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A Comparative Analysis of Scent-Marking, Social and Reproductive Behavior in 20 Species of Small Cats (*Felis*)[1]

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SYNOPSIS. Except for lions and cheetahs, members of family Felidae exhibit spatially and temporally dispersed social systems. However, this solitary existence does not preclude possession of a rich repertoire of communication signals. While patterns of communication have been examined in a number of the larger cats (*e.g.*, lions, cheetahs, tigers), those of the smaller cats (<20 kg) remain virtually unstudied. The purpose of this study was to examine behavior in the smaller members of the Family Felidae to determine the level of behavioral uniformity within the family and to ascertain whether systematic behavioral observations could be used as an effective bioassay to monitor reproduction. A comparative examination of the occurrence and rate of scent marking, social behavior (especially behaviors associated with copulation), and other reproductive parameters was made in 20 species of captive, small felids. In general, small felids exhibited remarkable uniformity in their behavioral repertoire, both with respect to scent-marking and social behaviors. While the frequency of social behaviors differed among species, their appearance and general order of occurrence was similar. This was especially apparent with regard to the copulatory sequence. Detectable behavioral changes occurred in association with reproduction, supporting the concept of using systematic behavioral observations as a viable, non-invasive assay for monitoring reproductive activity. Reproductively active felids scent marked more frequently than reproductively inactive cats. However, no single scent-marking behavior was a good indicator of reproductive activity. Rather, the relative change in rates of behaviors over time was a better indicator of reproduction. As with scent-marking behaviors, a change in the relative rates of some social behaviors was the most reliable indicator of reproductive activity. Comparative behavioral data also show promise for understanding the phylogenetic relationships of three proposed lineages within the family Felidae (*Panthera*, ocelot, and domestic cat).

INTRODUCTION

Members of the family Felidae comprise a unique group of highly specialized carnivores found on all continents except Australia and Antarctica. Characterized by relatively short muzzles, highly sectorial carnassials and sharp retractile claws, cat species range in size from small (1.5 kg) to very large (300 kg). Felids predominate in woodland and woodland-fringe terrain although some cat species can be found in nearly all terrestrial habitat types. Except for lions and cheetahs, most adult felids are intolerant towards adults of the same sex and commonly exhibit a spatially and temporally dispersed social system (Bekoff *et al.*, 1984). However, such solitary existence does not preclude the "asocial" members of the family Felidae from possessing a rich repertoire of communicative signals (Leyhausen, 1965; Eisenberg *et al.*, 1972; Kleiman and Eisenberg, 1973; Seidensticker *et al.*, 1973).

Detailed field observations of felid communication are limited to a few of the larger

[1] From the Symposium on *Basic Behavior Research in Zoos: A Link with the Wild* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1991, at Atlanta, Georgia.

TABLE 1. *History of cats studied.*

Common name	Scientific Name	Lineage [1]	Location [2]	Dates observed	Hours observed
Asian Cats					
Pallas' cat	*Felis manul*	domestic cat	Brkfld	24 Jun–18 Aug 84	25.50
sand cat	*F. margarita*	domestic cat	Brkfld	24 Jun–18 Aug 84	21.85
			Brkfld	24 Jun–27 Jul 84	16.59
			Brkfld	24 Jun–27 Jul 84	14.37
			WPZ	23 Feb–10 May 86	21.71
fishing cat	*F. viverrina*	*Panthera*	WPZ	2 Mar–10 May 86	17.05
			San Diego	30 Mar–9 Apr 88	7.50
			Cincin	[historical data only]	0.00
			Pt. Lympne	2 Apr–15 Apr 89	4.00
Temminck's golden cat	*F. temmincki*	*Panthera*	WPZ	23 Jun–29 Aug 87	21.92
			Pt. Lympne	2 Apr–15 Apr 89	4.50
jungle cat	*F. chaus*	domestic cat	Sacto	17 Feb–27 Apr 85	37.47
rusty-spotted cat	*F. rubiginosus*	*Panthera*	Cincin	17 Oct–28 Oct 88	3.50
			Pt. Lympne	2 Apr–15 Apr 89	3.00
Indian desert cat	*F. silvestris ornata*	domestic cat	Pt. Lympne	2 Apr–15 Apr 89	4.00
African Cats					
serval	*F. serval*	*Panthera*	WPZ	18 Jan–28 Mar 87	13.15
			San Diego	30 Mar–9 Apr 88	6.00
			Sacto	15 Feb–25 Apr 85	32.73
			NZP	1 Jul–8 Sep 85	31.03
			Pt. Lympne	[historical data only]	0.00
caracal	*F. caracal*	*Panthera*	Sacto	3 Apr–17 May 85	22.84
			Sacto	24 Feb–18 May 85	35.52
			Cincin	17 Oct–28 Oct 88	3.42
			Pt. Lympne	2 Apr–15 Apr 89	4.50
black-footed cat	*F. nigripes*	domestic cat	San Diego	[historical data only]	0.00
			Cincin	17 Oct–28 Oct 88	4.00
African golden cat	*F. aurata*	*Panthera*	Pt. Lympne	2 Apr–15 Apr 89	3.50
South American Cats					
Geoffroy's cat	*F. geoffroyi*	ocelot	WPZ	2 Nov 86–10 Jan 87	25.63
			Sacto	31 Jan–6 Mar 85	26.86
			NZP	7 Jul–5 Feb 85	27.69
jaguarundi	*F. yagouarundi*	*Panthera*	ASDM	26 Jan–5 Feb 88	8.97
			Cincin	17 Oct–28 Oct 88	3.25

TABLE 1. *Continued.*

Common name	Scientific Name	Lineage [1]	Location [2]	Dates observed	Hours observed
ocelot	*F. pardalis*	ocelot	ASDM	27 Jan–5 Feb 88	6.00
			Cincin	17 Oct–28 Oct 88	3.90
			Pt. Lympne	2 Apr–15 Apr 89	3.50
			Pt. Lympne	2 Apr–15 Apr 89	3.00
margay	*F. wiedi*	ocelot	ASDM	[historical data only]	0.00
			San Diego	[historical data only]	0.00
			Sacto	[historical data only]	0.00
Pampas cat	*F. colocolo*	ocelot	Cincin	17 Oct–28 Oct 88	3.25
			Cincin	17 Oct–28 Oct 88	4.17
European Cats					
Scottish wildcat	*F. silvestris grampia*	domestic cat	San Diego	30 Mar–9 Apr 88	6.00
Siberian lynx	*F. lynx wrangeli*	*Panthera*	Pt. Lympne	2 Apr–15 Apr 89	3.00
North American Cats					
Canadian lynx	*F. lynx canadensis*	*Panthera*	Sacto	3 Mar–18 May 85	31.75
Worldwide					
domestic cat	*F. silvestris catus*	domestic cat	WPZ	3 Jan–30 Aug 87	168.40
				Total Number of Hours	685.02

[1] From Wayne *et al.*, 1989.

[2] 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; San Diego = San Diego Zoo, San Diego, CA; Cincin = Cincinnati Zoological Garden, Cincinnati, OH; Pt. Lympne = Pt. Lympne, Kent, England.

TABLE 2. *Marking behavior for male and female captive small felids.*

	Scientific name	Sex	Cheek rub	±SE	Head rub inanimate	±SE	Chin rub	Neck rub	Sharpen claws	±SE	Flehmen	±SE	Urine spray	±SE	Scrape with hind feet	Tail quiver	n
Asian Cats																	
Pallas' cat	*Felis manul*	male							0.15	0.12	0.03	0.03	0.47	0.21	+		1
		female	0.11	0.06					0.23	0.07	0.02	0.02					2
sand cat	*F. margarita*	male	1.83	0.53	0.26	0.15			0.23	0.07	0.26	0.12	1.17	0.47			4
		female	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*	male	0.05	0.05	0.24	0.12			0.54	0.21	2.77	0.54	1.39	0.20			3
		female	0.05	0.05	0.05	0.05			0.20	0.08	1.09	0.46	1.50	0.43			3
Temminck's golden cat	*F. temmincki*	male	2.10	0.71	0.09	0.09	+	+	0.72	0.24	2.26	0.36	6.14	0.97	+		2
		female	2.17	1.81	0.71	0.52		+	0.30	0.13	0.39	0.23	0.17	0.12			2
jungle cat	*F. chaus*	male	0.22	0.12					0.01	0.01	0.10	0.08	0.40	0.23			1
		female	0.11	0.11					0.17	0.11	+						1
rusty-spotted cat	*F. rubiginosus*	male							+		+		+				3
		female						+			+		+				3
Indian desert cat	*F. silvestris ornata*	male							+				+				1
		female															1
African Cats																	
serval	*F. serval*	male	0.65	0.37			+		0.15	0.08	1.39	0.61	2.81	0.75	+	+	3
		female	0.54	0.20			+		0.05	0.02	0.39	0.12	4.89	1.86	+	+	3
caracal	*F. caracal*	male	0.05	0.03					0.18	0.07	0.53	0.27	3.08	0.71	+	+	4
		female	0.14	0.09					0.14	0.06	0.27	0.15	0.21	0.11			4
black-footed cat	*F. nigripes*	male	+				+	+			+		+			+	2
		female											+			+	2
African golden cat	*F. aurata*	male						+								+	1
		female							+		+		+			+	3
South American Cats																	
Geoffroy's cat	*F. geoffroyi*	male	0.07	0.04			+	+	0.40	0.13	0.45	0.12	1.05	0.33	+	+	3
		female	0.10	0.06	0.20	0.16	+	+	0.10	0.04	0.01	0.01	0.03	0.03			3
jaguarundi	*F. yagouarundi*	male	+					+	+		+		+		+		2
		female						+	+		+				+		3
ocelot	*F. pardalis*	male	+		+		+	+	+		+		+		+		4
		female	+		+			+	+		+						4
Pampas cat	*F. colocolo*	male	+				+				+		+		+	+	2
		female															2

TABLE 2. *Continued.*

	Scientific name	Sex	Cheek rub	±SE	Head rub inanimate	±SE	Chin rub	Neck rub	Sharpen claws	±SE	Flehmen	±SE	Urine spray	±SE	Scrape with hind feet	Tail quiver	n
European Cats																	
Scottish wildcat	*F. silvestris grampia*	male											+			+	1
		female	+		+			+	+								2
Siberian lynx	*F. lynx wrangeli*	male							+				+				1
		female															1
North American Cats																	
Canadian lynx	*F. lynx canadensis*	male	0.16	0.07	+				0.09	0.05	0.21	0.10	5.57	2.36		+	1
		female	0.13	0.09					0.08	0.04			1.96	0.91		+	1
World Wide Distribution																	
domestic cat*	*F. silvestris catus*	male	5.14		0.03		0.01	0.79	0.48		0.90		0.01		+		2
		female	2.73		0.00		0.00	9.24	0.62		0.30		0.02				21

* Domestic cats were only observed when males were paired with estrous females.

cat species: lions (Schaller, 1972), cheetahs (Caro and Collins, 1987), tigers (Sunquist, 1981; Smith *et al.*, 1989), cougars (Seidensticker *et al*, 1973). Additional data have been obtained via observations of captive animals: snow leopards (Freeman, 1983), tigers (Kleiman, 1974), and cheetahs (King, 1983). Substantially less information exists about the smaller members of the family Felidae. "Small cats" are defined here as those species with an adult body weight of less than 20 kg (Emmons, 1991, p. 62). The nocturnal pattern of activity, the use of densely vegetated habitat, wide-ranging movements, and often wariness because of intense hunting pressures preclude obtaining this information *in situ* for most felids, and especially the small cats.

The purpose of this study was to examine behavior among the smaller members of the Family Felidae to determine the level of behavioral uniformity within the family and to ascertain whether systematic behavioral observations could be used as an effective bioassay to monitor reproduction. To investigate these questions, comparative examination of the occurrence and rate of scent marking, social behavior (especially behaviors associated with copulation), and other reproductive parameters was made across 20 of the 29 species of captive small felids. This number represents all but 3 of the species of small cats currently held in North American and European zoos.

METHODS

Data were collected on a total of 134 individuals (65 males, 69 females) representing 20 *Felis* species from eight zoological institutions. Information on species and number of animals observed as well as where, when, and how long each was observed is included in Table 1. Other information on subjects and their respective captive environments are detailed in Mellen (1989, 1991, 1992).

Behavioral data were collected via direct observation using all occurrences of selected behaviors sampling methods (Altmann, 1974). Behaviors associated with scent marking, drawn from Mellen (1988), were defined as follows:

cheek rubbing: cheek of cat is rubbed against an inanimate object

"sharpening" claws: claws of front paws are used to scratch a surface (usually wood)

urine marking: cat urinates on vertical surface; tail is usually held straight up and sometimes the distal third is vibrated or appears to quiver; behavior sometimes includes scraping substrate with hind feet

flehmen: open-mouth grimace following the sniffing of an object or cat.

Other solitary behaviors included:

head rubbing: head (forehead region) of cat rubbed against an inanimate object

neck rubbing: cat vigorously rubs/scrapes lateral portions of neck against an inanimate object or along substrate.

Social behaviors included the following:

spit/hiss/growl vocalizations: cat orients to another cat and emits a spit/hiss/growl vocalization

strike/strike at with paw: cat strikes or strikes at (*i.e.*, no contact is made) another with its paw

mounting: for the male, mount is dorsoventral with nape bite and straddling of the female with both front feet and hind feet: "pelvic" thrusting, stepping with hind feet, and/or intromission may occur; for the female, lordosis posture, treading with hind feet, deflecting tail to one side, and "copulatory cry" may occur

lordosis: female lowers her forequarters while elevating her hindquarters; tail is often moved to one side

social head rubbing: head (forehead region) is 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 cat

social sniffing: cat sniffs any region other than the anogenital region of another cat

following: cat follows within two body lengths of 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 one another (usually both are in a sitting position); cats are within one to two body lengths of each other and stare directly at each other; this behavior is usually preceded and/or followed by an agonistic interaction; duration is variable (10 sec to 2 min).

Behavioral observations were made during regular visitor hours at each zoo, between 09:00 and 17:00 local time. This time frame was chosen because a major purpose of this study was to determine if behavioral observations could be used as an effective assay for monitoring reproductive functions. While these predominantly nocturnal/crepuscular cats may have exhibited a substantial portion of their behavior at night, the author wanted to determine if behaviors exhibited by the cats during regular zoo hours (the time period when most zoo personnel/volunteers/students are present to make such observations) could be used to detect reproductive activity.

Data on reproductive parameters, length of estrus, gestation, mean litter size, sex ratio of litter, *etc.*) were obtained by reviewing medical, keeper, and ISIS (International Species Information System) records.

RESULTS

Behaviors associated with scent marking

A summary of data on behaviors associated with scent marking are presented in Table 2. Average rates for each behavior are presented for those cats that were studied for at least 8 weeks. Some behaviors associated with scent marking were noted outside of a formal observational setting (and thus not quantified); their occurrence is indicated by a plus (+) sign.

Cheek rubbing.—Most species of cats observed in the present study cheek rubbed (Table 2) and the rate at which cheek rubbing occurred was about equal for both males and females (Fig. 1a). In general, cheek rubbing occurred more frequently among reproductively active pairs (Fig. 1a).

Head rubbing.—No trends were apparent with regard to the relative rates of head rubbing between the sexes or between repro-

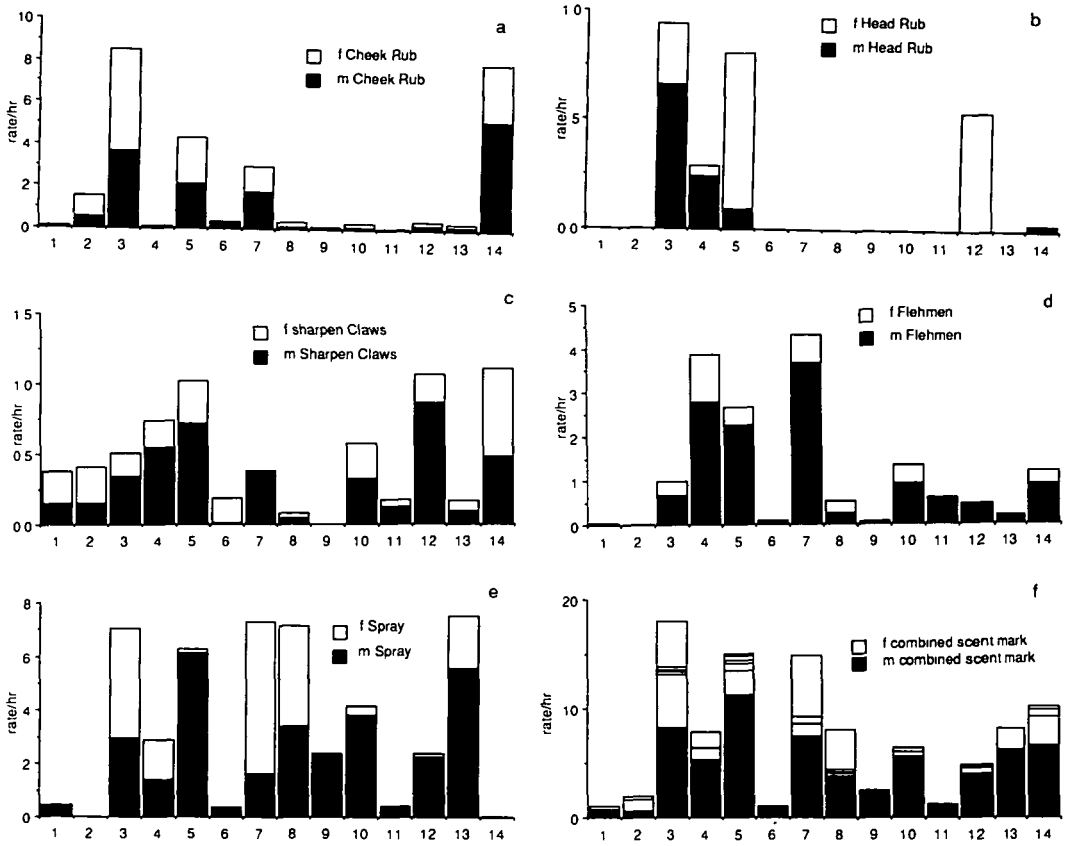

FIG. 1. Average rates of selected scent-marking behaviors which allow for comparisons of those individuals that demonstrated reproductive activity to those individuals that were not reproductively active. **Bold** print indicates data from those pairs in which the female was in estrus during some portion of the observation set. m = male; f = female; 1 = Pallas' cat (Brkfld); 2 = sand cat (Brkfld); **3 = sand cat (WPZ)**; 4 = fishing cat (WPZ); **5 = Temmincks' golden cat (WPZ); 6 = jungle cat (Sacto); 7 = serval (WPZ)**; 8 = serval (NZP, Sacto); 9 = caracal (Sacto); **10 = caracal (Sacto)**; 11 = Geoffroy's cat (WPZ); **12 = Geoffroy's cat (NZP)**; 13 = Canadian lynx (Sacto); **14 = domestic cat (WPZ)**.

ductively active *versus* inactive individuals (Fig. 1b). When data from Table 2 are compared to those compiled by Wemmer and Scow (1977), head rubbing was observed in relatively fewer species in the present study. However, Wemmer and Scow (1977) describe head rubbing, including 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 exposure to novel odors, the probability of observing these behaviors may have been reduced.

Neck rubbing.—Neck rubbing is similar to Wemmer and Scow's description (1977) of recumbent head rubbing and was observed in apparent response to the urine marks of a mate. This behavior also was seen frequently in both males and females examined in the present study during introductions of pairs and when a female was in estrus (see Mellen, 1989).

"Sharpen" claws.—This behavior was observed in most species examined in the present study (Table 2; Fig. 1c). Sharpening claws occurred at a somewhat higher rate in males than females and its relative occurrence does not seem to be related solely to reproductive activity. It was a frequently observed behavior, seen both as a component of scent-marking behavior (*e.g.*, occurring in the same areas as urine marking) and as apparent "displacement" when an estrous

TABLE 3. *Occurrences of social behaviors in small felids.*

	Sex	Spit	Hiss	Growl	Strike at	Strike with paw	Bite	Mount	Nape bite	Lordosis	Social head rub	Social groom	Ano-genital sniff	Social sniff	Follow	Displace	Ap-proach	Chase	Face off
Asian Cats																			
Pallas' cat	male		+		+									+		+	+	+	+
	female		+		+	+	+					+	+	+	+	+	+	+	
sand cat	male	+	+	+	+	+		+	+			+	+	+	+	+	+		+
	female	+	+	+	+	+				+			+	+	+	+	+	+	+
fishing cat	male		+		+	+							+	+	+		+		+
	female		+			+	+						+	+	+	+	+	+	+
Temminck's golden cat	male			+	+	+	+	+	+		+	+	+	+	+		+	+	+
	female		+	+	+	+	+			+	+	+	+		+	+	+		+
jungle cat	male		+	+	+			+	+			+	+	+	+	+	+	+	
	female			+	+	+				+		+	+	+	+		+	+	
rusty-spotted cat	male							+	+			+	+	+	+		+		+
	female		+	+		+				+	+		+	+	+		+		+
Indian desert cat	male																		
	female																		
African Cats																			
serval	male		+	+								+	+	+	+	+	+		+
	female		+	+	+	+	+				+	+	+	+	+	+	+	+	+
caracal	male		+	+	+			+	+			+	+	+	+	+	+		
	female		+	+	+	+	+			+	+	+	+	+	+	+	+	+	
black-footed cat	male	+	+	+											+		+		+
	female	+	+	+	+														+
African golden cat	male																		
	female		+	+	+	+							+	+		+	+		
South American Cats																			
Geoffroy's cat	male		+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+
	female		+		+	+	+			+	+	+	+	+	+		+	+	+
jaguarundi	male		+	+								+	+	+	+	+	+	+	+
	female		+	+		+	+				+	+		+			+	+	+
ocelot	male				+		+	+	+		+	+	+	+	+		+		+
	female		+	+	+	+	+			+	+	+	+	+	+		+	+	+
Pampas cat	male	+	+			+		+	+		+	+	+	+			+		
	female	+	+		+	+	+					+	+	+			+		

TABLE 3. *Continued.*

	Sex	Spit	Hiss	Growl	Strike at	Strike with paw	Bite	Mount	Nape bite	Lordosis	Social head rub	Social groom	Ano-genital sniff	Social sniff	Follow	Displace	Ap-proach	Chase	Face off
European Cats																			
Scottish wildcat	male																+		
	female*					+					+				+		+		
Siberian lynx	male			+															
	female																		
North American Cats																			
Canadian lynx	male					+							+			+			
	female		+									+					+		
World Wide Distribution																			
domestic cat	male		+		+	+	+	+	+		+	+	+	+	+	+	+	+	+
	female	+	+	+	+	+	+			+			+	+	+	+	+	+	+

* Hormonally implanted to prevent pregnancy.

female repeatedly and vigorously threatened a male.

Flehmen.—Observations made during the present study support the general pattern described elsewhere (*e.g.,* Wemmer and Scow, 1977; Wright and Walters, 1980; Hart and Hart, 1985). Typically, a urine mark is approached, sniffed, and then the cat exhibits a flehmen response. When a small cat flehms, it raises its head and drops its lower jaw so that the mouth is half open. The cat appears almost immobilized, has a staring look, and breathes slowly. In this study, both sexes of most species were observed to flehm (Table 2) but males exhibited a consistently higher rate than females (Fig. 1d). Males of most species examined showed a rise in the rate of flehmen during those periods when copulations were observed.

Urine marking.—Males of all species observed and females of most species observed urine marked, *i.e.,* sprayed urine on a vertical surface (Table 2; Fig. 1e). Males of most species sprayed urine at a higher rate than did females. A notable exception was female servals.

In the present study, two behaviors performed often in association with urine marking or spraying were as follows: 1) scraping with the hind feet, and, 2) "tail quiver." Table 2 identifies which species exhibited each of these behaviors. When spraying urine, virtually all species observed raised their tails vertically while spraying. In some species, the terminal third of the tail sometimes twitched or quivered during the spraying.

Social behavior of captive small felids

Cats communicate with one another via a combination of visual, auditory, and olfactory signals. The previous section on scent-marking behaviors addressed some aspects of olfactory communication. Auditory communication was not examined in this study because observations often were made through glass barriers or in situations with substantial background noise that prevented collection of systematic data on vocalization. (See Peters and Wozencraft, 1989, for a review of vocal communication in felids.) However, visual communication was measured with respect to selected social

TABLE 4. *Reproductive data for captive small felids.*

	Scientific name	Duration of mounts[1] (min)	Length of estrus[3] (days)
Asian Cats			
Pallas' cat	*Felis manul*	—	—
sand cat	*F. margarita*	8.83 ± 2.13 (n = 13)	5.25 ± 0.75 (n = 2)
fishing cat	*F. viverrina*	—	—
Temminck's golden cat	*F. temmincki*	—	6.00 ± 0 (n = 2)
jungle cat	*F. chaus*	2.50 (n = 1)	—
rusty-spotted cat	*F. rubiginosus*	0.92 ± 0.11 (n = 8)	≥4 but <6 days (n = 1)
Indian desert cat	*F. silvestris ornata*	—	—
African Cats			
serval	*F. serval*	—	4 (n = 1)
caracal	*F. caracal*	2.00 ± 0.5 (n = 3)	5 (n = 1)
black-footed cat	*F. nigripes*	—	—
African golden cat	*F. aurata*	—	—
South American Cats			
Geoffroy's cat	*F. geoffroyi*	1.14 ± 0.25 (n = 3)[2]	2.50 ± 0.50 (n = 2)
jaguarundi	*F. yagouarundi*	—	3.17 ± 0.75 (n = 6)
ocelot	*F. pardalis*	1.50 (n = 1)	4.63 ± 0.63 (n = 6)
margay	*F. wiedi*	—	4 (n = 1)
Pampas cat	*F. colocolo*	—	—
European Cats			
Scottish wildcat	*F. silvestris grampia*	—	—
Siberian lynx	*F. lynx wrangeli*	—	—
North American Cats			
Canadian lynx	*F. lynx canadensis*	1.50 (n = 1)	—
Worldwide Distribution			
domestic cat	*F. silvestris catus*	2.64 ± 0.32 (n = 48)	5.13 ± 0.24 (n = 15)

[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.
[6] See Mellen, 1989.
[7] n = number of litters.
[8] Males.females.sex unknown.
[9] Females' date of birth to birth of 1st litter produced; male's date of birth to 1st litter sired.

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 indicate reproductive activity, discussion of social behaviors will be limited to that context.

Social behavior represents only 1–2% of the time budgets of small cats in captivity (Mellen, 1989), so the rates of occurrence of various social behaviors were very low. Table 3 lists the social behaviors observed during the present study with an indication of whether or not each species exhibited each behavior. These data are meant to provide an overview of the occurrence of selected social behavior among these species of cats and to demonstrate the relative uniformity of these cats' behavioral morphology.

Reproductive data for captive small felids

The study of captive animals facilitates the determination of a wide variety of reproductive parameters that would be difficult, if not impossible, to gather *in situ*. In the process of gathering behavioral data at eight zoological institutions, the author had an opportunity to glean information regarding a wide variety of reproductive param-

TABLE 4. *Extended.*

Length of estrous cycle[4] (days)	Gestation[5] (days)	Birth season[6]	Litter size[7] (Mean ± SE)	Sex ratio of litter[8]	Age at maturity[9] (wks)
–	–	yes	3.57 ± 0.53	7.13.5	F 57.43
46 (n = 1)	66.5 ± 0.50 (n = 2)	no	2.92 ± 0.21	18.22.33	M 67.67
–	70 (n = 1)	no	2.61 ± 0.28	12.15.5	F 63.14
39 (n = 1)	–	no	1.11 ± 0.11	5.4.1	–
–	63 (n = 1)	–	4 (1 litter)	0.0.4	–
–	67.6 ± 2.0 (n = 4)	no	1.55 ± 0.25	5.3.6	F 68
–	–	yes?	2.75 ± 0.14	10.26.2	–
–	–	no	2.45 ± 0.21	22.9.5	–
54 (n = 1)	–	yes	2.13 ± 0.75	11.13.1	F 113
–	–	yes?	1.71 ± 0.18	5.5.2	F 50.43
–	–	–	–	–	–
20 (n = 1)	71 (n = 1)	no?	2.31 ± 0.13	14.7.7	–
53.63 ± 2.41 (n = 8)	–	yes	1.83 ± 0.24	9.4.9	F 74.86
25.11 ± 4.33 (n = 9)	83 (n = 1)	no	1.64 ± 0.21	19.21.9	F 133.85
–	84 (n = 1)	no	1.00 ± 0.00	6.9.2	–
–	–	no	1.31 ± 0.13	9.7.1	–
–	–	yes	2.50 ± 0.22	9.8.8	–
–	–	yes	2.56 ± 0.50	11.11.1	–
–	–	–	–	–	–
15.10 ± 0.70 (n = 9)	62.9 ± 0.74 (n = 8)	yes	4.75 ± 0.25	16.18.4	F 42.00

eters from zoological records. Table 4 contains a compilation of selected reproductive data obtained during the present study including length of estrus, gestation, mean litter size, sex ratio of litters, and age at first maturity. The data in Table 4 are original and do not synthesize published information.

Copulatory behavior.—The copulatory behavior of small cats shows marked similarities among the species that have been studied. Their copulatory pattern has been described as one with "no lock, no intravaginal thrusting, ejaculation on a single insertion, and multiple ejaculations" (Dewsbury, 1972; Lanier and Dewsbury, 1976).

In this study, nine species of small cats were observed to copulate. The typical copulatory sequence recorded was as follows: the male approached the female, grasped her by the nape, mounted by straddling the female first with the front feet and then with the hind feet. The female responded to the nape bite by adopting a lordosis posture and moving her tail to one side; the female sometimes also treaded with her hind feet. At this point, the male occasionally began stepping with his hind feet, often simultaneously rubbing against the female's flanks. The latter may induce the female to adjust or to exaggerate her lordosis posture. The male then began "pelvic" thrusting. (Lanier and Dewsbury [1976] term this behavior "extra-vaginal pelvic thrusting" and believe it to function in detecting the vaginal orifice.) In the present study, "pelvic" thrusting typically lasted one–five min. In most instances, the male maintained a firm grasp on the female's nape throughout the mount. Intromission is apparently signalled by a "copulatory cry" given by the female; this vocalization was typically a low, barely audible growl. Five to ten seconds after the

TABLE 4. *Extended.*

	Young reared by mother in captivity?	2nd generation young produced in captivity?	Data based upon:
Asian Cats			
Pallas' cat			7 litters to 5 pairs of 4.4 cats
sand cat	yes	yes	25 litters to 6 pairs of 5.5 cats
fishing cat	yes	yes	13 litters to 4 pair of 4.4 cats
Temminck's golden cat	yes	yes	9 litters to 2 pairs of 2.1 cats
jungle cat	yes	yes	1 litter to 1 pair of 1.1 cats
rusty-spotted cat	yes	yes	9 litter to 3 pair of 3.3 cats
Indian desert cat	yes	yes	16 litters to 3 pairs of 3.3 cats
African Cats			
serval	yes	yes	15 litters to 5 pairs of 3.5 cats
caracal	yes	yes	8 litters to 5 pairs of 4.5 cats
black-footed cat	yes	yes	9 litters to 4 pair of 3.4 cats
African golden cat	yes	no	
South American Cats			
Geoffroy's cat	yes	yes	14 litters to 3 pairs of 2.3 cats
jaguarundi	yes	yes	12 litters to 4 pairs of 4.3 cats
ocelot	yes	yes	28 litters to 9 pairs of 7.8 cats
margay	yes		17 litters to 3 pairs of 3.3 cats
Pampas cat	yes	yes	13 litters to 3 pairs of 3.2 cats
European Cats			
Scottish wildcat	yes	yes	10 litters to 3 pairs of 2.3 cats
Siberian lynx	yes	—	9 litters to 1 pair of 1.1 cats
North American Cats			
Canadian lynx	—	—	0 litters to 1 pair of 1.1 cats
Worldwide Distribution			
domestic cat	yes	yes	8 litters to 8 pairs of 2.8 cats

female emitted this vocalization, she threw the male off her back, often threatening him, and began vigorously rolling on her back. Rolling on the back typically lasted five to thirty seconds. Both the male and female usually then groomed their own anogenital regions. Numerous mounts were observed in the present study, but it was assumed that intromission occurred only when mounts were followed by a "copulatory cry" and rolling by the female.

The most reliable indicator of estrus and/or reproductive activity identified in this study was a *change* in the relative rates of some behaviors. Figures 2 and 3 illustrate this observation.

DISCUSSION

While the initial intent of this study was to determine whether systematic behavioral observations could serve as an effective assay for monitoring reproductive activity, this very applied research question also resulted in the acquisition of substantial basic information about the behavior of a wide range of felid species. Discussion of of these behaviors in the context of previously published information is presented below.

Behaviors associated with scent marking

Urine, feces, and glandular secretions 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).

Cats presumably rub saliva onto inanimate objects during 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 differentiate phases of the estrous

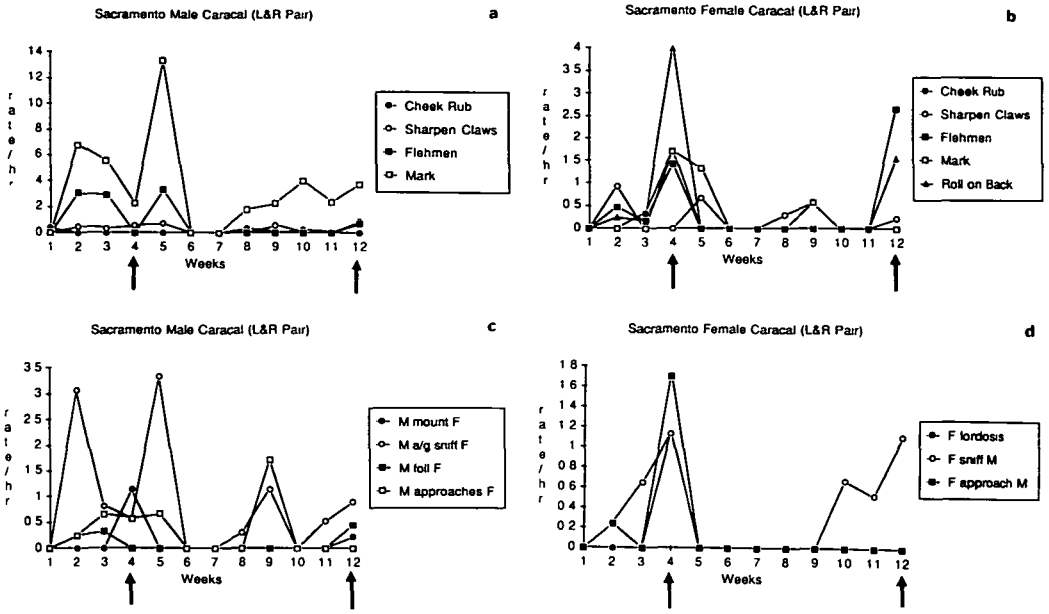

FIG. 2. Rates of selected behaviors exhibited by a pair of reproductively active caracals (*Felis caracal*). Arrows indicate those weeks in which reproductive activity was observed. a/g sniff = anogenital sniffing; foll = following.

cycle of females from cheek gland secretions (Verberne and DeBoer, 1976). Reiger (1979) and Reiger and Walzthonz (1979) contend that cheek rubbing in the Felidae functions not as a "marking" behavior (*i.e.*, laying down a scent), but rather to pick up scent from the substrate. They further suggest that cheek rubbing serves as a visual display.

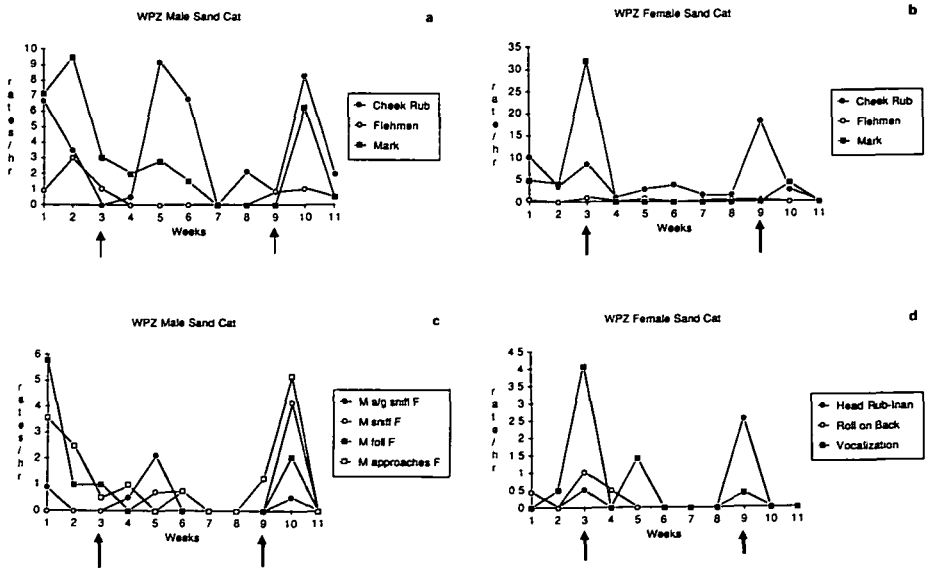

FIG. 3. Rates of selected behaviors exhibited by a pair of reproductively active sand cats (*Felis margarita*). Arrows indicate those weeks in which reproductive activity was observed. a/g sniff = anogenital sniffing; foll = following; Head Rub-Inan = head rubbing an inanimate object.

Data from the present study suggest that cheek rubbing serves all three functions; 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). See also Mellen (1989).

Claw "sharpening" probably does *not* function to "sharpen" claws per se, but rather may facilitate removal of loosened claw sheaths and may also serve to leave a visual signal by modifying or disturbing the substrate (Wemmer and Scow, 1977). Data from the present study support this interpretation.

The flehmen response, its relationship to the vomeronasal organ (VNO), and the role of the VNO have been systematically investigated in domestic cats (Verberne, 1976). Cats utilize the VNO, an accessory olfactory system, through the flehmen response to examine 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.

A flehmen response may be universal among the Felidae (Ewer, 1973). In this study, both sexes of most species were observed to exhibit a flehmen, providing support for Ewer's suggestion. Male domestic cats are reported to flehm more frequently than females (Hart, 1985); the present study demonstrated that in virtually all pairs observed, the male's rate of flehmen was higher than the female's. This study also indicates that the occurrence of flehmen is a good indicator of reproductive activity; males of most species studied exhibited a sharp rise in the frequency of flehmen responses two to three days prior to when copulations were observed.

In felids, the most conspicuous scent-marking behavior is performed by spraying urine against vertical objects (Fiedler, 1955; Verberne, 1976; Schaller, 1972; Verberne and Leyhausen, 1976; Leyhausen, 1979). In the present study, males typically sprayed urine at a higher rate than did females. Although urine appears to be used to mark a felid's territory, the urine spot itself seems not to be a deterrent. Instead it provides temporal information and may reduce the probability of confrontation (Hornocker, 1969; Schaller, 1972; Fox, 1974; DeBoer, 1977).

Wemmer and Scow (1977) suggest that the tail is raised just prior to spraying to help direct and position the spray. They further add that quivering or twitching of the end of the tail may serve as a visual signal or may simply be an automatic manifestation coupled with urine emission. During the present study, the tail quiver was not observed to accompany every bout of spraying. The cats instead exhibited a tail quiver during sprays that appeared particularly "vigorous" in execution.

Detectable behavioral changes in scent marking occurred in association with reproduction, supporting the concept of using systematic behavioral observations as a viable, non-invasive assay for monitoring reproductive activity. In general, reproductively active felids display a higher rate of scent-marking behavior. However, no *single* scent-marking behavior was a good indicator of reproductive activity. Rather, the relative change in rates of some behaviors over time were the best indicators of reproduction. When plotted over time, some scent-marking behaviors or some combinations of those behaviors typically showed a dramatic increase in association with those periods when copulations were observed. The scent-marking behaviors that showed increases in association with reproductive activity differed with species, sex, and individual.

Social behavior of small cats

While small felids vary widely in the habitats they use and the prey items they exploit, these cats are remarkably similar with regard to the behavioral mechanisms they use to communicate with conspecifics. The relative frequency of social behaviors differed, but their appearance and the general order of occurrence was similar among the species observed. For example, the copulatory sequence among the felid species observed in the present study is similar to other felid species, including the larger cats (Ewer, 1973; Lanier and Dewsbury, 1976; Leyhausen, 1979). As with scent-marking behavior, no

single social behavior measured could reliably predict copulation, but when the change in relative frequencies of these social behaviors were plotted over time, selected social behaviors were observed to increase simultaneously in association with observed copulations. In this study, the most reliable indicator of estrus and/or reproductive activity was a *change* in the relative rates of some behaviors.

Behavioral patterns associated with the three lineages of Felidae

Comparative behavioral data also show promise for understanding the phylogenetic relationships of three proposed lineages within the family Felidae. When behaviors of small cats are examined in the context of these three proposed lineages, *i.e., Panthera,* ocelot, and domestic cat (Collier and O'Brien, 1985), some intriguing patterns emerge. One example involves the behavior scraping with the hind feet which was observed in most species within the ocelot and *Panthera* lineages, but was seen in only one species within the domestic cat lineage, Pallas' cat. Pallas' cat is a species that may represent the sister group of the remainder of the domestic cat lineage (see Wayne *et al.,* 1989).

A second example involves the occurrence of a nape bite during copulation. Traditionally, one of the most pronounced dichotomies between "large" and "small" cats has been the absence of the nape bite during copulation in the large cats. Indeed within the domestic cat lineage, the nape bite often seems to be necessary for the male's ability to safely and successfully copulate (personal observation). In this study males of two species (the male ocelot [ocelot lineage] and male Temminck's golden cat [*Panthera lineage*]) displayed an intermediate behavior: each was observed to initiate a mount with a nape bite, but release the grip on the female's nape during the mount, grasping the nape again at or near the time of intromission. It has been speculated that the absence of the nape bite in the larger cats (*e.g.,* lions, tigers, jaguars) is due to the potential risk of injury to the female by the male's extremely large canine teeth (Lanier and Dewsbury, 1976; Wemmer and Scow, 1977). The absence of a sustained nape bite during the mount in the golden cat may represent a transitional state between the sustained nape bite found in the domestic cat lineage and the lack of a nape bite in the *Panthera* lineage. The intermediate condition displayed by the ocelot poses intriguing problems that beg a more detailed phylogenetic analysis. These examples indicate that a thorough examination of comparative behavioral data might contribute significantly to hypotheses developed using recent molecular data (Wayne *et. al.,* 1989) and help elucidate the relationships of groups within the family Felidae.

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