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Scent Rubbing in Carnivores

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Every dog owner is familiar with the reaction of his pet to a dead fish. The animal intensely sniffs the carcass, then flexes its forefeet and rolls over on its back. Lying on its back, the animal rolls to and fro on the carrion. This scent rubbing behavior is well known among other carnivores too, most of them performing it on objects with a strong smell!

In this paper I survey the available literature on scent rubbing in carnivores, describe the behavior, and investigate possible explanations for the origin and function of scent rubbing.

During scent rubbing the animal stretches and turns its neck, causing contact between the animal's body and the environmental object on which scent rubbing is executed, with this movement the area of contact changes from a more cranial to a more caudal part of the animal's body. From this basic form of scent rubbing, several new forms evolved that will be described below. The various forms of scent rubbing led to different names in the literature for basically the same kind of behavior. Synonymous terms for scent rubbing are: body rubbing, neck sliding, cheek rubbing; Einreiben, Sichreiben, Parfumiern, Impragniern.

Scent rubbing is only one behavior pattern which a scent source elicits from a carnivore. Beside scent rubbing, odorous objects are covered with urine or feces (mustelids, Herter and Ohm-Kettner, 1954; *Vulpes* vulpes, Henry 1977; *Alopex lagopus,* Fox, 1971). In cats, odorous objects elicit Flehmen. In some cases cats cover objects with soil (Knappe, 1964; Verberne, 1964; Verberne, 1970; Leyhausen, 1973; Rieger 1978a).

The scent rubbing behavior transfers scent substances from the environment onto the animal's body, thus burdening a carnivore with scent (Schneider, 1952). This self burdening is sometimes a very intensive behavior. Thus anal gland secretions were noticed in the neck fur of *Hyaena hyaena,* the spot where this species usually scent rubbed (Rieger, 1977, unpublished observations). Until now, a generally accepted interpretation of the meaning of scent rubbing is not available. This might be due to various forms of scent rubbing that were not recognized as being phylogenetically related.

MATERIAL

Table 1 lists the available references on scent rubbing in carnivores. This list does not claim to be complete. It is obvious that in some large carnivore families, e.g. the mustelids, few references concerning scent rubbing were found. This might be influenced by insufficient knowledge of the literature bearing on these carnivore groups. Nevertheless, some carnivore families do not scent rub as frequently as others (Goethe, 1964).

A serious handicap is always connected with review papers. As the information on different animals species was not collected in the same way — i.e. some papers were based on casual observations, others on thorough investigations over several years — a behavior pattern common in one species was not reported from others, although it was suspected to occur. Thus the only purpose of the present paper can be to draw attention to some behavioral tendencies connected with scent rubbing.

Although the references to scent rubbing are few, they do allow us to answer the following questions:

(1) Which body areas are scent rubbed?

(2) What scent sources elicited scent rubbing?

(3) In what situations do carnivores scent rub?

RESULTS

Scent Rubbed Body Areas (SRBA)

The SRBA that primarily comes into contact with smelling environmental objects during scent rubbing are: lips, chin, throat, cheeks, neck, shoulders, backside of the head, chest, flanks and back. The preferred SRBA varies from one carnivore family to another sometimes varying within families (Table 2). While some species scent rub only a few body areas, others scent rub more or less the whole area between chin and back.

Among ursids, the brown bear, *Ursus arctos,* has an extended SRBA that ranges from the cheeks to the back. Procyonoid species seem to scent rub infrequently. The only references available where for two species, the coati, *Nasau spec.,* and the kinkajou, *Potos flavus.* For other members of this family, scent rubbing was never noted *(Bassaricyon spec.,* Poglayen-Neuwall, 1965; *Ailurus fulgens,* Keller, 1977, personal communication). Except for the tayra, *Eira barbara,* and the wolverine, *Gulo gulo,* scent rubbing in mustelids is rare (Goethe, 1964).

Viverrids scent rub body areas between lips and shoulders, plus flanks and back. The paradoxurinae scent rub more cranial body areas, i.e. cheeks and neck, and occasionally flanks too, whereas herpestinae prefer to scent rub back and backside of the head. Both hyena species for which references were available scent rub neck, shoulders, and back on odorous environmental objects. Felids prefer cranial body areas for scent rubbing. The cheeks especially are regularly scent rubbed, but chin, neck, shoulders and back are scent rubbed too.

Besides these primary SRBAs there exist secondary SRBAs in some species. Schneider (1952) described how a coati, *Nasua spec.,* transferred scent substances with its hands onto its belly and tail.

Scent Sources Eliciting Scent Rubbing

The scent sources that were known to elicit scent rubbing behavior in carnivores can be divided into five groups (Table 3):

(1) **food:** e.g. meat, fish, carrion, intestines, stomach contents, vomit, pellets, *Citrus*-fruits.
(2) **chemicals;** e.g. benzine, cheese, cigarettes, cod-liver oil, formiat, hair-oil, insecticides, menthol, perfumes, pine resin, turpentine, trimethylamine.
(3) **cat mint:** Parts of the *Nepeta cataria* plant or its scent 'nepetalactone' (Palen & Goddard, 1966; Todd, 1962) and *Valeriana spec.*
(4) **urine** and **feces** of other species, such as ungulates, birds, etc.
(5) **scent markings** of conspecifics or the scent rubbing animals themselves.

Some cases of scent rubbing, or of behavior similar to scent rubbing, did not belong to one of the five groups described above. Schneider (1932) observed a young wolf rubbing and rolling on a dead conspecific and Schaller (1972) observed similar behavior in an African wild dog. Also a male lion was seen rolling on a lion cub (Schaller, 1972), and a mungo (Ducker, 1965) and a pine marten (Herter & Ohm-Kettner, 1954) were seen rolling in water.

Individuals of many canid, viverrid, and hyenid species scent rub on sources belonging to the 'food' group. Canids, viverrids and felids in particular reacted toward scents of excrements and urine of prey animals. Hyenas and cats orient scent rubbing frequently towards scent markings.

Table 1 Scent rubbing references

Family	Genus	Species	References
Canidae	Canis	lupus	Fox, 1969; Mech, 1970; Schneider, 1932; Zimen, 1978
		familiaris	Graf & Meyer-Holzapfel, 1974, Rieger, unpublished observations
		latrans	Gier, 1975
		aureus	Heimburger, 1959
	Lycaon	pictus	Schaller, 1972
	Alopex	lagopus	Fox, 1971; Heimburger, 1959
	Vulpes	vulpes	Fox, 1969; 1971
	Fennecus	zerda	Gauthier-Pilters, 1962
	Nyctereutes	procyonides	Heimburger, 1959
	Chrysocyon	brachyurus	Hammerling & Lippert, 1975; Kleiman, 1972
	Otocyon	megalotis	Kleiman, 1966
	Urocyon	cinereoargentus	Fox, 1969; 1971
	Speothos	venaticus	Kleiman, 1972
Ursidae	Ursus	arctos	Ewer, 1973; Hediger, 1949; Krott :& Krott, 1963; Schneider, 1952; Tschanz et al. 1970
	Helarctos	malayanus	Schneider, 1952
Procyonidae	Nasua	spec.	Schneider, 1932; 1952
	Potos	flavus	Poglayen-Neuwall, 1962
Mustelidae	Gulo	gulo	Goethe, 1964
	Eira	barbara	Poglayen-Neuwall & Poglayen-Neuwall, 1977; Wemmer 1971
	Martes	martes	Herter & Ohm-Kettner, 1954
Viverridae			
Viverrinae	Civettictis	civetta	Bearder & Randall, 1978; Ewer, 1973; Ewer & Wemm Wemmer, 1971, 1977
	Viverricula	indica	Ducker, 1965
	Genetta	genetta	Ducker, 1965, Gangloff & Ropartz, 1972
		tigrina	Wemmer, 1977
	Prionodon	linsang	Gangloff, 1975
Paradoxurinae			
	Nandinia	binotata	Ducker, 1965; Vosseler, 1928; Wemmer, 1971, 1977
	Paradoxurur	spec.	Gangloff, 1975; Wemmer 1977
	Paguma	larvata	Wemmer, 1971, 1977
Herpestinae			
	Herpestes	paludinosa	Ducker, 1965
	Mungo	spec.	Schneider, 1932
	Helogale	undulata	Zannier, 1965
	Suricata	suricatta	Ewer, 1963
Hyaenidae	Hyaena	hyaena	Rieger, 1977, Schneider, 1932
	Crocuta	crocuta	Bearder & Randall, 1978, Kruuk, 1972, Schneider, 1926, 1932

Felidae	Leopardus	wiedii	Petersen, 1976
	Felis	libyca dom.	Leyhausen, 1965a, 1965b, 1973; Palen & Goddard, 1966; Todd, 1962; Verberne 1970
	Leptailurus	serval	Rieger, 1978b
	Lynx	rufus	Wemmer in McCord 1974
	Puma	concolor	Bogue & Ferrari, 1976; Schneider 1932
	Uncia	uncia	Rieger, 1978b, in preparation; Wemmer & Scow, 1977
	Panthera	tigris	Kleiman, 1974; Rieger, 1978b; Schaller, 1967, 1972
		pardus	Schloeth, 1956; Rieger, 1978b
		leo	Anonymus 1962; Eaton, 1972; Rieger, 1978b; Schaller, 1972; Schenkel, 1966
	Acinonyx	jubatus	Eaton & Craig, 1973

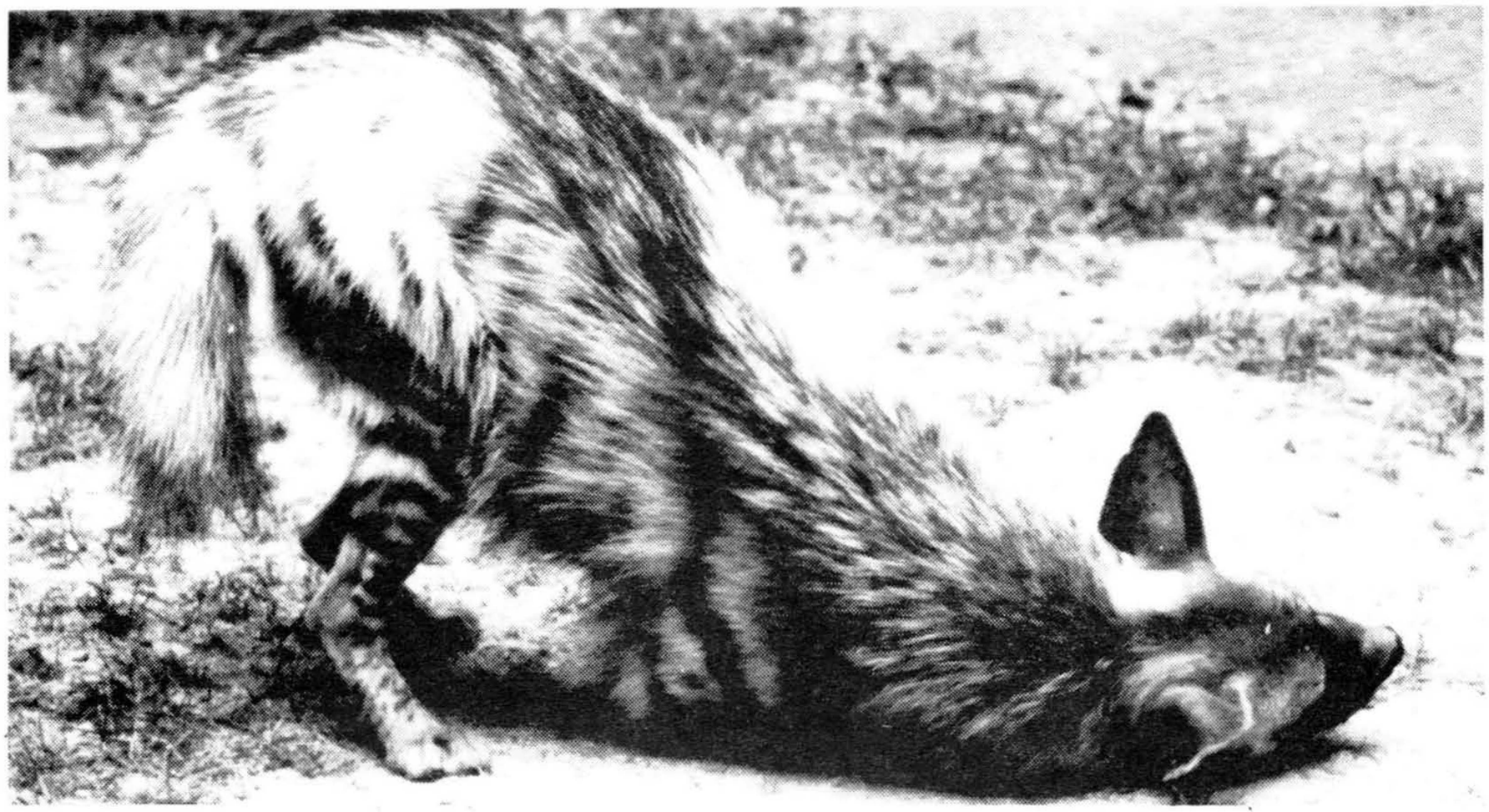

Figure 1: Scent rubbing striped hyaena, *Hyaena hyaena*.

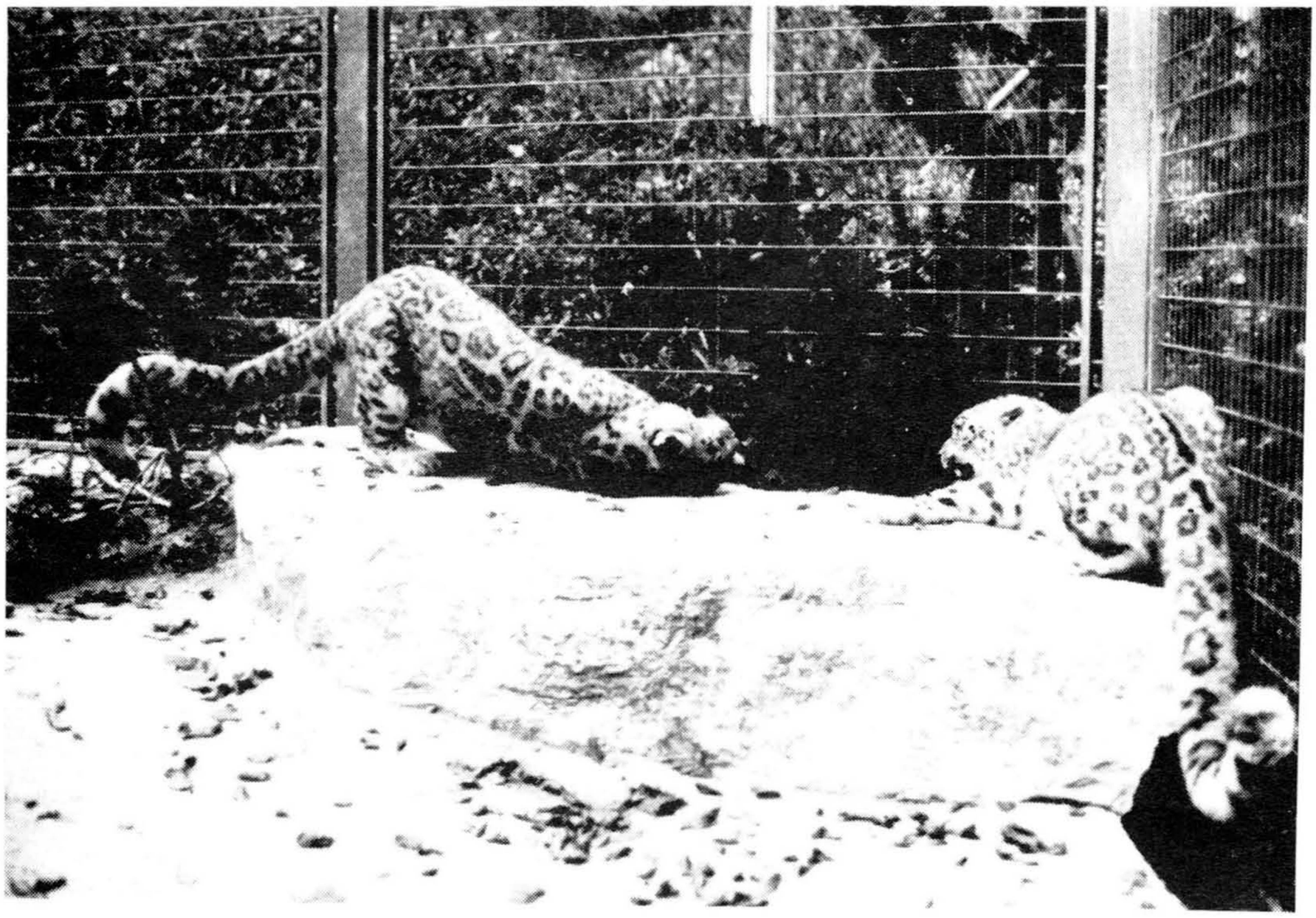

Figure 2: Scent rubbing movements in ounces, *Uncia uncia,* functioning as an appeasement behaviour.

Table 2: Scent rubbed body areas (SRBA) in carnivores.

1: lips, 2: chin, 3: throat, 4: cheeks, 5: neck, 6: shoulders, 7: backside of the head, 8: chest, 9: flanks, 10: back

Species	1	2	3	4	5	6	7	8	9	10
Canis lupus	.	.	.	.	x	.	.	.	.	x
Canis familiaris	.	.	.	.	x	x	.	.	.	x
Canis latrans	.	.	.	.	.	x	.	.	.	.
Canis aureus	.	.	.	.	x	.	.	.	.	x
Lycaon pictus	.	.	.	.	.	.	.	.	.	x
Alopex lagopus	.	.	.	x	x	.	.	.	x	x
Vulpes vulpes	.	.	.	.	x	.	.	.	.	x
Fennecus zerda	.	.	.	x	x	x	.	.	x	x
Nyctereutes procyonides	.	.	.	x	x	x	.	.	.	x
Chrysocyon brachyurus	.	.	.	.	x	.	.	.	x	x
Otocyon megalotis	.	.	.	.	.	.	.	.	.	x
Urocyon cinereoargentus	.	x	.	x	x	.	.	.	.	.
Speothos venaticus	.	x	x	x	x	.	.	.	.	.
Ursus arctos	.	.	.	x	x	x	x	x	.	x
Helarctos malayanus	.	.	.	.	x	.	.	.	.	x
Nasua spec.	.	.	x	.	.	.	.	.	.	x
Potos flavus	.	.	.	.	.	.	.	.	.	x
Gulo gulo	.	.	.	.	.	.	.	.	.	x
Eira barbara	.	.	x	x	x	x	.	.	.	x
Martes martes	.	.	.	.	.	.	.	.	.	x
Civettictis civetta	.	x	x	x	x	x	.	.	.	x
Viverricula indica	.	x	.	x	.	.	.	.	.	x
Genetta genetta	.	.	.	.	.	.	.	.	x	x
Genetta tigrina	x	.	.	.	.	.	.	.	.	.
Prionodon linsang	.	.	.	.	x	.	.	.	x	.
Nandinia binotata	.	.	.	x	x	.	x	.	.	x
Paradoxurus spec.	.	x	.	.	.	.	.	.	x	.
Paguma larvata	.	.	.	x	x	.	x	.	.	.
Herpestes paludinosa	.	.	.	.	.	.	.	.	.	x
Mungo spec.	.	.	.	.	.	.	.	.	.	x
Helogale undulata	.	.	.	.	.	.	x	.	.	.
Suricata suricatta	.	.	.	.	.	.	.	.	x	.
Hyaena hyaena	.	.	.	.	x	x	.	.	.	x
Crocuta crocuta	.	.	.	.	x	x	.	.	.	x
Leopardus wiedii	.	x	.	x	.	.	.	.	.	.
Felis libyca dom.	.	x	.	x	.	.	.	x	.	x
Letailurus serval	.	.	.	x	.	.	.	.	.	.
Lynx rufus	.	.	.	x	.	.	.	.	.	.
Puma concolor	.	.	.	.	.	.	.	.	.	x
Uncia uncia	.	.	.	x	.	.	.	.	.	x
Panthera tigris	.	.	.	x	.	.	.	.	.	.
Panthera pardus	.	.	.	.	.	.	.	.	.	x
Panthera leo	.	.	.	x	x	x	.	.	.	x
Acinonyx jubatus	.	.	.	x	.	.	.	.	.	

Table 3 Scent substances on which carnivores scent rub.

Species	Food	Chemicals	Cat Mint	Urine/feces	Scent marks
Canis lupus	x	x	.	.	.
Canis familiaris	x	.	.	x	x
Canis latrans	x	x	.	.	.
Canis aureus	x	x	.	.	x
Lycaon pictus	x	.	.	x	.
Alopex lagopus	.	.	.	x	.
Vulpes vulpes	.	.	.	x	.
Fennecus zerda	.	.	.	x	x
Nyctereutes proc.	x	x	.	x	x
Chrysocyon brachyurus	x	.	.	.	x
Urocyon cinereoarg.	.	.	.	x	x
Ursus arctos	.	x	.	x	x
Helarctos malayanus	.	x	.	.	.
Nasua spec.	.	x	x	.	.
Potos flavus	x	.	.	.	.
Gulo gulo	.	.	.	x	.
Eira barbara	x	.	.	.	x
Civettictis civetta	x	x	.	x	.
Viverricula indica	x	x	x	x	.
Genetta genetta	.	x	.	.	.
Genetta tigrina	.	x	.	.	.
Nandinia binotata	x	.	.	x	x
Paradoxurus spec.	x	.	.	.	.
Paguma larvata	x	.	.	x	x
Helogale undulata	.	.	.	.	x
Suricata suricatta	.	.	.	.	x
Hyaena hyaena	x	x	.	.	x
Crocuta crocuta	x	.	.	.	x
Felis libyca dom.	.	x	x	.	x
Leptailurus serval	.	.	.	.	x
Lynx rufus	x	.	.	.	.
Puma concolor	x	.	.	.	.
Uncia uncia	x	.	x	x	x
Panthera tigris	.	.	.	x	x
Panthera pardus	.	.	.	.	x
Panthera leo	x	.	x	x	x
Acinonyx jubatus	.	.	.	.	x

Cat mint or catnip, as its name implies, is particularly attractive to felids as a scent source. But not every cat species scent rubs on cat mint (Ewer, 1973). The only species that, to my knowledge, scent rubs on cat mint are the house cat, the ounce, and the lion (on *Lippia javanica (Verbenaceae)* Schaller, 1972). Other carnivores such as the coati, *Nasua spec.* (on valerian, Schneider, 1952) and the small Indian civit, *Viverricula indica,* showed reactions similar to the catnip behavior of felids.

'Chemical' comprised scent sources which the carnivores in question were normally unfamiliar with. These artificial scents are perceived by humans too. Experiments first performed by Schneider (1932, 1952) tested the reactions of carnivores towards chemicals. In such experiments it would be possible to quantify the reactions of test animals, assuming that all experiments proceeded under similar conditions. The results presented in Table 3 do not correspond to this presupposition. Thus they only allow us to conclude that 13 carnivore species reacted with scent rubbing when exposed to the chemicals mentioned above.

Situations in which Carnivores Scent Rubbed

We lack comprehensive information of situations in which carnivores scent rub (Table 4). Species of four carnivore families scent rubbed before, during, and following feeding. Species of three families scent rubbed in connection with scent marking. Here, the felids and the brown bear are worth mentioning. Both of them integrated their species specific scent rubbing behavior into their scent marking pattern (Hediger, 1949; Rieger, 1978b; Rieger & Walzthony, in press; Tschanz et al., 1970). While only one cat species, the ounce *(Uncia uncia),* was said to scent rub following agonistic interactions (Rieger, 1978b, in preparation; Rieger & Walzthony, in press), fenecs (*Fennecus zerda),* and genets *(Genetta genetta),* scent rubbed during aggressive behavior (Gangloff & Ropartz, 1972; Gauthier-Pilters, 1962). Most felids scent rub together with scent marking, and it is a common observation that scent marking terminates agonistic behavior in carnivores.

Scent rubbing in several carnivore species has been correlated with social behavior. Brown bear, felids, and fenecs increase their scent rubbing frequencies, with or without releasing scent sources, during estrus (Eaton & Craig, 1973; Gauthier-Pilters, 1962; Leyhausen, 1973; Palen & Goddard, 1966; Schneider, 1952; Tschanz et al., 1970). Social canids (Type III, according to Fox 1975) frequently scent rub on scents while more solitary species (Type I, II) cover scents with urine or faeces (fox, 1975; Henry, 1977). Graf & Meyer-Holzapfel (1974) mentioned that male dogs in aggressive mood rolled on a rival's urine.

The available information on carnivore scent rubbing behavior suggests the following four presuppositions for the occurence of this behavior:

(1) Scent rubbing is restricted to terrestrial carnivores. The more arboreal procyonids never scent rub or do so only in exceptional circumstances, (e.g. on artificial scent sources). Clearly arboreal viverrids such as the binturrong, *Arctictis binturong,* were never seen scent rubbing (Huf, 1966; Schneidermann, personal communication).
(2) The generalized form of scent rubbing is correlated with an animal's diet. Pure vegetarians as the red pandas, *Ailurus rulgens,* were never seen scent rubbing. It is unkown whether other specialized feeders, such as the termite eating aardwolf, *Proteles cristatus,* scent rub or not.
(3) Scent rubbing was only reported from carnivore species of a certain size. In mustelids, the two comparatively large species, the wolverine, *Gulo gulo,* and the tayra, *Eira barbara,* were seen scent rubbing, and only one species of the large number of small mustelids was seen scent rubbing (pine marten, *Martes martes).* In other carnivore families with small and large species, e.g. viverrids and felids, more accurate information concerning scent rubbing came from observations of large species.
(4) Scent rubbing was never reported from aquatic carnivores. This supports the idea that scent rubbing serves to transfer scent substances from the environment onto the animal's body, rather than to impregnate environmental objects with scent gland secretions. Scent substances in the fur of an aquatic carnivore would be washed out and thus lose any possible function.

Table 4 Activities during which carnivores scent rubbed.

Species	Feeding	Scent marking	Agonistic behaviour
Fennecus zerda	.	.	x
Nyctereutes proc.	.	x	.
Chrysocyon brachyurus	x	.	.
Ursus arctos	.	x	.
Potos flavus	x	.	.
Civettictis civetta	x	.	.
Parasoxurus spec.	x	.	.
Genetta genetta	.	.	x
Felis libyca dom.	.	x	.
Leptailurus serval	.	x	.
Uncia uncia	.	x	x
Panthera tigris	.	x	.
Panthera pardus	.	x	.
Panthera leo	x	x	.
Acinonyx jubatus	.	x	.

DISCUSSION

The following hypotheses on the evolution of scent rubbing are proposed:
(1) The phylogenetically oldest SRBA is the back and rolling is the behavior corresponding to it (Wemmer, 1977). Two observations support this assumption: (a) Today the back is the most frequently used SRBA in carnivores (Table 2), and (b) In conformity with Haeckel's biogenetic rule is the observation that, although some young carnivores roll on scents, adults of the same species usually no longer scent rub their backs (e.g. brown bears, Krott & Krott, 1963).
(2) The phylogenetically oldest scents which release scent rubbing are connected with a carnivore's animalic diet, which is supported by the following observations (a) foods release scent rubbing in most carnivore species (Table 3), and (b) many carnivores scent rub before, during, and following feeding (Table 4).

We assume 'rolling on food substances' to be the most generalized form of scent rubbing. But this behavior changed its form and its releasers during evolution. Beside the SRBA on a carnivore's back, new SRBAs on more cranial areas, such as shoulders, neck and head, were introduced. And besides releasers from the food substances group, others, such as excrements of potential prey animals and other odorous environmental substances, among them also species specific scent marking secretions, were introduced as scent rubbing releasers. Thus, in the evolution of scent rubbing the new cranial SRBA and scent marking secretions as releasing scents evolved together. As carnivores had a tendency to deposit their scent marks on places somewhat above ground, there was a need for scent rubbing behavior patterns that allowed the animal to contact these scent marking sites with its body. The agility of cranial SRBA, such as shoulders, neck and head, increased compared to the agility of the back SRBA. Thus scent marks higher above ground could be used as scent rubbing releasers.

Species, genera, and families of carnivores reached different grades of this scent rubbing specialization. While there are no carnivore species that exclusively roll on food substances, others displayed only extreme forms of scent rubbing.

Brown bear: Rolling behavior in adult brown bears could only be released with strong odors of the 'chemical' group (Table 3, Schneider, 1952). Brown bears integrate scent rubbing into their scent marking behavior. They micturated standing erect, rubbing their shoulders on their scent marking trees. Then they scent rubbed their shoulders in the fresh urine and again rubbed their shoulders and necks on their scent marking trees (Hediger, 1949; Tschanz et al., 1970).

Felids: The cat species emancipated their scent rubbing behavior too, as the following examples demonstrate:
(1) Only the pantherines roll more or less regularly, whereas the felines roll only exceptionally on extremely powerful scents, i.e. cat mint. Felids scent rub their cheeks especially (Table 2). As the rolling frequency is small compared to the cheek rubbing frequency, these two behavior patterns are not recognized as being phylogenetically related. The idea arose that felids scent mark with their cheek rubbing behavior, i.e. they transfer secretions of cheek skin glands onto environmental objects. But Rieger & Walzthony (in press) could not prove the existence of scent skin glands in cat cheeks.
(2) With few exceptions species specific scent marking secretions and powerful chemicals release scent rubbing. The releasing molecule of cat mint, nepetalactone, is thought to be similar to the species specific pheromones (Todd, 1962).
(3) In some cat species at least, there was a loosening in the exact orientation of the scent rubbing behavior towards odorous environmental objects. Ounces several times were seen sniffing the urine of a conspecific. They then walked a few steps and rolled **beside** the urine place (Rieger, in preparation).
(4) Scent rubbing behavior in cats occurs in different behavior patterns. Other than during the scent marking pattern, felids show the scent rubbing movements, especially cheek rubbing, in agonistic and sexual contexts. Following an agonistic interaction, an animal rubs its head on the nearest protruding object (Rieger, 1978b, in preparation). Females in estrus display their willingness for copulation with rolling and intensive cheek rubbing.

In the last two situations described, feline scent rubbing movements were not oriented towards scent. Thus these scent rubbing movements no longer function to transfer scents from the environment onto the animal's body. They were ritualized and seemed to function as visual displays, in some situations functioning as appeasement behavior (Rieger, in preparation; Schaller, 1967, 1972).

Until now, only formal aspects of scent rubbing have been discussed. Nothing has been said of the behavior's function. Several hypotheses on the significance and origin of scent rubbing were found in the literature:

(1) One idea of the origin of scent rubbing suggests that it might be a vestige of a scent marking behavior: "As among Mammalia scent glands are very well known at several places in the skin, it might be possible that during evolution several glands disappeared but the association rubbing movements remained" (Verberne & Leyhausen 1976:196).

(2) Ewer & Wemmer (1974:376) showed that, at least in the species they studied, scent rubbing is "not concerned with setting an ownership mark on food which is not going to be consumed at once."

(3) Several authors described scent rubbing together with comfort behavior, and by that implied a possible relationship between the two behavior patterns (Ducker, 1965; Gangloff, 1975; Schaller, 1972).

(4) Zimen (1972, 1978) suggested that scent rubbing might function as an odor camouflage which allows a carnivore to cover its own body odor and thus be able to approach a potential prey animal at close range without being detected.

(5) Fox (1971:187) presented two different interpretations of scent rubbing functions. First, that "rolling in certain materials . . . may reduce novelty by the odor mingling with the animal's body odor and also habituating to the strange odor as it 'wears' it."

(6) Fox's (1971:187) second interpretation of scent marking function is that scent rubbing might increase social attractiveness of a particular animal: "It may be postulated that social canids returning with a strange odor to conspecifics will experience more social investigation than if they were not 'wearing' this olfactory attractant."

I want to mention the following considerations concerning these six interpretations of scent rubbing function. (1) To the best of my knowledge there were only two carnivore species with scent glands in those body areas that are scent rubbed. These are the kinkajou which used mandibular and throat glands for scent marking (Poglayen-Neuwall, 1966), and the African dwarf mongoose which scent marks with cheek glands (Rasa, 1972, 1973). Some authors assert that cats have cheek glands with which they scent mark during cheek rubbing (Verberne & deBoer, 1976; Verberne & Leyhausen, 1976; Prescott 1971). But no such glands were found in histologically treated cat cheek skin (Montagna, personal communication; Rieger & Walzthony, in press). If we accept Johnson's (1973:521) definition of scent marking: "Scent marking is behavior by which glandular secretions are deposited on the ground or onto objects in an animal's environment," then scent rubbing, during which scents were transferred from the environment onto the animal's body, cannot be described as scent marking.

The interpretation that scent rubbing might be a vestige of phylogenetically old scent marking behavior came from students of the felids, the carnivore family with the highest form of scent rubbing emancipation. In this family, scent rubbing behavior was integrated in the scent marking pattern. Brown bears which also integrated scent rubbing into their scent marking pattern were also thought to have enlarged skin glands in their main SRBA, but an investigation of a brown bear shoulder skin did not provide any evidence supporting this assumption (Hediger, personal communication).

(2) It cannot be overlooked that a strong relation exists between feeding and scent rubbing which might support the interpretation of scent rubbing as an indication of ownership. But this interpretation again took for granted that scent rubbing transferred scents from the animal onto the food. No doubt, some scent molecules are transferred in this direction, but more important is the scent transport in the opposite direction. These theoretical considerations were proven by the observations of Ewer & Wemmer (1974).

(3) During comfort behavior species of several mammalian orders (e.g. Perissodactyla, Artiodactyla, Proboscidea) rub their bodies against evironmental objects or roll on the ground. Because these movements are similar to scent rubbing, some authors treated carnivore scent rubbing behavior under the heading of comfort behavior. If scent rubbing should be part of a comfort behavior, we must assume that together with scent rubbing, other elements of comfort behavior, e.g. nibbling, licking, scratching, occur. But neither in those carnivores whose behavior I am familiar with, nor in the literature, can I find a relationship between scent rubbing and comfort behavior. Thus we are obliged to reject this interpretation of the origin of scent rubbing.

Interpretations 4, 5, and 6 above have one trait in common. Each one takes into consideration that, during scent rubbing, odors from an animal's environment are transferred onto the animal's body. The new scents on the animals are then addressed to individuals of other species, individuals of the same species, or to the carrying animal itself. Only experiments can prove which interpretations of scent rubbing are correct. At least some references support hypothesis 5 and 6. Some authors stress the fact that the carnivores they studied scent rubbed on new, unkown objects (e.g. Bogue & Ferrari, 1976; Glickman & Sroges, 1966; Kleiman, 1966), supporting the idea that scent rubbing might reduce novelty.

Several observations support hypothesis 6, that scent rubbing increases social attractiveness. In descriptions of carnivore encounters, Schloeth (1956) reported a male fox sniffing the back of a female conspecific. He also observed a female fox sniffing the back of a female conspecific. A similar occurance was described by Rabb (1968, in Mech 1970). Also, when meeting, striped hyenas sniff at the mid-back area of a conspecific (Rieger 1978a). In all these species, the back is a well used SRBA.

Fox's (1971) second interpretation of the function of scent rubbing, saying that the behavior in question increases social attractiveness, presupposes that a scent rubbing carnivore has relatively frequent encounters with conspecifics. This allows us to assume that social carnivores scent rub more frequently than solitary species. This assumption is correct, as least for the phyologenetically oldest SRBA on a carnivore's back. Social canids scent rub more on the back while solitary canids (type I, II) prefer rubbing more cranial SRBA (Table 2). Felids roll too, but the most frequently used SRBA in felids is the cheek. Only for the most social cat species, the lion, were several references to scent rubbing the back found.

The positions of the SRBA point toward a possible function of scent rubbing. Parts of a carnivore's body between its back and its chin were scent rubbed (Table 2). The information stored on these SRBA were primarily accessible to smell and taste sensory organs. Anatomical reasons make it difficult to for a carnivore to contact most of its SRBA with its nose or mouth. This led me to conclude that at first the carrier of such SRBA is not identical with the recipient of the scent information stored on the SRBA. There is a tendency to scent rub only those parts of the animal's body which are far above ground. Thus only carnivore species greater than a minimum limit scent rub, and the SRBA are located on those body parts having the greatest vertical distance from the ground when the animal is standing or walking.

The location of SRBA on an animal's body allows an easy diffusion of scent molecules. For the phylogenetically oldest SRBA on a carnivore's back we must assume that other individuals were recipients of the scent information. These individuals might belong to the same species as the carrier of the scent. In this case the primary function of scent rubbing would be to enhance social attraction or attraction to a carcass located by the scent carrying individual (R. Eaton, personal communication). Or the scent recipient might be individuals of other species, especially potential prey animals. In this second case, scent rubbing would function as odor camouflage. The carnivore's own body odor would be covered or mixed with scent from the environment.

Scent molecules diffusing from more cranial SRBA, e.g. neck and cheek, might produce a field of scent in front of the nose of the animal itself. Interestingly enough, cranial SRBA are often scent rubbed on species specific scent marks (e.g. felids, type I, II canids). Thus we might assume that scent rubbing cranial SRBA on species specific scent marks had a reassurance fuction, similar to the function of some scent marks (Ewer 1968).

Abstract: *Scent rubbing behavior in carnivores is described, along with a possible phylogenetic relationship between the various forms of this behavior. The phylogenetically oldest form of scent rubbing is rubbing of back and neck on scent sources belonging to the food group. From this basic scent rubbing behavior evolved those behavior patterns which are directed to urine/feces or species specific scent marks. Besides this evolution of the scent sources which elicit scent rubbing, there were also changes in the body areas rubbed on the scent. In modern forms of scent rubbing, more cranial body areas are used, e.g. cheek, chin, and throat. These interpretations led to the conclusion that feline cheek rubbing is not a scent marking behavior, but a scent rubbing behavior.*

LITERATURE CITED

Anonymus. 1962. *Das Tier* 2 (2):5.

Bearder, S.K. and R.M. Randall. 1978. The use of fecal marking sites by spotted hyenas and civets. *Carnivore* 1 (2):32-48.

Bogue, G. and M. Ferrari 1976. The predatory 'training' and captive-reared pumas. *World's Cats* 3 (1):36-45.

Ducker, G. 1965. Das Verhalten der Viverriden. *Handbuch der Zoologie* 8, 10 (20a):1-48.

Eaton, R.L. 1972. Predatory and feeding behavior in adult lions: the deprivation experiment. *Zeitschrift fur Tierpsychologie* 31:461-473.

Eaton, R.L. and S.J. Craig. 1973. Captive management and mating behavior of the cheetah. *World's Cats* 1:217-254.

Ewer, R.F. 1963. The behavior of the meerkat, *Suricata suricatta* (Schreber). *Zeitschrift fur Tierphsychologie* 20:570-607

— 1968. *Ethology of Mammals.* Logos Press, London.

— 1973. *The Carnivores.* Weidenfeld and Nicholson, London.

— and C. Wemmer 1974. The behavior in captivity of the African civit, *Civettictis civetta* (Schreber). *Zeitschrift fur Tierpsychologie* 34:359-394.

Fox, M.W. 1969. Ontogeny of prey-killing behavior in Canidae. *Behavior* 35:259-272.

— 1971. *Behavior of Wolves, Dogs and Related Canids.* Harper and Row, New York.

— 1975. Evolution of social behavior in canids. Pp. 429-460, *In:* M.W. Fox, (Ed.),: *The Wild Canids.* Van Nostrand Reinhold, New York.

Gangloff, B. 1975. Beitrag zur Ethologie der Schleichkatzen (Banderlinsang,*Prionodon linsang* (Hardw.) und Banderpalmenroller, *Hemigalus derbyanus* (Gray). *Der Zologische Garten* 45:329-376.

— et P. Ropartz 1972. Le repertoire comportemental de la genette *Genette genetta* (Linne). *La Terre et la Vie* 4:489-560.

Gauthier-Polters, H. 1962. Beobachtungen an Feneks *(Fennecus zerda* Zimm.).*Zeitschrift fur Tierpsychologie* 19:440-464.

Gier, H.T. 1975. Ecology and behavior of the coyote *(Canis latrans).* Pp. 247-262, *In:* M.W. Fox, (Ed.), *The Wild Canids.* Van Nostrand Reinhold, New York.

Glickman, S.E. and R.W. Sroges. 1966. Curiosity in zoo animals. *Behavior* 26:151-188.

Goethe, F. 1964. Das Verhalten der Musteliden. *Hanbuch der Zoologie* 8, 10 (37),1-80.

Graf, R. and M. Meyer-Holzapfel. 1974. Die Wirkung von Harnmarken auf Artgenossen beim Haushund. *Zeitschrift fur Tierpsychologie* 35:320-332.

Hammerling, F. und W. Lippert 1975. Beobachtungen des Geburts- and Mutter- Kind-Verhaltens beim Mahnenwolf *(Chrysocyon brachyurus)* uber ein Nachtsichtgerat (Infrarot-Beobachtungsanlage) *Der Zoologische Garten* 45:393-415.

Hediger, H. 1949. Saugetier-Territorien und ihre Markierung. *Bijdragen tot de Dierkunde 28:172-184.*

Heimburger, N. 1959. Das Markierungsverhalten einiger Canidan. *Zeitschrift fur Tierpsychologie* 16:104-113.

Henry, J.D. 1977. The use of urine marking in the scavenging behavior of the red fox *(Vulpes vulpes). Behavior* 61:82-106.

Herter, K. und I. Ohm-Kettner 1954. Ueber die Aufzucht und das Verhalten zweier Baummarder *(Martes martes L.). Zeitschrift fur Tierpsychologie* 11:113-137.

Huf. K. 1966. Ueber das Verhalten des Binturong *(Arctictis binturong* Raffl.). *Portugaliae Acta Biologica* 9:249-304.

Johnson, R.P. 1973. Scent marking in Mammals. *Animal Behavior* 21:521-535.

Kellner, R. 1977. Beitrag zur Ethologie des Kleinen Pandas *(Ailurus fulgens,* Culvier, 1825). Dissertation, University of Zurich, 1-122.

Kleiman, D.G. 1966. Scent marking in the Canidae. *Symposia of the Zoological Society of London* 18:167-177.

— 1972. Social behavior of the maned wolf *(Chrysocyon brachyurus)* and bush dog *(Speothos venaticus):* A study in contrast. *Journal of Mammology* 52:791-806.

— 1974. The estrous cycle in the tiger. *World's Cats* 2:60-75.

Kanppe, H. 1964. Zur Funktion des Jacobsonschen Organs (Organon vomeronasale Jacobsoni). *Der Zoologische Garten* 28:188-194.

Krott, P. and G. Krott 1963. Zum Verhalten de Braunbaren (*Ursus arctos* L. 1758) in den Alpen. *Zeitschrift fur Tierpsychologie* 20:160-206.

Kruuk, H. 1972. *The Spotted Hyena.* University of Chicago Press, Chicago.

Leyhausen, P. 1965a. Soziale Organisation und Dischtetoleranz bei Saugetieren. Pg. 142-168, *In:* K. Lorenz, und P. Leyhausen (1968): *Antriebe tiersischen und menschlichen Verhaltens.* Piper, Munchen.

— 1965b. The communal organization of solitary mammals. *Symposia of the Zoological Society of London* 14:249-263.

— 1973. *Verhaltensstudien an Katzen.* 3rd Edition. Parey, Berlin.

McCord, C.M. 1974. Courtship behavior in free-ranging bobcats. *World's Cats* 2:76-89.

Mech, L.D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species.* Natural History Press, Garden City.

Palen. G.F. and G.V. Goddard 1966. Catnip and oestrous behavior in the cat. *Animal Behavior* 14:372-377.

Petersen, M.K. 1976. Behavior of the margay. *World's Cats* 3 (2):39-59.

Poglayen-Neuwall, I. 1962. Beitrage zu einem Ethogramm des Wickelbaren *(Potos flavus* Schrever). *Zeitschrift fur Saugetierkunde* 27:1-44.

— 1966. On the marking behavior of the kinkajou *(Potos flavus* Schreber). *Zoologica* 51:137-141.

— and I. Poglayen-Neuawall 1965. Gefangenschaftsbeobachtungen an Makibaren *(Bassaricyon* Allen, 1876). *Zeitschrift fur Saugetierkunde* 30:321-366.

— and — 1977. Postnatal development of tayras (Carnivora: *Eira barbara* L., 1758). *Zoologische Beitrage* 22:345-405.

Prescott, R. 1971. unpublished talk.

Rasa, O.A.E. 1972. Aspects of social organization in captive dwarf mongoose. *Journal of Mammalogy* 53:181-185.

— 1973. Marking behavior and its social significance in the African dwarf mongoose, *Helogale undulata rufula. Zeitschrift fur Tierpsychologie* 32:293-318.

Rieger, I. 1977. Markierungsverhalten von Streigenhyanen, *Hayaena hyaena* im Zoologischen Garten Zurich. *Zeitschrift fur Saugetierkunde* 42:307-317.

— 1978a. Social behavior of striped hyenas at the Zurich Zoo. *Carnivore* 1 (2):49-60.

— 1978b. Scent marking behavior of ounces. *Uncia uncia. Int. Snow Leopard,* Panthera uncia, *Pedigree Book* 1:77-102.

— in preparation. Sozialverhalten von Irbissen in Zoologischen Garten.

— und D. Walzthony. in press. Markieren Katzen beim Wangenrieben?

Schaller, G.B. 1967. *The Deer and The Tiger — A Study of Wildlife in India.* University of Chicago Press, Chicago.

— 1972. *The Serengeti Lion — A Study of Predator-Prey Relations.* Univeristy of Chicago Press, Chicago.

Schenkel, R. 1966. Zum Problem der Territorialitat und des Markierens bei Saugern — am Beispiel des Schwarzen Nashorns und des Lowens. *Zeitschrift fur Tierpsychologie* 23:592-626.

Schloeth, R. 1956. Zur Psychologie de Begegnung zwischen Tieren. *Behaviour* 10:1-80.

Schneider, K.M. 1926. Ueber Hyanenzucht. *Die Pelztierzucht* 2, (8):1-4, (9):9-11, (10):12-14.

— 1932. Das Flehmen (III. Teil). *Der Zoologische Garten* 5:200-226.

— 1952. Einege Bilder zur Paarung der Fleckenhyanen, *Crocuta crocuta* Erxl. *Der Zoologische Garten* 19:135-149.

Todd, N.B. 1962. Inheritance of the catnip response in domestic cats. *Journal of Heredity* 53:54-56.

Tschanz, B., M. Meyer-Holzapfel und S. Bachman 1970. Das Informationssystem bei Braunbaren. *Zeitschrift fur Tierpsychologie* 27:47-72.

Verberne, G. 1970. Beobachtungen und Versuche uber das Flehmen katzenartiger Raubtiere. *Zeitschrift fur Tierpsychologie* 27:807-827.

— and J. DeBoer 1976. Chemocommunication among Domestic Cats, Mediated by the Olfactory and Vomeronasal Senses. I. Chemocommunication. *Zeitschrift fur Tierpsychologie* 42:86-109.

— and P. Leyhausen 1976. Marking behaviour of some Viverridae and Felidae — Time interval analysis of the marking pattern. *Behaviour* 58-192-253.

Vosseler, J. 1928. Beobachtungen am Fleckenroller *(Nandinia binotata* (Gray)). *Zeitschrift fur Saugetierkunde* 3:80-91.

Wemmer, C. 1971. Scent-marking and anointing: Behavioral parallelism in Mammals. *Text of a Talk to be presented at the 1971 Meeting of the AAAS.*

— 1977. Comparative ethology of the large-spotted genet (*Genetta tigrina)* and some related viverrids. *Smithsonian Contribution in Zoology.* 239:1-93.

— and K. Scow 1977. Communication in the Felidae with Emphasis on Scent Marking and Contact Patterns. Pp. 749-766, *In:* T. Sebeok, (Ed.),: *How Animals Communicate,* Indiana University Press, Bloomington

Zannier, F. 1965. Verhaltensunteruchungen an der Zwergmanguste *Helogale undulata rufual* im Zoologischen Garten Franfurt am Main. *Zeitschrift fur Tierpsychologie* 22:672-695.

Zimen, E. 1972. *Wolfe und Konigspudel — Vergleichende Verhaltensbeobachtungen.* Piper, Munchen.

— 1978. *Der Wolf — Mythos und Verhalten.* Meyster, Wien und Munchen, 333 pp.

Copy of the ERRATA Sheet mailed together with CARNIVORE II (1), including only a few of the corrections from the galley proof

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ERRATA
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Page 17, under title: Reiger to Rieger
Page 17, left, 3rd para., bottom two lines: Parfumiern to Parfuemiern
Page 17, right, 2nd para., line 4: Nasau to Nasua
Page 18, far right under references, line 23: Ewer & Wemm to Ewer & Wemmer 1974
Page 20, far left, 8th line up from bottom: Letailurus to Leptailurus
Page 22, left, 12th line up from bottom: rulgens to fulgens
Page 23, right, 1st para., line 5: association to associated
Page 24, Lit. Cited, last reference: Journal of Mammalogy 52 to 53
Page 25, left, 1st word: Kanppe to Knappe
Page 25, first citation after Rieger: Streigenhyanen to Streifenhyanen