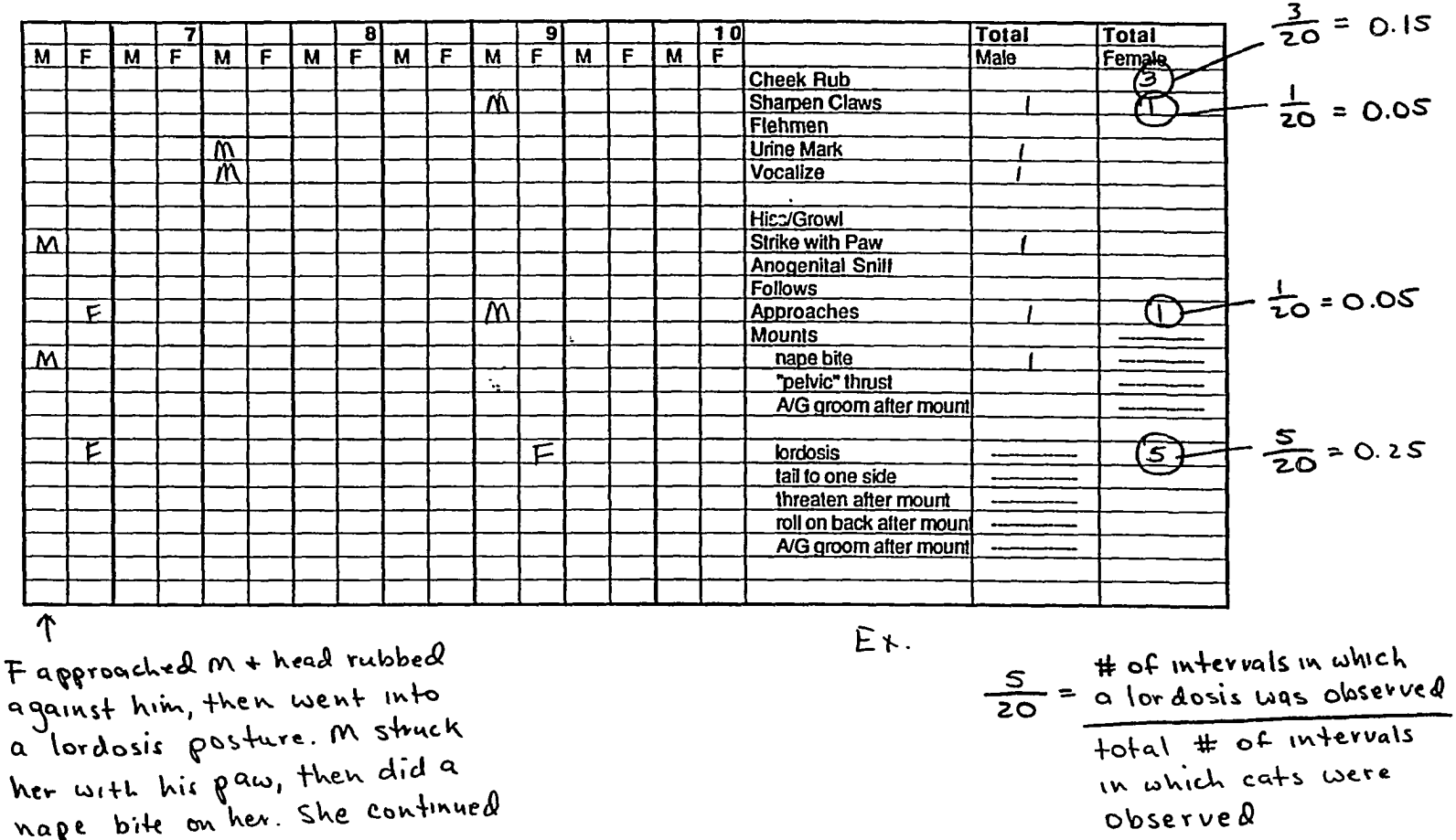

Figure 2. (cont) Completed data sheet illustrating how data are collected, tallied, and converted to proportions

IV. Graphing the data

The data collected can be graphed daily or weekly. In the examples presented below, data are graphed daily. The first step in graphing data is to convert the raw scores, i.e., the tallies on the data sheet representing the number of intervals in which each behavior was observed, to proportions. The simple math used to convert raw data to proportions is illustrated in Figure 2 next to the **Total** columns.

The total number of intervals in which a particular behavior was observed is divided by the total number of intervals in which the cats were observed. In the sample data sheet (Figure 2), a lordosis posture was scored 5 times for the female, i.e., during 5 intervals the female was observed to exhibit a lordosis; the cats were observed for a total of 10 minutes or 20 30-second intervals. Thus, the proportion of intervals in which the female exhibited a lordosis is 5/20 or 0.25. These same calculations are done for each behaviors exhibited by the male and the female. These proportions are then graphed over time. Figure 3 illustrates how these data might be graphed. Typically, data for the male and the female are graphed separately for ease of interpretation.

V. Interpreting the data

Once observations have been made over several months and then graphed, patterns should emerge if the female is cycling, i.e., coming into estrus. Estrus is suggested whenever there is a substantial change in behavior. Typically, the occurrence of scent marking in the female increases dramatically as does the occurrence of all social behaviors initiated by both the male and the female.

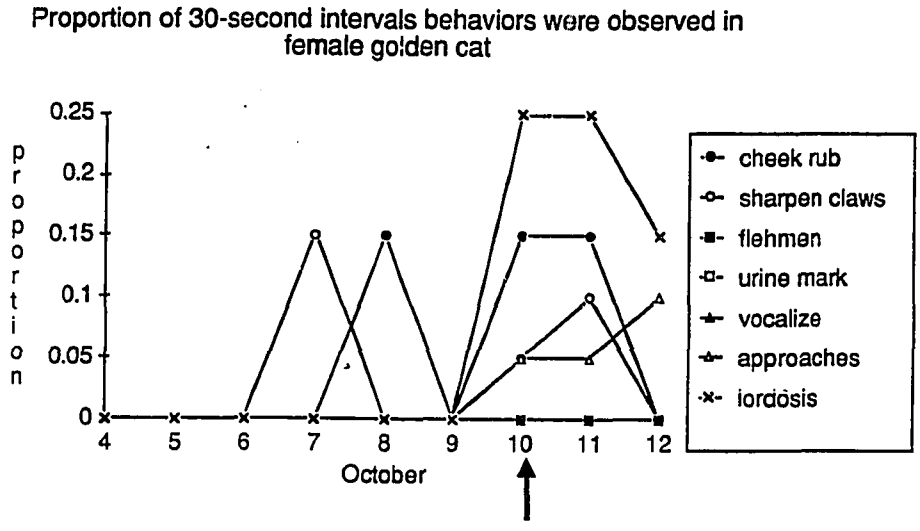

Figure 3. Hypothetical data set for golden cats. Data were collected using a one/zero sampling method, converted to proportions, and graphed over time. Arrow indicated October 10th and represents those sample data presented in Figure 2.

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