

COMMUNICATION IN THE FELIDAE WITH EMPHASIS ON SCENT MARKING AND CONTACT PATTERNS

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Introduction

It is ironic that students of social behavior and communication have not shown as much interest in cats as the general public has. Fewer than a third of the thirty-six living species of cats have been studied from an ethological standpoint. Because of the scarcity of information, most studies have been of a general nature, and few have been addressed to particular aspects of communicative behavior. Critical, detailed investigation of auditory, visual, and tactile modes of interaction is to our knowledge greatly under-represented. At the time of writing there are only a handful of studies published on olfactory aspects of communication (Fiedler, 1957; Palen and Goddard, 1966; Verberne, 1970). For reviews of cat behavior the reader is referred to Leyhausen's pioneering studies (1956, 1960) and the more recent works of Schaller (1967, 1972). This paper is not intended as such a review, but reports on certain aspects of communication involving contact directed to objects or companions. It is hoped that our statements concerning the ecological determinants and design features of felid communication will stimulate more complete analysis than we can now offer.

Methods

Our studies have taken place at the Chicago Zoological Park (Brookfield Zoo). Unsystematic observations have been made during the past two years on the following species: African lion (*Panthera leo*), Indian tiger (*P. tigris*), leopard (*P. pardus*), jaguar (*P. onca*), snow leopard (*P. uncia*), clouded leopard (*Neofelis nebulosa*), cheetah (*Acinonyx jubatus*), puma (*Puma concolor*), lynx (*Lynx lynx canadensis*), sand cat (*Felix margarita*), wildcat (*F. silvestris*), Pallas' cat (*F. manul*), golden cat (*Profelis temmincki*), leopard cat (*Prionailurus bengalensis*), fishing cat (*P. viverrinus*), margay (*Pardofelis wiedii*), Jaguarundi (*Herpetailurus yagouaroundi*). A focal animal method of observation (Altmann, 1974) has been employed to monitor social interaction in two litters of Pallas cat containing four (one male, three female) and five (one male, four female) young, respectively. Daily observations of varying length (ten to eighty minutes) were made on two litters of leopard cat (two male, two female, respectively) and one litter of sandcats (four male). In these cases we continuously sampled patterns of contact in all animals.

A brief review of felid natural history is necessary to understand the ecological setting to

which the felid mode of communication is adapted.

The Felid Habitus

The felid body plan is progressive, but its uniformity between species is striking when compared with most other families of Carnivores. The small size and forest habitats of most living cats are probably primitive adaptations for utilizing the relatively diverse small vertebrate fauna inhabiting such regions (Kleiman and Eisenberg, 1973). The most economical scheme for exploiting such prey is a system of solitary land tenure. The cat occupies a more or less exclusive hunting ground and probably encounters other community members infrequently. The mother family, the most complex social unit, is but a brief, usually seasonal association. High-intensity vocalization and locus-specific marking with scent are the two predominant methods by which various species space themselves and avoid confrontations (Muckenhirn and Eisenberg, 1973; Schaller, 1967, 1972). In more open habitats movement may be regulated by vision (Leyhausen, 1965a). It is also likely that neighbors recognize one another, and that the "brotherhood" is characterized by a loose social hierarchy in which the territory insures even the lowest-ranking cat of priorities in resources and space (Leyhausen 1965a).

Since nearly all cats can kill prey as large as themselves, hostilities between conspecifics are potentially lethal (Leyhausen, 1960, 1965b; Schenkel, 1968; Schaller, 1972). This fact has been instrumental in evolving a more stereotyped repertory of distance signals on the one hand, and a highly graded repertory of proximal signals on the other. Furthermore, there is a parallel between the dependence on vision and audition in the localization and capture of prey, and the linkage of visual (facial expression) and auditory signals in proximal agonistic interactions.

Secondly, the feline estrous cycle and induced ovulation place several constraints on courtship. During proestrus the female becomes hyperactive and announces her emerging receptivity by rubbing and calling (Rabb, 1959; Michael, 1961). This attracts a number of males, and severe rivalry, which is manifested by a seemingly disproportionate amount of display relative to combat, gives rise to a dominant animal (Ewer, 1973). The female's repulsion of the male diminishes after further repeated intense and often strikingly dramatic transactions. Induced ovulation requires that the female copulate repeatedly, often over a period of days before ova are produced and conception can occur (Ewer, 1973; Schaller, 1972). Often as the sexual motivation of the female waxes, that of the male wanes (Ewer, 1974). Sexual exhaustion of the first male may result in his retirement from further involvement, and another male may then step in. The observation that males are more tolerant of one another than are females may in part be explained by the adaptiveness of nonfatal inter-male competition during these circumstances (Leyhausen, 1965a; Berrie, 1973; Provost et al., 1973). In summary, the usual solitary existence of the mature but sexually inactive cat breaks down when females come into estrus and become highly attractive to males. The proximity of rival males provokes intensive display and fighting. Further agonistic behavior develops between the dominant male and female. In these contexts and in occasional territorial disputes motivational differences between animals are resolved through intense and highly modulated interactions.

Some General Features of Felid Communication

In view of the paucity of information for a variety of species, it is difficult to make generalizations. However, the available information

suggests several parallels and contrasts with other carnivore groups.

There are six calls that are common to the repertoires of most small cats that have been studied and these can be grouped into categories of discrete and graded call types. Some physical properties of these calls are listed in Table 1. All of these vocalizations, with the exception of spitting, vary in intensity, duration, and emission rate. Spitting and hissing share features of broad nontonal energy distribution. Sonographed examples of the two calls can be arranged on a continuum from long, moderate intensity hisses to brief, loud, and explosive sounding spits. However, most examples fall at the extremes of the continuum, and therefore the labeling of two basic calls seems justified. Whether the variants are lumped or split, the call(s) cannot be considered graded because the variation between extremes does not involve qualitative differences. Intermediates exhibit quantitative variation within the same physical parameters.

Graded calls among the small cats display several characteristics. Call transitions often occur without an interruption in the air column. This produces a usually short intermediate segment of sound that shares certain characteristics of the preceding and following calls. This kind of noninterrupted, inter-call gradation has been described for a number of small carnivores (Wemmer, in press) and primates, particularly open-habitat terrestrial forms (Marler, 1965, 1967). The features of this kind of acoustical grading are to be distinguished from the temporally discrete (interrupted) but graded calls of other mammals (e.g., red colobus monkey: Marler, 1970).

A second feature of these graded vocalizations is that gradation often seems to be one-directional. For example, howling (an harmonic call) may arise from growling (a pulsed call) and terminate with a scream (a noisy, high-frequency call) followed by a rapid volley of spitting. Rising

excitation and sound intensity seem to be common concurrent features of such sequences. When growling is resumed it is usually after an interruption in sound production. Extensive sonographic analysis is needed, however, to confirm this observation, for each call type may be considerably modulated in frequency, intensity, and noise level. As Schaller (1972) noted, the repertoire of cats is smaller than it seems because discrete signals are uncommon.

These calls share certain features with the graded vocalizations of terrestrial primates discussed by Marler (1965, 1967). They are addressed to conspecifics at close range and are accompanied by highly varying facial expressions. The potential of such visual-vocal signal systems for communicating fine-grain motivational changes has been discussed by Marler. In cats these signals occur mainly during proximal agonistic interactions, territorial skirmishes, and preambles to copulation. The sounds may broadcast and attract neighboring cats, but this seems to be a secondary or inadvertent side effect. The discrete, high-intensity calls that serve to attract or space neighbors seem to be lacking, or are at most only poorly developed, among the small cats that have been studied. Toms are certainly attracted by the discrete and repeated miao of the estrous domestic cat, but this call cannot be compared on relative grounds with the roaring and sawing calls of the great cats.

This leads us to consider the sensory assortment of the feline signal repertoire. Based on Leyhausen's (1960) studies of the domestic cat, Eisenberg (1973) tabulated twenty-five visual patterns (facial expressions, tail and body postures), sixteen of which occur in combination. There were eight vocal patterns and three olfactory patterns, and to this list can be added about seven contact patterns (body rubbing, clasp, mount, bite, lick, pat, hind leg pump). A similar profile emerges from Schaller's (1972) lion

study; there are at least seventeen visual patterns, thirteen vocalizations (including graded series), seven contact patterns, and five olfactory patterns. On the basis of this cursory examination, vision and audition seem to be the two top-ranking signal modalities, a pattern that agrees with the general impression that cats are essentially sight- and sound-oriented animals.

Scent Marking

Urine, feces, and glandular exudates of the skin are potential carriers of chemical information in nearly all terrestrial mammals. In the Felidae feces seem to lack the widespread communicative significance that they have in the canids, but urine is undoubtedly an important information carrier. The five patterns of object-oriented contact that can be distinguished vary in expression between species and possibly between sexes; interspecific postural differences and variation in sequencing also exist, but detailed studies on these aspects are lacking.

Urination occurs in a squatting or standing position. The latter is nearly a universal male felid trait, but it is also seen in the females of some species (Table 2). It is assumed that retro-ingent urination against upright objects (*Harn-Spritzen* of Leyhausen, 1956; spraying or urine spraying of Schaller, 1967, 1972) has evolved specifically as a scent-marking pattern. The urine is spread over a larger area than if deposited on the ground; it can be sniffed at head level; and according to the diffusion model of Bossert and Wilson (1963), a point source of scent above ground can produce an active space as much as twice as large as a scent source at ground level.

Ewer and Wemmer (1974) have also pointed out that the height of a scent mark can be used to judge the sex of the owner; however, this information might be redundant to sex identifiers in the scent itself. The upheld tail at times touches part of the object to be sprayed, suggest-

ing that it assists in orienting the direction of the spray (Fig. 1a). More often than this, however, the terminal part of the tail undergoes a marked erratic twitching lasting several seconds. The pattern occurs in snow leopard, lynx, leopard cat, and domestic cat, but is apparently absent in the other Pantherinae. While Schaller states that spraying is purely an olfactory pattern in lions, the conspicuous character of this movement in the above-mentioned cats implies it may also have a visual signal function. Alternately it may simply be an autonomic manifestation of urine emission. Schaller (1972) states that in lions one to twenty jets of urine are emitted during the assumption of the characteristic stance and that it travels three to four meters.

Defecation is similar between sexes and species, but its association with other patterns of behavior differs between species. In many small felids (particularly the genus *Felis*) feces are deposited in areas where they can be covered by repeated scratching motions of a forefoot. Larger cats (*Panthera*) make no attempt to cover feces; defecation does not occur in conspicuous areas and is not locus-specific, as it is in many other carnivores. Lindemann (1955) reported that both the European wildcat and the lynx bury their feces at specific localities within their territories, but leave them uncovered on stones and tree stumps in the spaces between territories (*Niemandsländstreifen*). In the lynx these "rendezvous" sites are eagerly sought out during the mating period by all adult conspecifics (Lindemann, 1955).

While anal scent glands occur in most small cats, the burying of feces suggests that anal scent secretion does not take place during defecation, as it does in certain rodents. Adamson (in Schaller, 1967) reported that anal scent was voided during urine spraying in her female lion Elsa, and Schaller (1967) observed that tiger urine deposited by spraying has a strong musky odor compared with urine deposited in a squat-

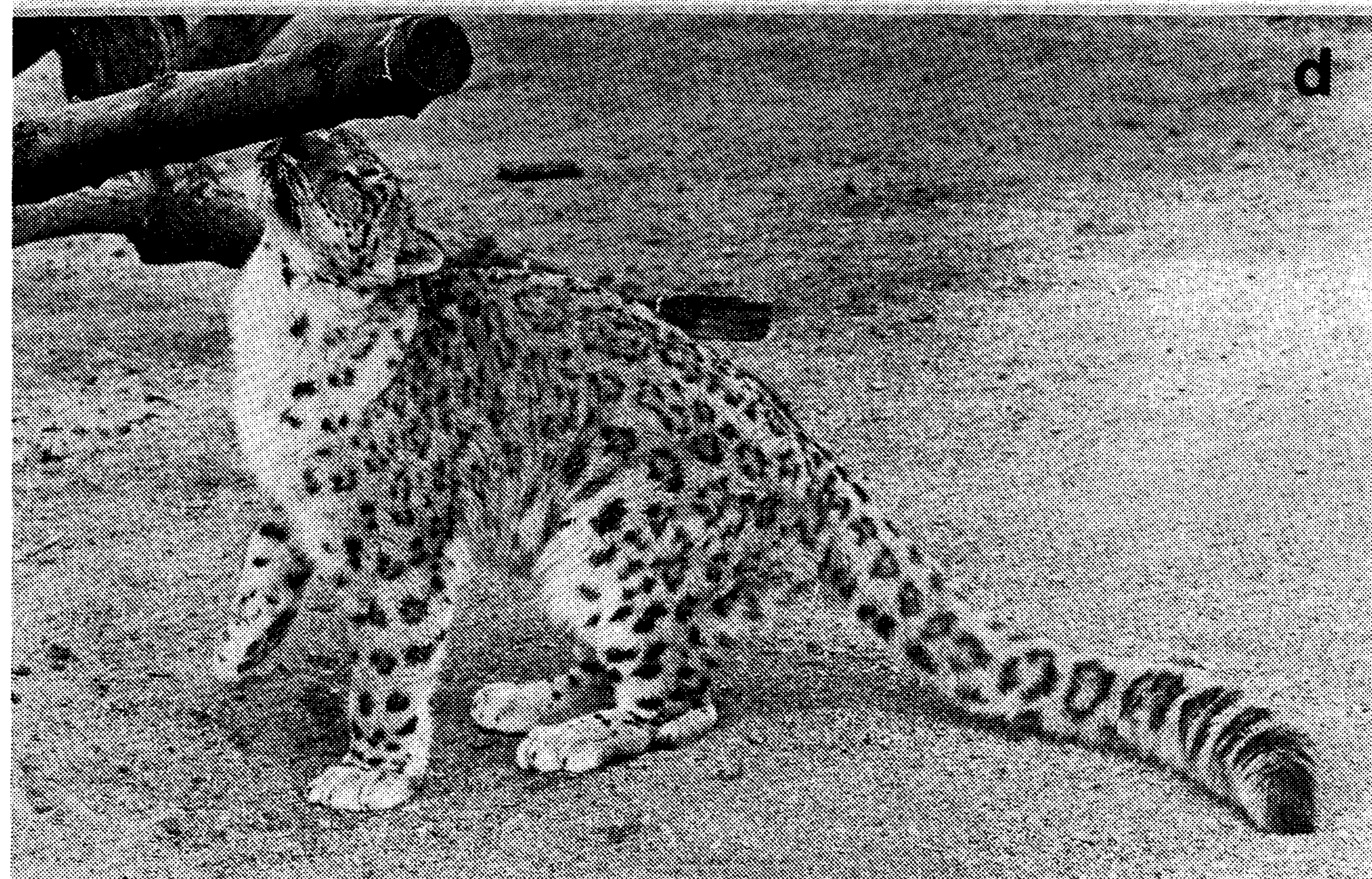
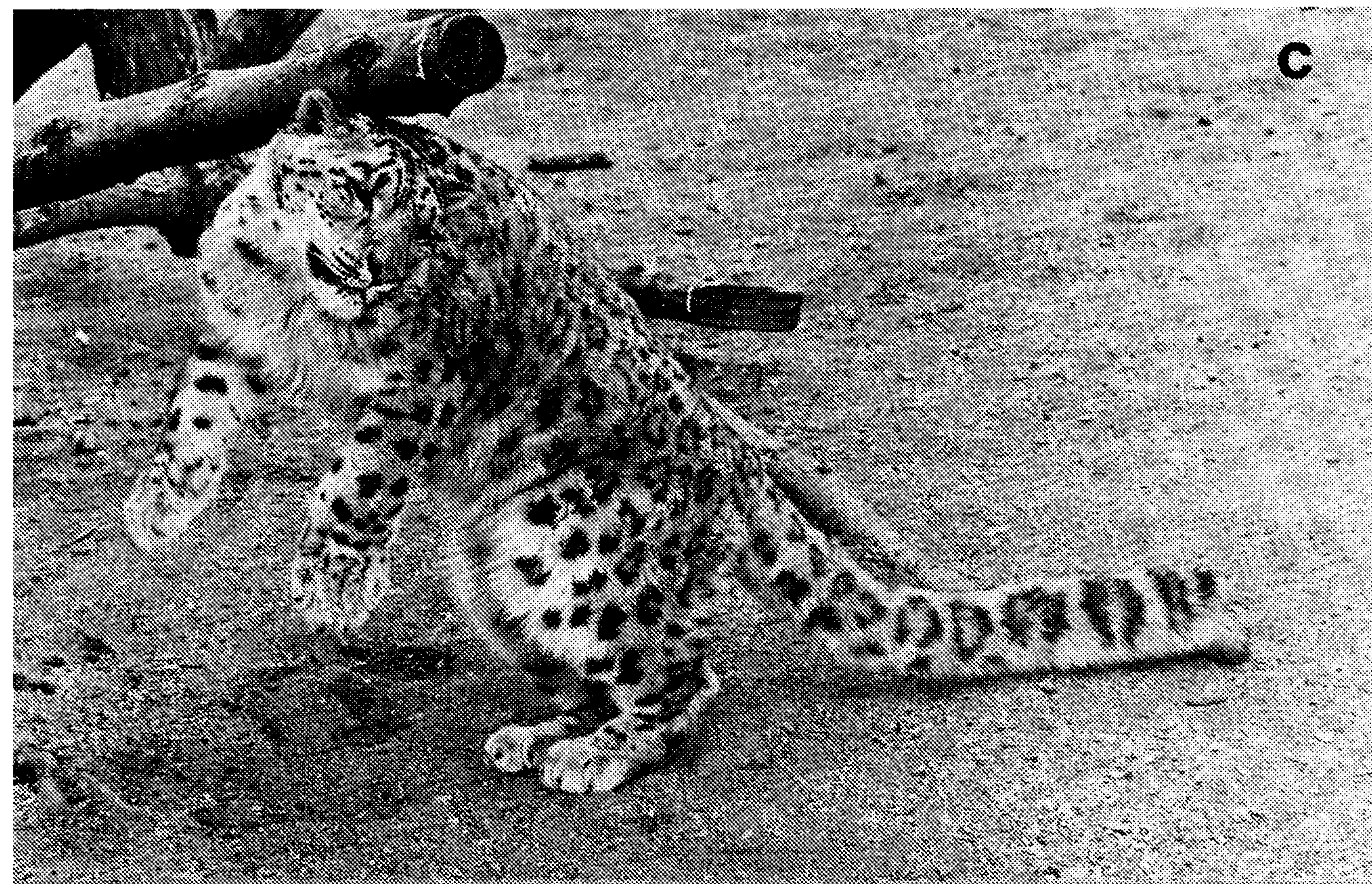
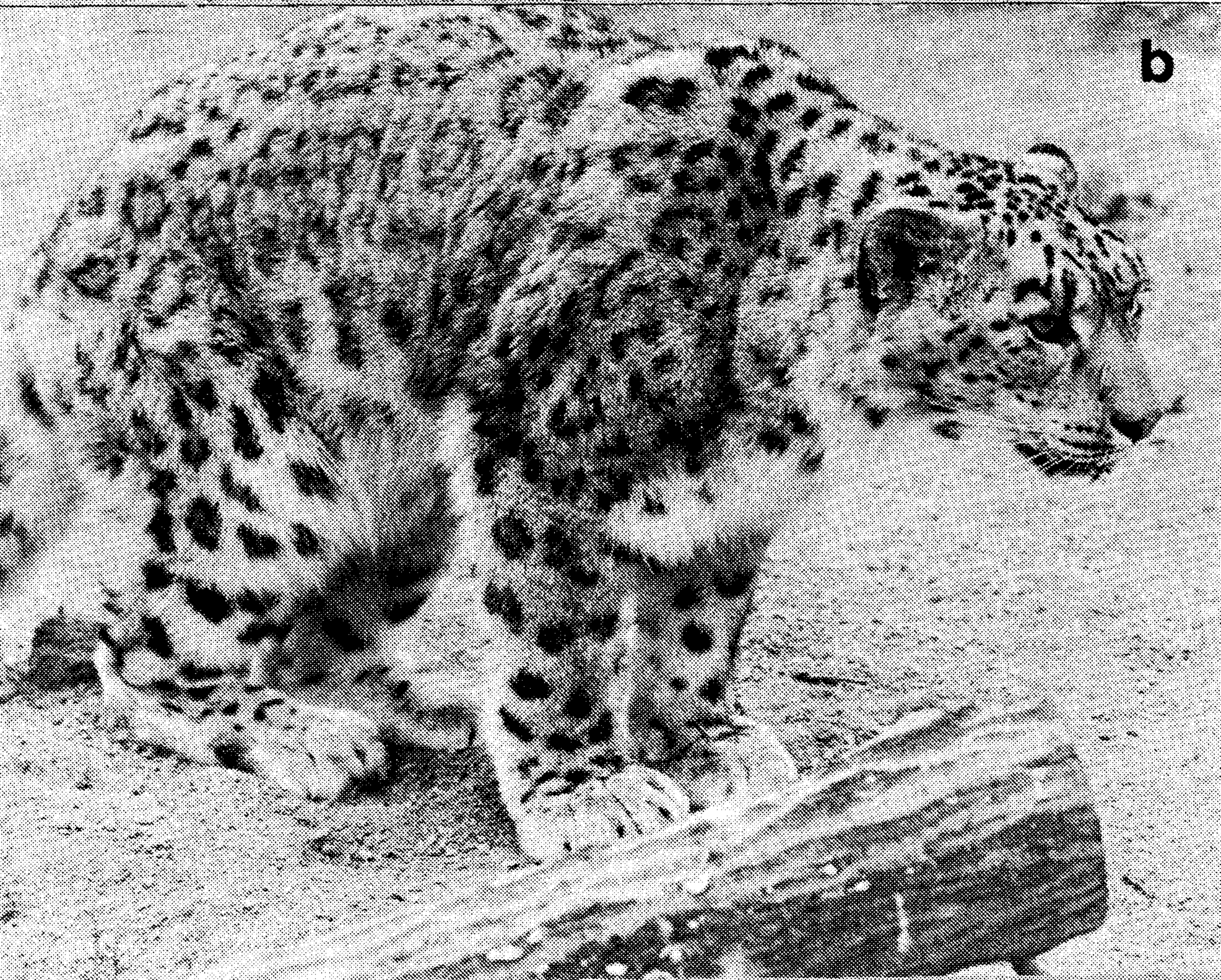


Fig. 1. Scent-marking patterns in a male snow leopard (*Panthera uncia*): a. Urine spraying (notice position of tail). b. Scuffing with the hind feet. c. Sniffing of leg prior to head and neck rubbing. d. Head and neck rubbing. The animal must rise up on its hind legs to touch the elevated branch.

Table 1

Some physical properties of vocalizations
common to members of the genera *Felis*, *Prionailurus*, and *Lynx*.

Vocalization	Harmonic structure	Duration	Relative intensity	Frequency modulation
Hiss	—	Variable but usually brief	Moderate	—
Spit	—	“Fixed”	Moderately loud	—
Purr	—	Variable, but usually long and repeated	Soft	—
Growl	—	Variable, but usually long and repeated	Moderate	+
Miau	+	Variable	Moderately loud	+
Scream	+	Variable	Loud	+

Table 2

Distribution of scent-marking patterns in various *Felidae*.

Species	Urine spraying		Feces	Scuffing (scraping)
	M	F		
African lion (<i>Panthera leo</i>)	+	—	Scattered haphazardly, not buried	+
Tiger (<i>P. tigris</i>)	+	+	Scattered and covered	+
Leopard (<i>P. pardus</i>)	+	—	Occasionally deposited on a scrape made by scuffing	+
Jaguar (<i>P. onca</i>)	+	—		
Puma (<i>Puma concolor</i>)	—	—	Deposited on scrapes	+
Snow leopard (<i>Panthera uncia</i>)	+	—	Scattered, not buried	+
Clouded leopard (<i>Neofelis nebulosa</i>)	+			—
Cheetah (<i>Acinonyx jubatus</i>)	+	—	Occasionally deposited on scrapes	+
Canada lynx (<i>Lynx lynx</i>)	+	+	Localized and covered and uncovered	?
Bobcat (<i>Lynx rufus</i>)	+	—	Localized deposits	?
Fishing cat (<i>Prionailurus viverinna</i>)	+	?	In water ?	—
Leopard cat (<i>P. bengalensis</i>)	+	—	Scattered, buried	—
Margay (<i>Pardofelis wiedii</i>)	+	—	Not buried	+
Golden cat (<i>Profelis temmincki</i>)	+	?	?	?
Jaguarundi (<i>F. yagouaroundi</i>)	+	—	?	+
Pallas cat (<i>F. manul</i>)	+	—	Feces covered	—
Sand cat (<i>F. margarita</i>)	+	—	Feces covered	—
Domestic cat (<i>F. catus</i>)	+	—	Covered	
Wildcat (<i>F. silvestris</i>)	+	—	Locus specific	—

ted posture. He attributed this to a granular white precipitate, but even in captivity where spraying can be viewed at close range it is not possible to witness the emission of the anal scent, and it is possible that the white precipitate seen was actually the glycerides excreted in the urine by the cats.

Scuffing (scraping, treading) with the hind feet is commonly associated with urination (Fig. 1b). The animal squats on its hindquarters with

the entire length of its hind feet touching the ground. Then each foot is alternately thrust backward while the claws are usually extended. Upon completion of this scuffing motion the foot is almost always lifted as it is brought forward. Occasionally one foot may repeat the scuffing motion up to six times before the other foot comes into action (snow leopard). The emphasis of the contact along the length of the foot probably varies between species, as a number of varia-

Table 2 (continued)

Head rubbing	Claw raking	Recumbent head rubbing	Reference
+	+	+	Fiedler (1957), Schaller (1972)
+	+	+	Fiedler (1957), Schaller (1967)
+	+	+	Eisenberg (1970), Fiedler (1957), Muckenhirn and Eisenberg (1973), Schaller (1972)
+	+		Fiedler (1957), Wemmer and Scow (pers. obs.)
+	+	+	Fiedler (1957), Hornocker (1969), Seidensticker et al. (1973)
+	+	+	Hemmer (1968, 1972)
+	+	?	Hemmer (1968)
+	+	+	Eaton (1970)
+	+	+	Wemmer and Scow (pers. obs.), Lindemann (1955)
—	—	?	Provost et al. (1973)
+	+	+	pers. obs.
+	+	+	pers. obs.
+	+	+	M. Peterson (pers. comm.)
+	+		pers. obs.
+	+	+	Ewer (pers. comm.)
+	+	+	pers. obs.
+	+	+	Hemmer (1974), Wemmer and Scow (pers. obs.)
+	+	+	Lindemann (1955)

tions have been described in the Viverridae (Wemmer, in press). The tempo of the movement is moderately fast, but varies somewhat with the size of the species.

It can be seen in Fig. 2 that the variation within an individual is slight and manifests a typical intensity in rate of delivery, but not in bout length. The result of the movement is a characteristic scrape in which loosened soil is heaped at the posterior end. The movement may also scrape bark loose or scratch the surface of horizontal or diagonal logs (jaguarundi). Urination

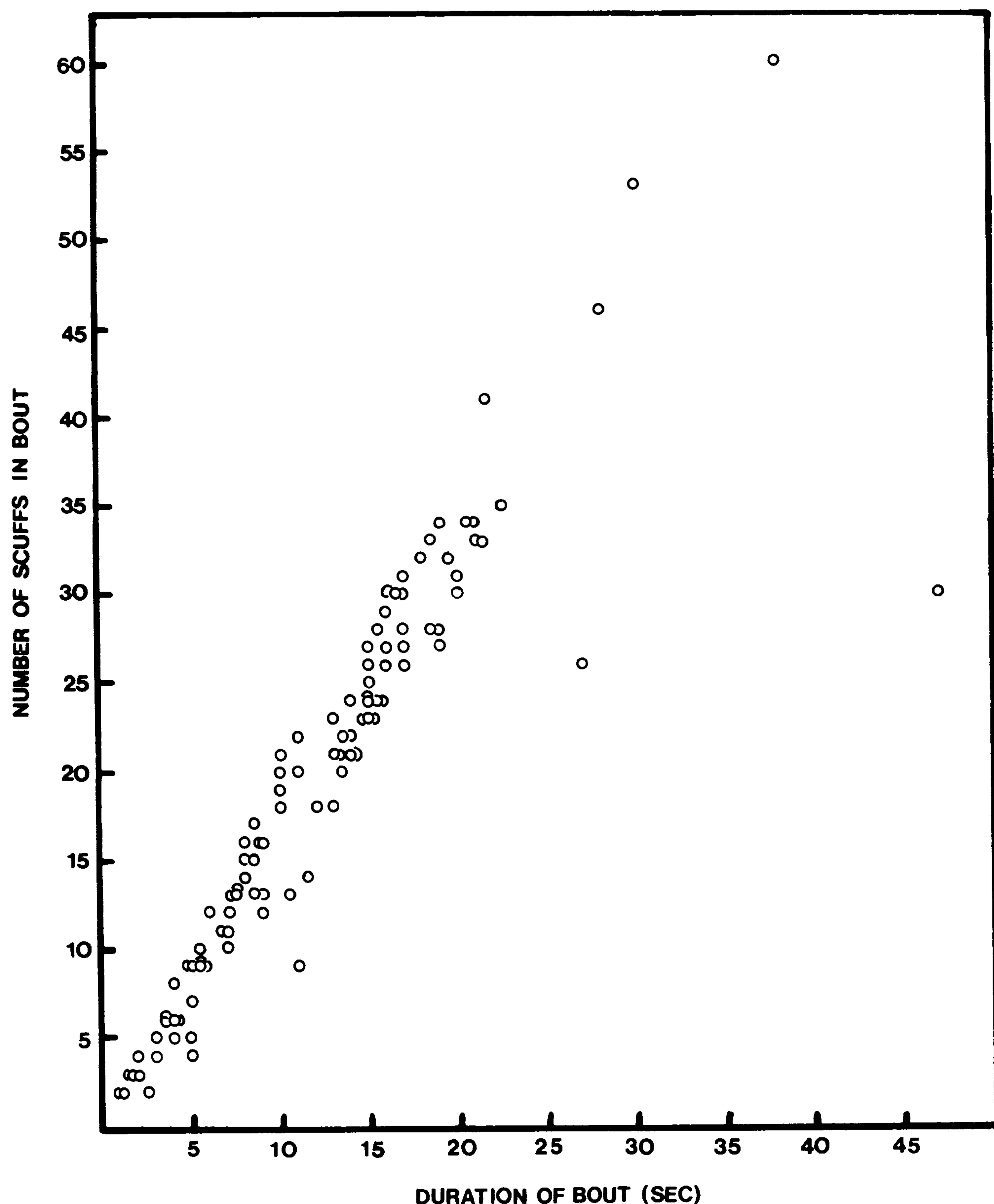


Fig. 2. The relationship between the number of scuffs composing a scuffing bout and the duration of the bout in a male snow leopard (*Panthera uncia*). Bouts varied from 1 to 47 sec and contained 2 to 60 individual leg movements (scuffs).

occurs for brief periods during or near the termination of the scuffing bout or after the movement has stopped. Urination during scuffing may be associated with a slight deceleration or even a brief pause in leg motion. The churning effect of the feet mixes urine into the soil, and distributes it along the length of the foot. The fur on the sides of the feet of captive snow leopards may acquire a yellowish tinge from the activity, but this may result from both unusually high levels of scuffing and its repeated occurrence at one site in captivity. In the African lion the urine often wets the hind legs (Schaller, 1972). Thus it may act as a solvent transferring pedal scent to the substrate.

Seidensticker et. al. (1973), who studied the mountain lion in the Idaho primitive area, found that nearly all the 86 scrapes examined were made by resident adult males, and that the frequency of scraping was highest in the overlap zone between the home ranges of two radio-tracked males. From one to six scrapes were found within a small area at each site; they were usually placed near but not on animal trails, and only 11 of the 86 sites were revisited. Feces or urine was detected at 17 of the sites, usually on the soil and needles heaped up by the scraping action. Whether scrapes are made with the fore- or hind feet is not known. The authors in this study concluded that scrapes demark the home ranges of adult males by indicating that the area is occupied.

Schaffer (1940) described glands in the feet of the domestic cat, but the extent and type of glandular development in the feet of other species is not known. Scrapes made by tigers are also defecated upon if only in small amounts; these scrapes are more evident and perhaps more commonly performed during the monsoon, while the feces persist longer than the scrape during the dry season (Schaller, 1967).

Head rubbing is associated with several postural variants and is almost always preceded by

sniffing (Fig. 1c, d) or licking and biting of the focal object, and by flehmen. Most commonly the face is rubbed as the animal stands beside a branch or rock at head level. The contact phase is often one-directional; it occurs as the body leans toward the object with the cheek or neck serving as the point of contact. Forward movement of the body is achieved by a combination of neck extension, walking, and leaning forward. Upon breaking contact the cat may assume a different position in relation to the object or may repeat the movement from the same starting point. The head, cheeks, and neck may also be turned and rotated as the animal stands still, sometimes securing the branch with the claws of a forefoot. A similar style is employed by a sitting cat. If the branch is elevated the cat will grasp it with one or both forefeet while standing upright on the hind legs. Rubbing and sniffing very often lead shortly to salivation. A clear watery saliva appears on the closed lips and is wiped onto the object and the cheeks and neck. A vigorous bout of rubbing virtually soaks these areas.

The cheeks and neck are also rubbed against novel or odoriferous substances on the ground. Here the cat reclines with the object between the forefeet. After the object is sniffed and licked, the sides of the head and neck are pressed against it and extended. The movement often alternates with sniffing, or licking and flehmen, and there is a tendency for the same side of the head to be used several times before switching to the opposite side. For example, the sequence of actions in an adult male snow leopard in response to an unknown scent in the soil was: sniff, right, right, left, sniff, left, pause (22 sec) sniff, right, sniff and lick, right, right, left, lick, left, stand. This recumbent rubbing, which is also characterized by salivation, may lead to rolling and writhing on the sides and back. There are two basic differences between recumbent head rubbing and the other versions. The former is clearly evoked by strong novel odors such as car-

rion, vomit, the feces of strange animals, and catmint. The latter pattern, which is part of the daily routine, characteristically occurs against objects that are also sprayed with urine.

Depending on the position of the tree trunk, claw raking is performed in an upright or a horizontal position. The cat generally grips the trunk with extended forelegs and depressed body, and the claws are then drawn backward simultaneously or alternately in strokes of variable length and speed. The motion often has a jerky quality that results from the intermittent snagging of the claws and raking. The action serves to remove loose claw sheaths but also leaves a visual and possibly an olfactory trace having social significance to other cats.

The occurrence of these patterns in different felid species is presented in Table 2, but there have been few studies on the temporal organization of scent-marking behavior. Urine spraying occurs by itself and in association with other patterns. Eisenberg (1970) reported that in the Ceylon leopard scraping (scuffing) and urine spraying occurred near the sloping trunks of trees in which clawing with fore- and hind feet (scuffing?) and cheek rubbing took place. In the snow leopard, cheek rubbing, scuffing, and spraying are often associated acts (Fig. 3); sniffing preceded cheek rubbing, scuffing, and spraying in a decreasing proportion of cases, while urine spraying and cheek rubbing were the most common and second most common terminal acts. In Pallas cats clawing and urine spraying are coupled together, and Schaller (1972) reports that head rubbing may precede spraying by male Serengeti lions, particularly at spraying sites used by other males.

Table 3 compares some attributes of the six different scent-marking patterns. Urine spraying is distinctive in being a one-directional marking pattern, which by itself does nothing to modify the sender's body odor. Clawing involves forelimb contact, but it is doubtful that much of the

Table 3

A comparison between characteristics of scent-marking and anointing patterns common to the Felidae.

Pattern	Material deposited	Substrate disturbance	Anointing material	Habitual site usage	Possible information potential
Urine spray	Urine	None	None	Yes	Individual identity, sexual identity and condition.
Head and neck rubbing	Saliva, skin exudates	None	Saliva, glandular exudates	Yes	Individual identity.
Scuffing	Urine, feces, skin exudates	Considerable	Urine	Yes	Individual identity, sexual identity and condition.
Clawing	Skin exudates	Considerable	None	Yes	Individual identity.
Recumbent head and neck rubbing	Saliva, skin exudates	Minimal	Carrion, feces, vomit, catmint	No	Individual identity, sexual identity and condition.
Rolling	Skin exudates	Minimal	Carrion, feces, vomit, catmint	No	?

cat's personal odor is imparted to the substrate. Like scuffing, however, the behavior may considerably modify the substrate, and it is likely that the odors emanating from the lacerated bark and scraped soil modify and present a "disturbance" to the olfactory landscape. This substrate modification probably creates a detectable secondary cue that intensifies perceptibility of the signal's location.

Cheek rubbing and scuffing, associated with urination, however, transfer body secretions (saliva and urine) to other body regions, namely, the head, cheeks, neck, shoulders, chest, and hind feet. These parts of the body are also targets of companion-oriented contact, a problem to be considered in the following pages. Recumbent rubbing and rolling, on the other hand, clearly differ from the above patterns in being directed to decomposing animal matter. They differ from each other in the extent to which the body is covered with the foreign scent, but it is important to remember that these behaviors may occur in tandem. In any case, an overriding result of either act is that the cat's body odor is

radically changed, and any trace of the animal's scent left at the site must be slight compared with the intensity of the foreign scent source.

In passing, mention should be made of motivation and function. The difficulty in understanding these aspects of felid scent marking is that marking is often not characteristically linked to other motivationally distinctive (aggressive, sexual, or fearful) behavior. Recumbent head rubbing and rolling is an exception. Todd (in Palen and Goddard, 1966) studied this pattern in domestic cats as a response to catmint; he showed that as a specific response to this plant its expression is controlled by a single allele, and he regarded it as a sexual display.

Palen and Goddard revealed that as a reaction to refined catmint (trans-cis-nepetalactone) rubbing and rolling were independent of sex and gonadal state. The occurrence of the pattern in the estrus female and as a reaction to this chemical led them to conclude that both conditions increase skin sensitivity on the head. Thus, the occurrence of catmint-evoked rubbing and rolling is noncyclical in both sexes, while in the

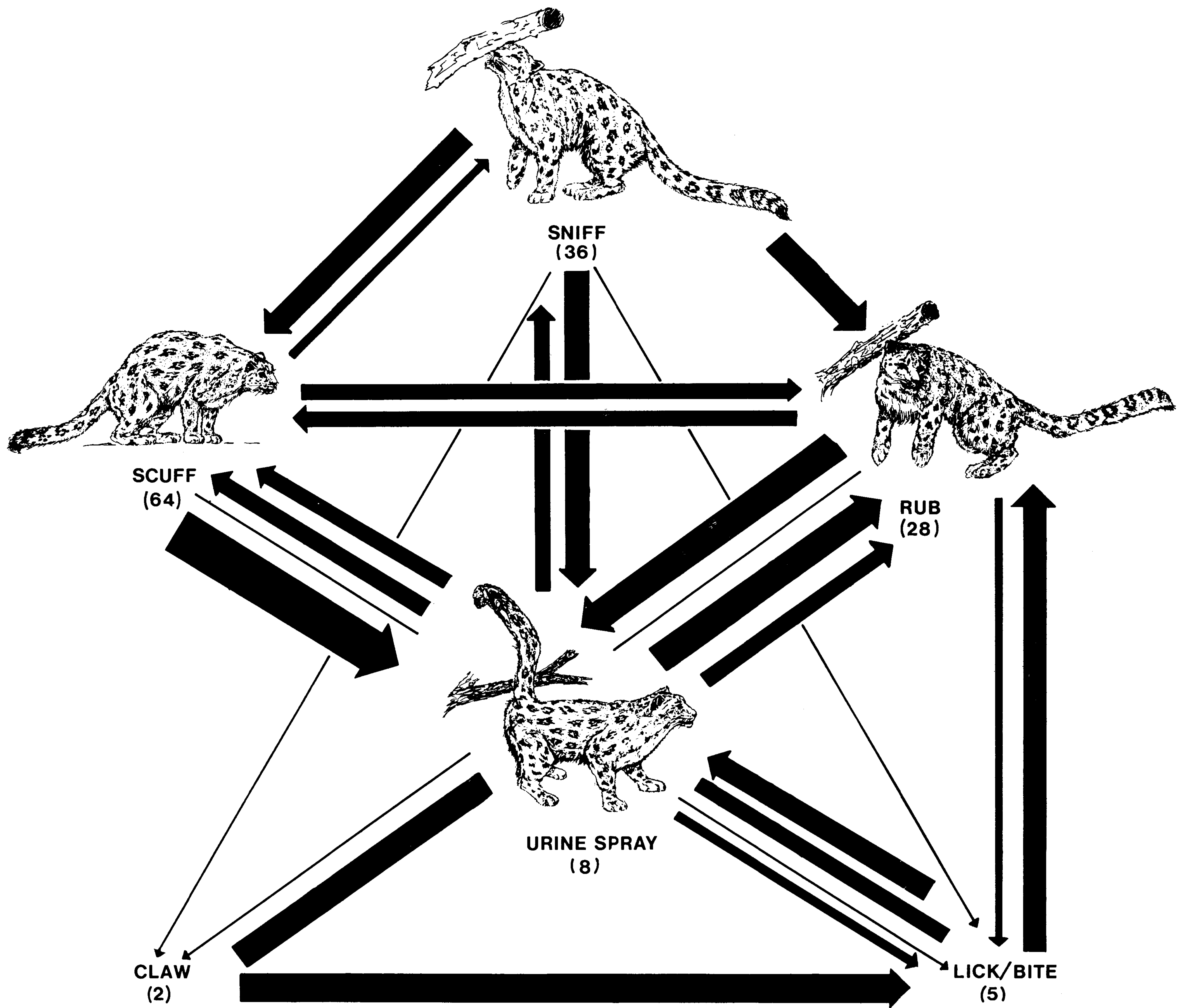


Fig. 3. Sequencing of scent-marking patterns in a male snow leopard (*Panthera uncia*). The thickness of the arrows is proportional to the percentage of transi-

tions from one pattern to another. For example the scuff-to-urine-spray arrow represents 66% of all transitions originating with scuff.

female spontaneous rubbing and rolling cycles with the estrous period. If the pattern evolved as an olfactory signal the male would be expected to sniff sites where the female has rubbed.

Palen and Goddard did not investigate the pattern from a zoosemiotic standpoint; however, Michael (1961) reported that the male watches

the proestrous female during this activity and attempts to mount her. The female's orgasmic postcoital rolling frequently provokes forelimb sparring with the male. Therefore the display appears to be visual rather than olfactory; when sniffing and licking occur in the sexual context they are directed to the female's head and neck,

and the vulva. Possibly the orientation to the anterior body areas is reinforced by heightened rubbing during proestrus.

Less is known concerning the other patterns. Leyhausen (1965a) remarked that while territory marking is often interpreted as having a warning function in solitary mammals, there is no indication that a cat is intimidated upon sniffing a companion's scent mark. The receiver's response is neither overt nor immediate, and probably depends on the identity of the owner and its relationship to the receiver. The owner of a fresh mark might be aggressively sought by a dominant male receiver, while the mark left by an estrous female might arouse sexual interest in the same animal. The assumption here that remains to be tested is that cats can identify individuals and sexual condition by olfactory traces in urine and skin secretion. Other hypotheses also require testing. When head rubbing follows urine spraying, is some additional information incorporated at the site? It is possible that different sequence-linked patterns simply overlap in message content and serve as cross-referencing or redundancy function (Birdwhistell, 1970)?

Companion-Oriented Contact

Contact between animals takes many forms, and probably not all of them are communicative. At one extreme there are the fleeting, infrequent, and seemingly inadvertent contacts that result from proximity due to a common concern or activity. An example is the crowding and bumping of bodies that accompany the flight of a family group into a burrow. Sender and receiver are difficult to delineate, and the points of contact often vary without a predominating pattern. Most contact, however, is clearly intentional, of variable duration, and specifically oriented to a part of the companion's body. It may be a single brief, one-directional act, but if

several points of contact exist between two or more animals, the bodies are usually aligned in characteristic configurations. The configurations restrict the range of targets selected for contact (Wemmer and Fleming, 1974). In the following pages the distributions of four contact patterns (rubbing, sniffing, biting, and patting with the forepaw) to the body targets of siblings are compared among the leopard cat, sand cat, and Pallas cat.

Body rubbing between siblings and between siblings and adults was infrequently seen in the leopard cats ($N=7$) and sand cats ($N=14$). However, 187 incidents of rubbing were recorded in the Pallas cats. In all three species the pattern resembles the body rubbing of domestic cats. The initiator presses the side of the head and neck or the torso against the companion's body. The position of the recipient's body (standing, sitting, lying) to an extent determines the area that is rubbed. Several juxtapositions are possible, but for simplicity we can consider four basic situations ranked in decreasing order of occurrence: body to body (79%), body to head-neck (8.5%), head-neck to head-neck (6.4%), and head-neck to body (5.3%). The body-to-body category is clearly divisible into two groupings. Kittens pressed their sides against the sitting or standing mother's breast and lower throat region on 81 occasions (43%), while the remaining body-to-body rubbing for the most part occurred between siblings and consisted of one cat's rubbing its side against the other's.

Of the remaining three patterns, sniffing was exhibited least often (Fig. 4). Though it is difficult to assess the relative importance of companion-oriented sniffing in different species, it is our impression that it is not as prevalent in these small cats as it is in other carnivores. For example, in meerkats observed under similar conditions the overall sniffing rate was 7.9/hr (data from Wemmer and Fleming, 1974). In the leopard cats the rate was 2.3/hr and in the Pallas cats

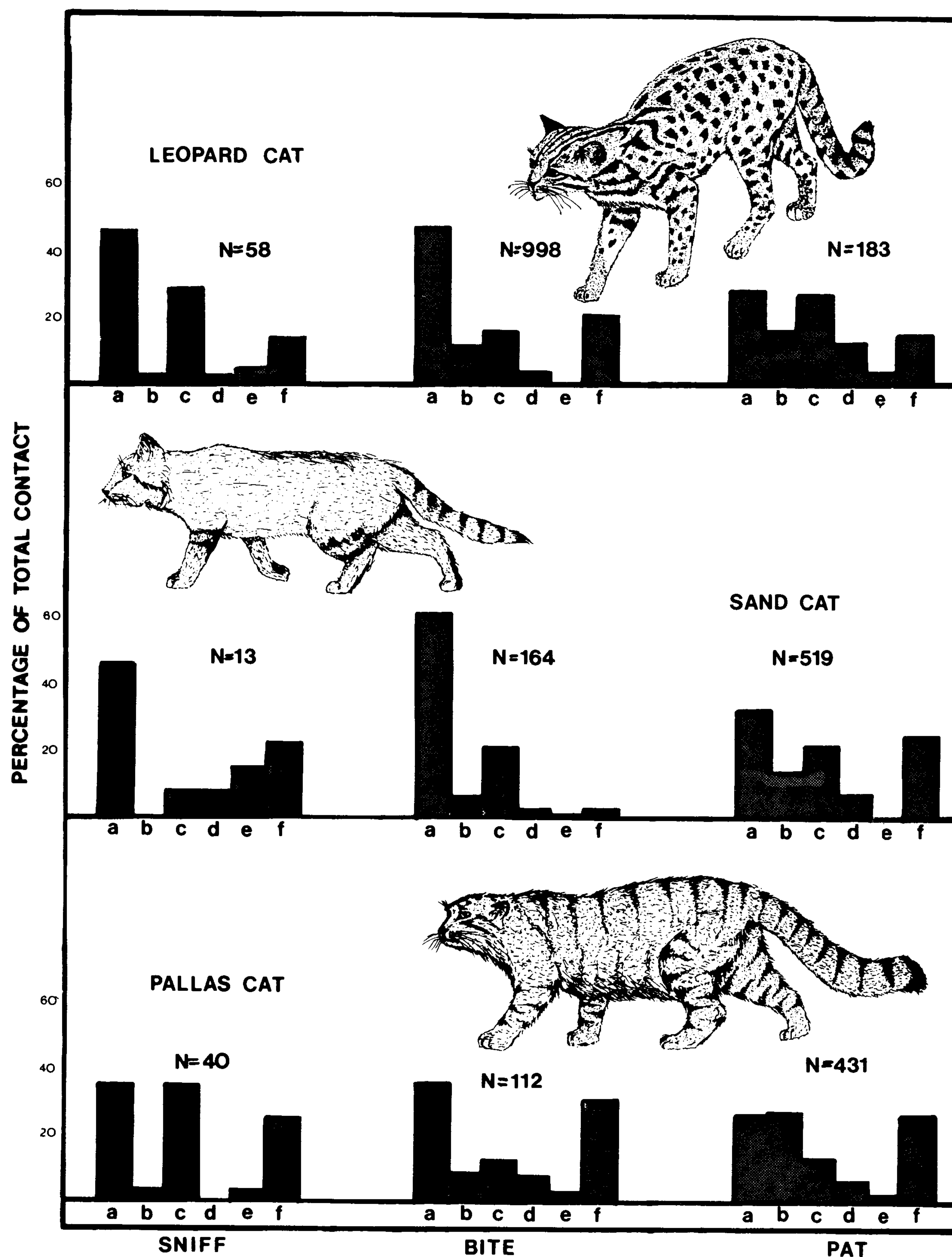


Fig. 4. The percentage distribution of sniffing, biting, and patting to general body areas of siblings in the leopard cat, sand cat, and Pallas cat. a = head-

neck, b = forelimbs (including feet), c = torso, d = hind limbs (including feet), e = ano-genital region, f = tail.

2.1/hr (data for sand cats are not in comparable form).

In all three species the head-neck and tail rank high among the general body areas sniffed (Fig. 4); however, there are differences among species. In the leopard cats and sand cats the head-neck was the area most often sniffed, while this area and the torso received equal attention in the Pallas cats. The torso was highly sniffed in

the leopard cats and least sniffed in the sand cats, but the sample size for the latter species was small. In all species the ano-genital region was infrequently checked, which is in marked contrast to other species of carnivores, particularly canids and viverrids (Ewer, 1973; Wemmer, in press; Wemmer and Fleming, 1974). Michael (1961) has observed in fact that the ano-genital region of anestrus domestic cats has a repelling

effect when sniffed by sexually mature males. When the histograms for these three species are compared statistically a significant positive correlation is found for the leopard cats and Pallas cats ($r_s = .940$, $P < .05$, Spearman rank correlation coefficient). Unfortunately, the small number of sand cat observations are inadequate for statistical treatment.

In all three species the head-neck is the most frequent biting target, with the torso ranking second and third in importance (Fig. 4). Pallas and leopard cats differ from the sand cat in that the tail is the second most common biting target. All other areas (limbs and ano-genital region) receive a relatively small portion of bites compared with these three areas. The ranked distribution of biting in the Pallas and leopard cats are identical, and a correlation of .829 ($P = .05$) was found between the sand cats and leopard cats, and sand cats and Pallas cats. When specific areas of the torso are considered there is no general agreement in biting (Fig. 5). Only in the sand cat did one body area receive more than 27% of all bites. In the leopard cat the rump was the favored target, and in the Pallas cat the side and belly. In all three species chest and haunches were always low-ranking targets. In comparison with the general picture no specific target predominates the torso (Fig. 5). Between species tests of specific head-neck and body targets (Fig. 5) produce relatively high correlations, but only Pallas cat and sand cat exhibit a statistically significant correlation at $P = .01$.

Fig. 4 shows that patting in the three species is directed mainly to the forebody, infrequently to the hind legs and ano-genital region, but more often to the tail. Ear, cheek, and neck stand out among the specific head-neck targets, while back and side predominate in the torso (Fig. 5). There are no significant correlations among head regions of the three species; however, values for leopard cats and Pallas cats, and leopard cats and sand cats were significantly correlated ($P > .01$, $> .05$, respectively).

Discussion

Scent transfer between cat and environment is mediated through elimination patterns and body contact with inanimate objects. Not all parts of the body are used in scent marking through contact. For example, the head and neck are employed in two distinct patterns by all the species reviewed, while scuffing seems to be restricted at least to the Pantherinae and cheetah, but is probably absent in the genus *Felis* (Table 2). The zone of contact between body and object has properties similar in some ways to a mechanical joint or an articular facet (I. Golani, pers. comm.). The relationship between the object and other, more distal body parts can vary considerably, but movement at the joint is more restricted. Contact between animals can be regarded in a similar way. The body has certain focal points for contact, and indeed it can be visualized as a field of valences; the shape or "relief" of the field may differ for different types of contact (sniffing, biting, or licking). The distribution of valences (or the form of the relief) is probably determined on the one hand by topographical features such as the location of sense organs and glandular areas, and on the other by characteristics of body movement and orientation to one another.

Recumbent head and neck rubbing in the felids has analogs of varying similarity in certain members of all but one family of the Carnivora, including three species of civet (Viverridae: Wemmer, in press; Ewer and Wemmer, 1974), the spotted hyena (Kruuk, 1972), various dogs (Fox, 1971), the polar bear, and the tayra (a member of the Mustelidae, pers. obs.). The specific use of the head and neck in these patterns suggests the hypothesis that the additional scent may enhance the attractiveness of those regions for certain types of contact received from companions. In all three cat species the head-neck region was the predominant sniffing target, though the tail also received considerable atten-

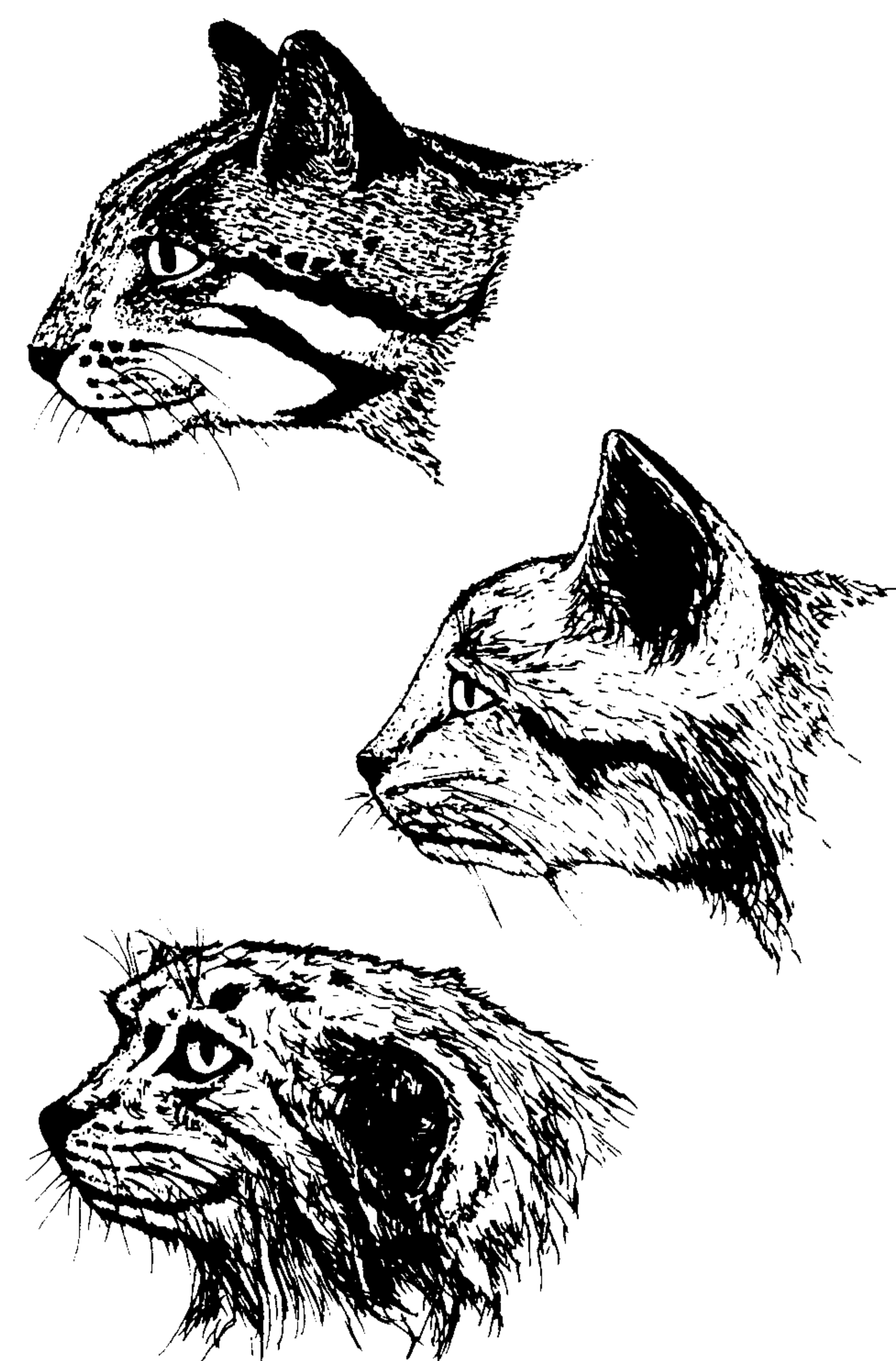
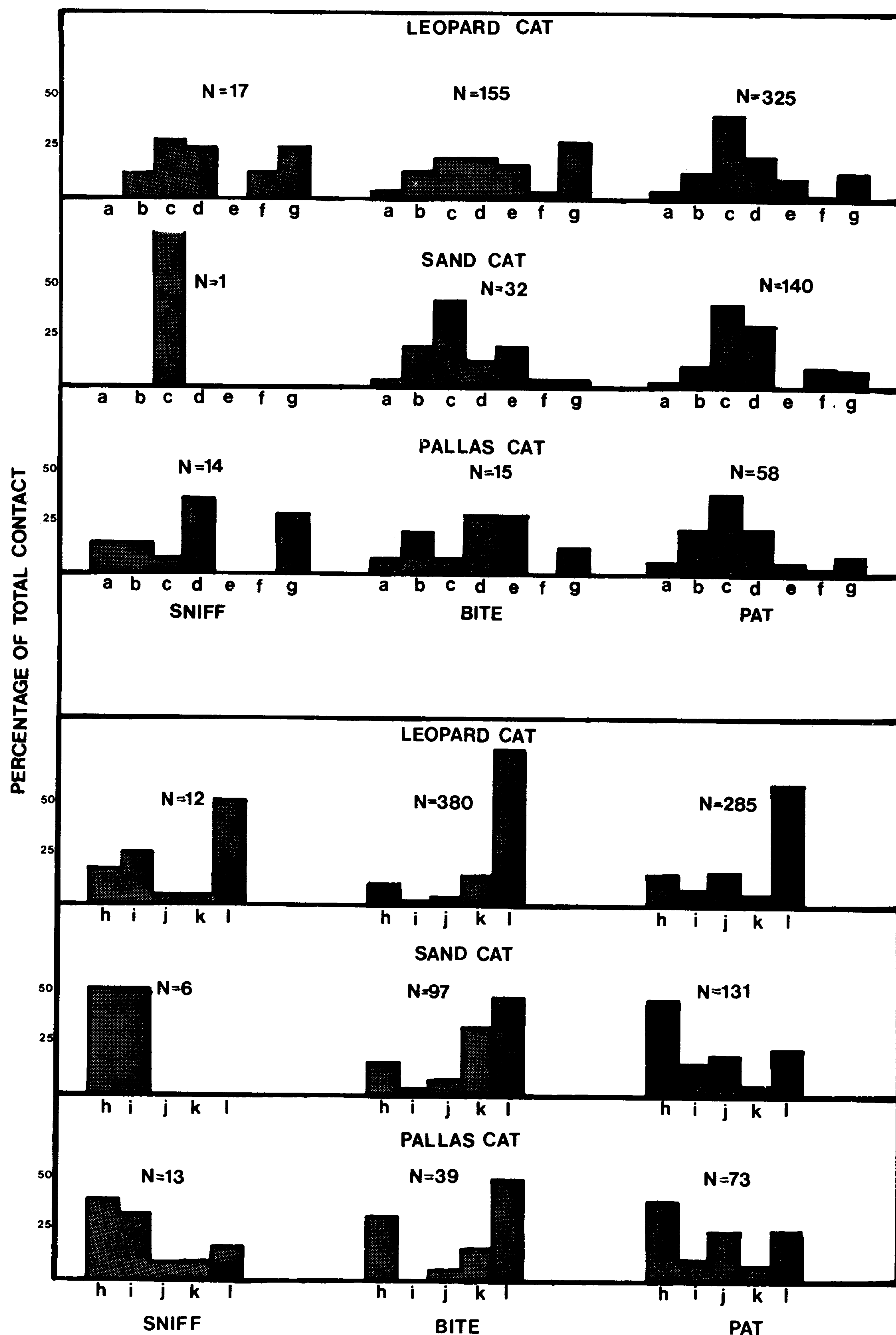


Fig. 5. The percentage distribution of sniffing, biting, and patting to specific regions of the torso (upper three lines) and to specific head regions (lower

three lines). a = chest, b = shoulder, c = back, d = side, e = belly, f = haunch, g = rump, h = ear, i = nose, j = cheek, k = throat, l = neck.

tion. The head-neck zone also received most of the bites, as well as a substantial proportion of pats from the forelimbs. The data do not make a compelling defense for the hypothesis. Furthermore, anointing is only occasionally seen even in captive situations, and rubbing, which

was frequently observed only in the Pallas cats, involved the head-neck zone but minimally (about 20%). In other words, support the hypothesis gains from the sniffing data is weakened by the biting and patting data.

Other species show similar trends whether

head and neck anointing is in their repertory or not. The African civet frequently and vigorously anoints the cheeks and neck with a variety of substances, including its food; up to 80% of all snaps and bites are directed to this contrastingly marked region, which is also presented to the biting animal. However, the same area receives less than 40% of all sniffing (Ewer and Wemmer, 1974; Wemmer, in press). In the genet, a viverrid carnivore in which anointing is weakly developed and neck presentation is absent, these areas receive about 70% of the bites and about 25% of the sniffing (Wemmer, in press). Head and neck rubbing is absent in the meerkat (a social-living mongoose), but these areas receive about 40% and 35% of all bites and sniffs (Wemmer and Fleming, 1974). In most of the examples the head is the most common sniffing target and the head and neck the prevailing biting target. The anterior location of the sense organs undoubtedly determines the predominance of these regions during contact, but skin secretions and possibly strange scents may provide olfactory information. This is supported by the observation that the ear is the most commonly sniffed part of the head in the Pallas cats and sand cats (Fig. 5). Schaffer (in Kleiman and Eisenberg, 1973) reports that the auditory meatus in cats is glandular, but his observations are based on the domestic cat, and interspecific differences are likely to exist.

The anal glands of the domestic cat and the sand cat are voided during traumatic experiences, and the scent has a pungent, unpleasant odor. There is no indication that the glands are used in scent marking, either alone or in combination with urine spraying. The anal region is glandular in many mammals, and in some species it is highly attractive to conspecifics (Fox, 1971). There are two situations in which cats are attentive to the ano-genital region. Mothers sniff and lick this region in their infants and ingest the milk feces, and males respond in a similar way to

the vulva of proestrous and estrous females. On the whole, however, cats are not particularly oriented to this part of the body.

Small felids dispatch their prey with a fatal bite to the nape of the neck; the orientation to the neck constriction is innate, but the precise orientation to the nape of the neck and the necessary pressure for a lethal bite must be learned through experience with live prey (Leyhausen, 1960, 1965b). The young cats of all three species directed their bites to the neck more often than to other parts, a situation that implies that this innate orientation is also operant in sibling interactions. However, the Pallas cats directed most bites to the throat, while the other two species oriented more strongly to the nape (Fig. 5). Differences in neck structure undoubtedly contribute to this behavioral contrast. The Pallas cat is a relatively short-necked species, and the condition is particularly pronounced in the kittens. The throat is probably more vulnerable than the nape, but postural differences during interaction probably also play a role.

There are other similarities and contrasts among species and patterns for which explanations are not apparent. The contact mapping method provides a refined description for a category of behavior that often receives little attention, but the general picture of contact we have presented is the sum of occurrences from various contexts and postural configurations during early development. Contact is also integrated with other concurrent communicative activities. No doubt a better understanding of target selection will be gained by relating mode and target of contact to these variables.

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Since the writing of this article, three important articles have appeared on the topic of felid olfactory communication that should be consulted by interested readers.