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COMPARATIVE ETHOLOGY OF THE LARGE-SPOTTED GENET, *GENETTA TIGRINA*, AND RELATED VIVERRID GENERA

by

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I. INTRODUCTION

The niche of the small semi-arboreal, solitary, and nocturnal insectivore-carnivore is occupied by the genus *Genetta* over most of Africa and southwest Europe. The dozen or so species comprising the genus are structurally coherent, exploit nearly all natural and cultivated habitats, and in many areas are a numerically dominant small carnivore. This success may be considered exceptional, for *Genetta* like *Didelphis* and *Tupaiia* is believed to be a relatively unmodified derivative of an ancestral form (GREGORY and HELLMAN 1939, COLBERT 1955). However, the view that the viverrines are the most structurally conservative viverrids is founded on the premise that tribosphenic molars, attenuated body form, and relatively unrestricted rotatory ability of manus and pes constitute features of the ancestral morphotype (GREGORY and HELLMAN 1939, COLBERT 1955, ROMER 1945). Since both fossil viverrines, such as the Oligocene and Miocene genera *Paleoprionodon* and *Stenoplesictis* and extant civets such as *Prionodon*, *Viverricula*, *Poiana*, and *Genetta* more or less share these features, the subfamily Viverrinae is considered to be the most central and basal viverrid group (WINGE 1941, THENIUS and HOFER 1960, GREGORY and HELLMAN 1939, COLBERT 1955, ROMER 1945). Whether, however, the lineage of the more terrestrial civets (*Viverricula*, *Viverra*, *Civettictis*) or the semi-arboreal civets (*Poiana*, *Genetta*, *Prionodon*) represents the least altered derivative of the common ancestor is equivocal, for the fossil record is inadequate. What little is known about *Poiana richardsoni*, however, suggests that a semi-arboreal habitus may more closely approximate the ancestral viverrine condition.

Besides displaying more cranial resemblance to Paleoprionodon than other extant genera (R. H. TEDFORD pers. comm.), Poiana is purported to build leafy arboreal nests (WALKER 1968), a trait interpretable as primitive by comparative carnivore standards. Furthermore, BOOTH (1954) has interpreted Poiana and other West African species with disparate distributions to be stabilized forest forms which reached an evolutionary climax before the appearance of the Dahomey Gap. Genetta's capacity for radiation and dispersal into woodland and savanna is a progressive feature which presumably emerged early in Genetta's lineage.

In the following sections, the genet should be regarded as a morphologically conservative and generalized solitary predator but not as a model antecedent of more specialized contemporary viverrids; rather, the genus displays a complex of morphological and behavioral characteristics some of which are considered to be fundamental to the evolution of more advanced or specialized forms. With this perspective in mind, the study attempts (1) to establish qualitative and quantitative behavioral characteristics, and to outline the principle features of the communication system of a population of captive genets, and (2) to compare certain behaviors of selected viverrids and interpret the results in light of known taxonomic affinities.

A. Intra-viverrid affinities

Because modern taxonomy strives to achieve evolutionary classification by delimiting taxa on the basis of common ancestry and subsequent divergence (MAYR 1968), behavioral evolution must ultimately rely upon morphologically founded appraisals of systematic position. Though behavioral criteria are often useful in elucidating relationship (LORENZ 1953, LAWRENCE and NOVICK 1963, McKINNEY 1965), their role in clarifying the affinities of higher taxa (families, orders) is minor. Unfortunately, the Viverridae have received so little attention that it is questionable whether the existing systematic schemes serve the practical needs of a sound classification. As many genera are rare or confined to remote tropical regions, this inadequacy is in part a result of a paucity of preserved specimens. In addition, a number of genera and perhaps one subfamily exhibit character mosaics which defy the simple construction of a scheme of filial relationship. While the pretense of a solution could be made by referring only to the most recent synopsis of families (ANDERSON and JONES 1967), the real problematical status of several genera dealt with herein would go overlooked.

Though a large number of viverrid species was available to me for comparative study, it became increasingly apparent during the course of the work, as it has to others (DÜCKER 1971, EWER pers. comm.), that the mongooses (Herpestinae) exhibit a more uniform and distinctive level of behavioral organization than the other viverrids. Similar observations were made by POCOCK (1916b) and GREGORY and HELLMAN (1939) who advised elevation of the mongooses to familial status on the basis of their uniformity in foot, dental, and glandular characteristics. This suggestion was endorsed by WURSTER and BENIRSCHKE (1968) who found that eight species and seven genera of mongooses examined karyotypically "... are all nearly identical to one another and, without exception, ... bear no satellited marker chromosome"(p. 374). In addition, EWER (in press) has noted that all four known herpestine genera have horizontal oval pupils, and states that this structure may be characteristic of the Herpestinae as a whole. A vertical slit pupil is found in all the other known viverrids with the exception of Paradoxurus whose pupil is a horizontal slit (WALLS, in EWER, in press) (Table 1). Lastly, RADINSKY (1971) has shown that in 25 of the 36 living genera representing all subfamilies, Cryptoprocta, the herpestines and the galidiines all possess a well developed cruciate sulcus, while the structure is small or absent in viverrines, paradoxurines, and hemigalines.

The existence of the Madagascan Galidiinae accounts for some of the difficulty of delineating the mongooses (Herpestinae) from the bulk of the viverrids. Cranially and in gross body form the subfamily shows strong linkage with the herpestines, but unlike the latter they possess the carnivore satellite chromosome (Table 1). CARLSSON (1910), who showed that Galidia elegans shares 14 anatomical features with the other Malagasy civets (including Cryptoprocta and Eupleres), 10 with the mongooses, and 7 with the viverrines, concluded that relegation of the Galidiinae to either the viverrids or herpestids would conceal its obscure affinities as a stem form that differentiated prior to the evolution of either the

Table 1. Comparisons of Some Major Features between Viverrid Subfamilies and "Problem" Species. [- = absence within the taxon; + = presence within the taxon, but not necessarily universal; ± = present in some members of the taxon (used when no character alternatives are listed).]

	Characteristics	Viverrinae	*Prionodon*	*Nandinia*	Paradoxurinae	*Fossa*	Hemigalinae	Galidiinae	Herpestinae	Cryptoproctinae
Skin glands	Perineal pouch	+	-	-	+	-	+	+	-	-
	Preputial pouch	-	-	+	+	-	-	-	-	-
	Anal gland	+	-	-	-	-	-	-	-	-
	Anal pouch	-	-	-	-	-	-	-	+	+
Feet	Plantigrade	-	-	+	+	-	+	+	+	+
	Sub-digitigrade	+	+	-	-	-	+	+	+	+
	Digitigrade	+	+	-	-	+	+	-	+	-
	Digit reduction	-	-	-	-	-	-	-	+	-
	Retractile claws	±	+	+	±	-	±	-	-	+
Teeth	Sectorial	+	+	-	-	+	+	+	+	+
	Tuberculate	+	-	+	+	-	-	-	+	-
	Molar reduction	+	+	-	-	-	-	-	-	+
Food habits	Carnivorous	+	+	+	+	+	+	+	+	+
	Omnivorous	+	-	+	+	+	+	+	+	-
	Piscivorous	+	-	-	-	-	-	-	+	-
	Insectivorous	+	+	-	+	+	+	+	+	-
	Myrmecophagic	-	-	-	-	-	+?	-	-	-
Coloration	Spotted	+	+	+	+	+	-	-	-	-
	Striped	-	-	-	+	-	-	+	-	-
	Banded	-	-	-	-	-	+	-	+	-
	Uniform	+	-	-	+	-	-	+	+	+
Misc. features	Marker chromosome	+	+	+	+	+	+	+	-	+
	Vertical pupil	+	+	+	±	+	+?	+?	-	+
Distribution	Africa	+	-	+	-	-	-	-	+	-
	Madagascar	-	-		-	+	-	+	-	+
	Asia	+	+	-	+	-	+		+	-
	Europe	+	-	-		-	-	-	+	-

herpestine or viverrine grade of organization. GREGORY and HELLMAN's decision to place the galidiines within the Viverridae is in keeping with their implicit belief that rate of evolution in viverrids (particularly viverrines) has been much slower than in herpestids.

Though the fossa (Cryptoprocta ferox) of Madagascar is distinctive at the subfamilial level, it too displays features of conflicting affinity. While POCOCK (1916a) gave the fossa familial status, GREGORY and HELLMAN, who placed it as a subfamily within the Felidae, believed it to be an excellent structural link between the primitive Viverrinae and the Felidae. This opinion was predicated on skeletal similarities. While its auditory region and dentition resemble the viverrines and felids respectively, its possession of an anal pouch (and the absence of the perineal gland) was seized upon by MIVART to ally this species with the mongooses (GREGORY and HELLMAN). Karyotypically, however, the fossa has more in common with the paradoxurines, hemigalines, and galidiines (WURSTER and BENIRSCHKE 1968). Without interpreting the fossa's affinity, it is clear that it is an early viverrid survivor displaying convergent or possibly archaic incipient felid features.

The African palm civet, Nandinia binotata, resembles the paradoxurines in both its gross body form and in its skull. On the basis of its more trenchant carnassials and cartilaginous auditory bulla, however, GREGORY and HELLMAN surmised that this civet branched off from the paradoxurine stem prior to frugivorous specialization. The existence of the subossified or cartilaginous entotympanic bone of the auditory bulla is generally regarded as a secondarily derived feature rather than a vestige of a miacid ancestry. The extraordinary nature of this structure and a preputial scent gland prompted POCOCK (1915b) to separate Nandinia as a family. Ironically, the species resembles the viverrines strongly in its possession of a sub-telocentric marker and a small acrocentric Y chromosome (WURSTER and BENIRSCHKE 1968).

The affinity of Asian linsangs (Prionodon) to the viverrines resembles that of Nandinia to the paradoxurines. While sharing features of body form with Genetta and karyotype with the viverrines in general, Prionodon lacks the metatarsal pads, the perineal gland, and the second upper molar. The differences were interpreted by POCOCK (1915a) as specializations justifying a distinct subfamilial status. GREGORY and HELLMAN relegate the linsang to a viverrine tribe (Prionodontini).

The fanaloka (Fossa fossa) in its possession of vestigial metatarsal pads and a genet-like hair pattern is superficially somewhat viverrine; karylogically and cranially it is distinctly hemigaline, while in gross body form it is remarkably fox-like. It is probably an early Asian hemigaline waif to Madagascar which has convergently acquired a fox-like habitus.

B. Behavioral classification and description

Ethological studies have classically relied upon both functional and motivational criteria in categorizing the activities constituting a species' behavioral repertoire. Many behavior patterns, however, can be relegated to several categories, others can be accommodated by none, and new criteria are invoked in order to categorize special cases (e.g., displacement activities). To design an objective systematic scheme with mutually exclusive categories is both difficult and over-reductionistic, because in most animals a large number of biological roles must be served by a number of movement patterns restricted by the mechanical and physiological properties of the species' body structure. As much as functional and motivational considerations may enhance a descriptive work an unequivocal understanding of these factors requires both experimental validation and a knowledge of the species in its natural realm. As these labors exceed the requirements of accurate description, it certainly seems more pragmatic and objective to systematize patterns of behavior on observable and measurable characteristics of form, rather than on deductive abstractions. Nevertheless, to discard the use of functional terms would be dogmatic and straining a point which should at best reflect a frame of mind. It will be noticed that though some new terms are used for descriptive categories, implicitly and explicitly functional terms, such as grooming, scent-marking, and play, are retained within the descriptions.

Behavioral description has for the most part been an empirical process; the events ethologists recognize and interpret as true behavioral units (action patterns) are assumed to represent functionally meaningful acts unabstracted by our own conceptual processes. At least in mammals, however, the question can be raised whether the discrete phasic properties of action continua accurately represent all the meaningful idmensions of animal conduct. Symposium titles such as "The search for natural units of behavior"* convey the distinct impression that (1) recognized behavioral units may be abstractions rather than true or complete representations of natural phenomena, (2) the types of units currently used have limited analytical utility, and (3) the elucidation of "natural units" will hopefully permit more insight into the meaning of animal behavior. With the exception of locomotion, which received early and exacting description by virtue of historical and esthetic interest (MUYBRIDGE 1957), most forms of mammalian behavior have not received the analytical descriptions exemplified by the BAERENDS' (1950) cichlid work or DANE et al (1959) and McKINNEY's (1961) studies on duck behavior. In essence, there have been no critical attempts to establish either indices of variability or typical intensity (MORRIS 1957) of mammalian displays (LE BOEUF and PETERSON 1969, being one exception).

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* A lecture presented by S. A. ALTMANN at a symposium titled "Analytic Problems in the Study of Animal Behavior." 67th Annual Meeting of the A.A.A.S. (1970).

The Eshkol-Wachmann Movement Notation Method (GOLANI 1969), which permits fine-grain temporal and spatial resolution of behavior, has remained an unexploited descriptive tool. By achieving rigorously objective description, the method provides a valuable alternative to the interpretive methods that have prevailed up to now, but from the standpoint of comparative ethology it requires very much time. Useful descriptions can be achieved more expediently. Not infrequently, however, descriptions are made in such general terms that they have limited utility. It is often necessary to know the postural and locomotory details as well as the basic mechanics of a motor pattern in order to appraise it comparatively. For this reason, photography is often as necessary for the analysis and description of body motion as sonograms are for the description of sound.

The classification used in this study is a phenetic one; patterns are lumped together on the basis of overall similarity in form. At the expense of reorganizing the conventional scheme of the ethogram, this system largely overcomes functional and motivational pigeonholing. For example, the patterns usually ascribed to the maintenance (or grooming) behavior category are herewith subdivided into classes of self- and object-oriented contact patterns. The latter category also includes behaviors which are otherwise classed as comfort movements (e.g., body rubbing) and scent-marking. As MAYR (1968) has remarked, no classification is absolute because the structuring of character sets always involves a subjective element. The present system clearly is not criteria-consistent. Although the orientation of the animal's body parts to one another and to the environment is a primary consideration, certain behaviors (e.g., vocalization) do not fit the scheme. The utility of the system, however, lies in bringing to attention certain elemental similarities in behavioral form.

C. Behavior in restricted environments: Some findings and assumptions.

As this study deals with the behavior of captive animals, it is imperative that its assumptions be outlined. That the captive condition precludes a realistic understanding of social structure and behavioral function is based on the belief that restricted environments cause abnormal behavior and prevent an awareness of the ecological setting to which the species' behavioral syndromes are adapted. There is little doubt that natural and captive environments and the conduct of the animals inhabiting them differ, but to assume that animal investigations in natural settings guarantee comprehension of the species' adaptation is unrealistic.

Environmental complexity and space are the primary dimensions in which the wild and captive condition differ, and the distinctions in behavior manifested under these two conditions are mainly of a quantitative rather than a qualitative nature (KUMMER and KURT 1965, ROWELL 1967). In the restricted environment, activity rhythms persist much as they do in nature, but relatively fewer activities occupy more time. Because of this, the resulting behavioral repertoires of confined animals often appear to be abnormal (MEYER-HOLZAPFEL 1968). However, the repetitive nature of captive activity probably reflects a fundamental compulsion to modify environmental variables, even if the animal's spatial relationship within the enclosure be the only tangible variable to work with (KAVANAU 1967). Hence, a relative stereotypy of the temporal structuring of daily activities is a characteristic common to animals living with or without spatial constraints (KAVANAU and RISCHER 1968, KAVANAU 1970). The various ways that animals modify their conduct in order to control the captive environment have been outlined by MORRIS (1964).

Modes of social interaction in captivity vary from bizarre, as in the case of animals reared under socially deprived or extraordinary conditions (INHELDER 1955, LANG 1958, HEDIGER 1950), to first order approximations of natural social affinities (KUMMER and KURT 1965, EISENBERG 1965, EISENBERG and GOULD 1969). In captivity as a whole it appears that the same range of behavior and presumptive communicatory patterns is used as in the wild, but intensity and frequency of interaction is elevated and types of interactions are distributed differently (ROWELL 1967). Though the corresponden of schedules, sequences, and time budgets for certain activities remains to be demonstrated for field and captivity, the qualitative expression of most behavior probably falls near the mode for the individuals comprising the species. Furthermore, the captive condition permits description and experimentation of social behavior in mammals whose solitary and/or nocturnal habits make such investigations in the field neither feasible nor practical even with the use of advanced electronic techniques. Thus, though ecological factors must largely remain obscure in captive studies, the nature of social interactions and affinities often reflect basic social tendencies. Lastly, it is important to remember that though we label our study topics with a symbol for an abstract concept, the biological species, the results, regardless of setting, encompass at most only individuals or populations.

II. MATERIALS AND METHODS

Table 2 presents personal history information concerning the 12 genets on which the results of this study are based. Nine of these animals were born in the Small Mammal House at the National Zoological Park, Washington, D.C. The origin of the parental pair remains unknown. However, comparison of skins and skulls of the previous offspring of this pair with specimens at the U. S. National Museum reveal a similarity to Genetta tigrina stuhlmanni, a subspecies inhabiting northwestern Tanzania (COETZEE in press). In addition, one male Genetta rubiginosa (= G. t. rubiginosa) from the vicinity of Bangui, Central African Republic, was obtained as a hand-reared specimen from Mrs. C. DOSCHER.

Kittens were always taken from their mother on the birth day or the day after and were confined to a box containing a heating pad and a blanket until able to move about by themselves. The first three hand-reared genets had unrestricted freedom in our home; subsequent animals were confined to one room for most of the day. The diet consisted of warm Esbilac (Bordens Company) mixed with water at recommended proportions and fed from a graduated (240 cc) nursing bottle designed for puppies (Evenflo Company). On two occasions this diet resulted in repeated vomiting that was remedied by changing to cow's milk mixed with egg yolk. Weaning was initiated by feeding raw morsels of meat from the nursing bottle nipple. Infants were triggered to urinate and defecate by massaging the perineum with a moist paper towel.

Table 2. Caging History of the Study Animals (*Genetta tigrina*).

Sex	Subject and date of birth	Cage locations, cagemates, periods of confinement, and dimensions in meters			
		University of Maryland		National Zoo	
♂	Parent Prior to 1966			♀P	Duration of study
♀	Parent Prior to 1966			♂P	Duration of study
♂	Kitzi 22-IV-1967	C,I	XI/1967-VI/1970 1.37 x 2.43 x 2.43	C	IX/1970-VI/1971 1.90 x 1.90 x 2.03
♀	Clawdina 22-VII-1967	K,I	XI/1967-VI/1970 1.37 x 2.43 x 2.43	K	IX/1970-VI/1971 1.90 x 1.90 x 2.03
♀	Ivy 22-VII-1967	C,K	XI/1967-VI/1970 1.37 x 2.43 x 2.43	Fe	IX/1970-VI/1971 1.90 x 1.90 x 2.03
♀	Monika 1-II-1968	Ma --	VIII/1968-XII/1968 1.37 x 2.43 x 2.43 XII/1968-VI/1970 1.47 x 2.43 x 2.43	--	IX/1970-VI/1971 .91 x .91 x 1.21
♂	Marvin[1] 1-V-1968	Mo	VIII/1968-XII/1968 1.37 x 2.43 x 2.43		
♂	Oscar 24-IV-1969	--	X/1969-VI/1970 1.37 x 2.43 x 2.43	E	IX/1970-VI/1971 1.90 x 1.90 x 2.03
♀	Elsie 14-V-1970			O	IX/1970-VI/1971 1.90 x 1.90 x 2.03
♀	Froda 5-VIII-1970			--	IX/1970-VI/1971 .71 x 1.21 x 1.21
♂	Felix[2] ?-I-1970	--	VII/1969-VI/1970 1.21 x 1.21 x 2.43	I	IX/1970-VI/1971 1.90 x 1.90 x 2.03

[1] Died during anesthesia in January, 1969.

[2] Wild born near Bangui, Central African Republic.

At weaning or some time later, the hand-reared genets were transferred to a laboratory at the University of Maryland. As the windows were open most of the year, the animals to some extent experienced local temperatures and humidity, except during thunder showers, cold spells, and winter when the windows were closed and the room maintained at about 13-19° C (55-60° F). During the summer when temperatures reached 20° C (80° F), an electric fan facilitated air circulation.

Cages of various size were used (Table 2; Figure 1a, b). All cages were provided with one or more elevated nest boxes, vertical, horizontal and diagonal branches of various diameters, and one or two pans containing corn-cob litter (Sanicel) which served as sites for urination and defecation. Diet consisted of chunk horsemeat and a vitamin additive (Pervinal, Thayer Laboratories) obtained from the National Zoological Park, supplemented with rats and mice, and occasionally hens' eggs, chicken embryos, chicks, and frogs. In the spring of 1970, all animals in my care were moved to the Division of Scientific Research at the National Zoological Park (Table 2), and maintenance was thereafter under the supervision of Mr. GENE MALINIAK.

Individuals of the following viverrid species were also studied: a pair of *Civettictis civetta* (African civet), two ♂♂ and a ♀ *Nandinia binotata* (African palm civet), a pair of *Paradoxurus hermaphroditus* (Asian palm civet), a ♂ *Paguma larvata* (Formosan masked civet), a pair of *Arctictis binturong* (binturong), a ♂ and two ♀♀ *Hemigalus hartwicki* (banded palm civet), two pairs of *Fossa fossa* (fanaloka), three ♀♀ *Galidia elegans* (Malagasy ring-tailed

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Figure 1. Genet Cages Used at the University of Maryland.

(a) A cage for single animals (.71 x 1.21 x 1.21 m),

(b) a large cage for 2 or 3 animals (1.37 x 2.43 x 2.43 m).

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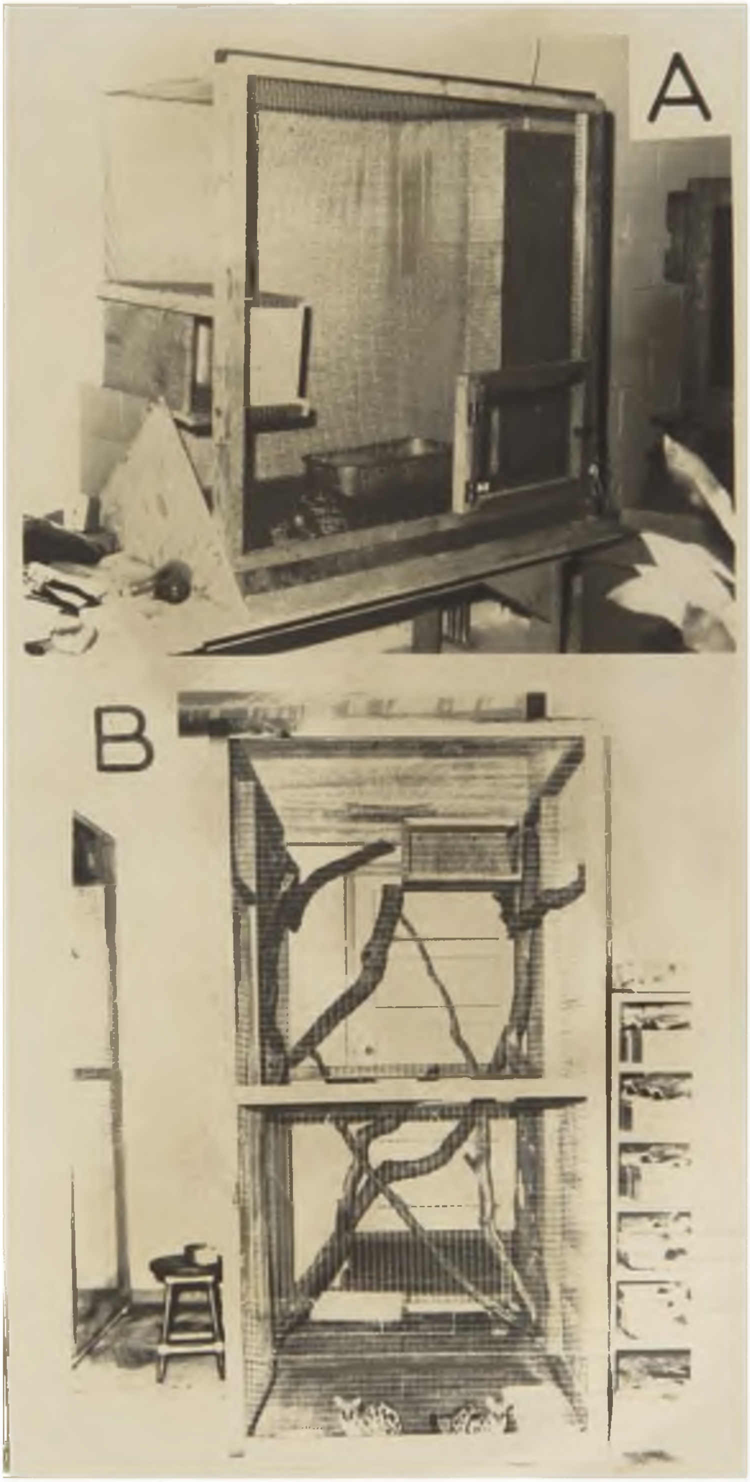

mongoose), and a ♂ Cryptoprocta ferox (fossa). Animals were observed in the National Zoo's Small Mammal House sporadically in the evenings of 1967 and 1968, regularly during the early morning in June, July, and August of 1968, and sporadically in the afternoon (at feeding time) from 1968 to 1971. I was also able to personally maintain several of these animals for closer observation. A ♂ Nandinia procured in 1967 from Kinshasa at about the age of 6 weeks was kept at home and later at the University of Maryland until 1970. An adult ♀ Nandinia was also held at the University from 1968 to 1970, as was the Paguma. In addition, a ♂ Fossa born in 1969 was hand-reared at home from the day of birth, and then held at the University until 1970. The ♂ Civettictis, obtained as a young adult in 1969 was also held for a year at the University and then transferred to the National Zoo when the young ♀ was received. (These animals were descendents of stock from Sierra Leone, MALLINSON 1969.) In addition to the standard meat diet, Civettictis, Nandinia, and Paguma in my care were fed fruits, such as melon, strawberries, apples, pears, oranges, grapes, and bananas.

Data for behavioral description were recorded in writing, on magnetic recording tape, on moving charts, and on still and ciné film. The equipment used included a Uher tape recorder (4000 Report-L) and microphone (Model M-514), an Esterline Angus Operations Recorder, Praktica and Pentacon 35 mm SLR cameras, a Pentacon 6 cm^2 SLR camera, and Bolex P-4 8 mm and H-16 Rex Reflex ciné cameras. Drawings were made from tracings of film projected on a Cabin Hilldem 8 mm viewer and an LW photo-optical Data Analyzer (Model

224-A). Drawings and descriptions are based in part upon selections from 443.9 m (1400 ft.) or 16 mm and 243.9 m (800 ft.) of 8 mm ciné film. Sound spectrograms of taped recordings were made using a Kay Electronic (Model 6061 A) Sonograph (85-8000 cps spectrum analyzer) and a Kay Electronic Missile Data-Reduction Spectrograph.

Further details of method are described under specific chapter headings.

III. NATURAL HISTORY OF THE GENUS GENETTA

The separation of the genus Genetta into three subgenera is based upon characters of the skull, teeth, and foot pads. The majority of species are placed within the subgenus Genetta and these are distinguished by the patterning of spots, spinal stripes and tail rings (in addition to cranial and dental criteria). Forest species are on the whole darker in color and have more spots than savanna forms (MATSCHIE 1902). Genetta victoriae appears to be a somewhat aberrant species tending towards large size and terrestriality. Its coloration shows considerable resemblance to that of the African civet (Civettictis civetta) with which it is sympatric (THOMAS 1901).

Members of the subgenus Pseudogenetta (villiersi, abyssinica) are characterized by relatively small size and the lack of hair in the depression between the interdigital and metacarpal pads. Paragenetta, represented by one species (johnstoni) is known only from skulls. The delicate dental structure of this species suggests its diet may consist largely of arthropods.

Genets occupy nearly all African habitats, but the range of habitat tolerance varies between species. Genetta victoriae, servalina, angolensis, johnstoni, and mossambica are primarily forest dwellers, while Genetta pardina occurs in forest-savanna ecotone, woodland and Guinea savanna. Drier non-forest areas are occupied by Genetta genetta, tigrina (sensu latu), villiersi, and abyssinica (COETZEE in press; BIGALKE 1968). Although DORST and DANDELOT (1970) state that G. villiersi inhabits forest, a large series of this species in the U.S. National Museum was collected in Sudan and Guinea savanna in Ivory Coast and Upper Volta.

At least in Botswana, Genetta genetta penetrates considerably drier areas than tigrina, though both species are often found together (R. H. N. SMITHERS pers. comm.). Displaying a tolerance to habitats ranging from low forest to woodland and savanna, G. tigrina has been collected from elevations as high as 2,560 m (8,500 ft.) on the slopes of Mt. Kenya (HOLLISTER 1918). It often appears to be a "culture-follower," being found in the vicinity of villages and cultivated land (RAHM 1966).

There appears to be a distinct sexual dimorphism in size in at least some populations of Genetta tigrina (i.e., stuhlmanni, pers. observation), but data are inadequate to make conclusive statements for other species. J. C. DE MENESES CABRAL (in COETZEE, in press) has found that in areas of low rainfall skull length in G. rubiginosa (= G. t. rubiginosa, s.l.) varies from an average of 87.5 mm in ♀♀ to 90 mm in ♂♂, while in high rainfall areas skulls of both sexes averaged 90 mm. Tables of the genet cranial measurements in ALLEN (1924) suggest sexual differences in skull dimensions may exist in G. victoriae and servalina as well.

Melanistic genets are sometimes seen in museum collections and zoos (SANDERSON 1940; G. MALINIAK pers. comm.). The natural frequency of the melanistic morph in the wild is unknown. At the National Zoo a wild type ♀ mated by a melano produced two wild-type offspring (G. MALINIAK pers. comm.).

All known species appear to be nocturnal and solitary, though pairs and family groups are occasionally seen. Evidence at present indicates that the most complex social unit is the mother family; its integrity is probably maintained only until the young are weaned. DÜCKER's (1957) observation of a parturient ♀'s antagonism towards its ♂ cage mate suggests that the sexes remain separate during the rearing of young. VERHEYEN's (1951) statement that the ♂ participates in providing food for the young contradicts the findings for many solitary small carnivores.

The exact nature of the social organization is unknown. Presumably a land-tenure system exists; however, information is sparse regarding activity and defense of the home area. In the course of capture and release work with genets inclined toward poultry thievery, CARPENTER (1970) recaptured 4 of 6 ♀ _G. rubiginosa_ (= _G. t. rubiginosa_ s.l.) at their original capture points within days after release from as far away as 20 miles. Six out of 11 ♂♂ were again taken at poultry runs, but none was recaptured at the original trapping site. He attributes the fact that most poultry thieves are ♂♂ to their greater mobility, and suggests that ♀♀, unlike ♂♂ may be territorial. COBB (1970), on the other hand, found that in Turkana, Kenya, genets frequently crossed paths; he is of the opinion that in this area at least genets are not strictly territorial. Locus-specific defecation, a trait often correlated with the territorial syndrome, also characterizes _G. tigrina_ (VERHEYEN 1951, RAHM 1966, CARPENTER 1970). More work is clearly needed to elucidate this aspect of natural history.

Breeding in G. genetta and G. tigrina (s.l.) occurs during the wet seasons in both Kenya (TAYLOR 1969) and Botswana (SMITHERS pers. comm.). TAYLOR (1969) collected lactating and pregnant ♀♀ in May and from September to December and believes the timing of reproduction during these rainy periods to be linked with an abundance of insects. Pregnant ♀♀ from Botswana were also taken during the warmer wet period from October to February (SMITHERS pers. comm.). Whether wild ♀♀ breed during both wet seasons is uncertain. However, a breeding pair at the National Zoological Park has regularly produced a litter of two in April or May and again in July or August, for the past six years. Females have two pairs of inguinal mammae, and the number of young born in the wild varies from two to four (HOLLISTER 1918, SHORTRIDGE 1934, ANSELL 1960, COPLEY 1950, ROBERTS 1951, VERHEYEN 1951).

The types of resting, parturition and rearing sites is probably influenced by habitat. Holes in trees above ground, in fallen logs, and burrows in kopjes and cliff areas seem to be usual locations (SHORTRIDGE 1934). ROWE-ROWE (1971) located 3 young G. genetta in a disused crow's or hawk's nest about 6 m above ground.

Feeding appears to be opportunistic with a strong predisposition for animal matter. SMITHERS (pers. comm.) has found that in a sample of 78 G. genetta from Botswana the 3 animal groups represented most frequently in stomachs were (in decreasing order) rodents, Orthoptera, and scorpions; in a sample of 30 G. tigrina from Botswana, rodents ranked first, and Coleoptera and Orthoptera second and third. COBB (1970) reports that on the basis of stomach contents, fecal samples, and observation the genets of Turkana, northern Kenya, feed primarily on birds which roost in the dominant shrub (*Salvadora persica*).

Nothing is known about the natural predators of genets; they are presumably preyed upon by larger carnivores and birds of prey, and are sought by human populations for food and fur. According to DEKEYSER (1955), *Genetta villiersi* is killed by the Bassari of Itiolo, Senegal, for its tail which is used in ceremonial rituals.

Genetta's climbing ability is probably an important niche parameter, not only in potentiating escape into arboreal refuge, but in availing sources of food and cover which would not be accessible to strictly terrestrial animals.

IV. CONDITION AT BIRTH AND DEVELOPMENT

Figure 2 presents a representative growth curve and the developmental appearance of some morphological and behavioral changes. Two genets at birth weighed 72.6 g (Ma) and 69.6 g (Mo), or 2-4% of the parental weight (♂ = 2523.0 g; ♀ = 1672.6 g). By the time of weaning young animals probably weight 10-16% of the adult size, assuming 6 weeks of age to be an accurate estimate of the natural time of weaning.

As noted elsewhere (DÜCKER 1965, ROWE-ROWE 1970), young are born in a moderately altricial condition; eyes and ears are closed, locomotary coordination is poor, but the body, except for the ano-genital region, is well haired. This is the usual neonatal condition in Carnivora.

Infant pelage is dark and somewhat woolly (Figure 16a); the soft quality of the hair is retained but by the time the animals are 2 months old the hair acquires a lighter color. This juvenile pelage is completely replaced with the more coarse and dense adult pelage by the age of 6 months. There is no apparent progression of hair repalcement during molt; individual hairs drop out diffusely, a pattern that may be partially conditioned in captive genets by artificial feeding and photoperiod (LING 1970).

Though the order of events in Figure 2 agrees for each known individual in this study and elsewhere (DÜCKER 1965, ROWE-ROWE 1970), considerable variation exists in the ages at which morphological changes occur. For example, whereas DÜCKER (1965) recorded eye opening at the ages of 5-12 days, none of my animals' eyes opened

Figure 2. A growth curve (individual I) and morphological development in 8 hand-reared genets. *A*) walking with belly clearing the ground, *B*) eye opening, *C*) ear opening, *D*) quadrupedal squatting stance during urination and defecation, *E*) weaning.

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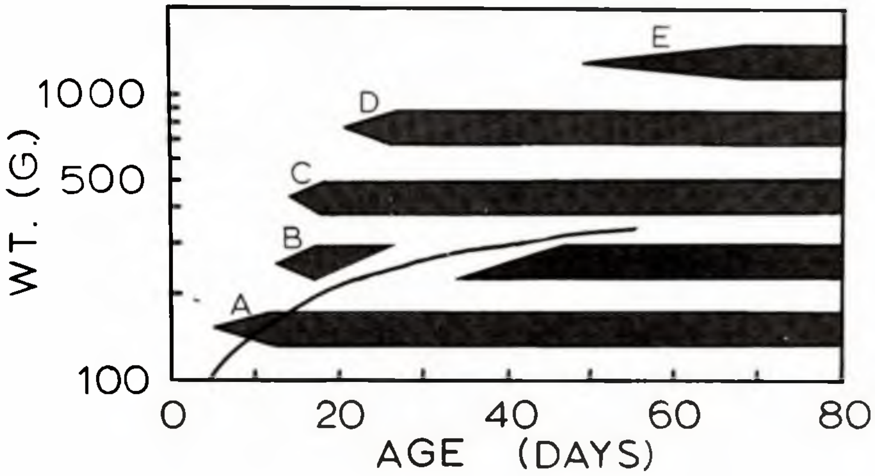

earlier than day 12 or later than day 17 (N = 8). Likewise DÜCKER's animals' ears opened at the age of 8 days while my three records were for the ages of 14, 17, and 18 days (subjects E, K, Fr).

Tooth eruption begins with the incisors at about the age of 3 weeks, followed by the canines and the premolars. For each tooth type, the upper dentition appears first. Accurate determination of the age at which infants are able to urinate and defecate independent of outside stimulation is difficult because urine flow is often triggered during perineal contact when crawling, and when infants nuzzle their own or their siblings' relatively bare anogenital regions. Individuals Ma and Mo and I and C were consistently seen to mutually stimulate urination by genital nuzzling until about 4 weeks old. A quadrupedal elimination stance was first seen assumed at about the age of 3 weeks (N = 6).

DÜCKER's (1965) and ROWE-ROWE's (1970) observations of weaning at ca. 6 weeks of age is probably a close approximation to the natural time of occurrence. The delayed ages of weaning in most of my animals resulted from an initial reluctance to take solid food.

V. THE BEHAVIOR OF SOLITARY ANIMALS

The following descriptions encompass behavior patterns that appear in a variety of contexts, social ones not excluded. The term "solitary" then is in a sense inadequate, though it indicates that these behaviors do not require the presence of a conspecific as a source of stimulation or as a social referent. Many of the patterns appear to be released by such generalized stimulus properties that their occurrence is not context-specific, though most of them appear predominantly in certain circumstances. Distinctions in motivation and function clearly exist, and many patterns have a direct or indirect role in social communication. The difference between these behaviors and those whose occurrence is more exclusively linked to an association with other animals is one of degree rather than kind.

A. The Primary Senses

1. Eyes. *Genetta tigrina* has moderately large semi-frontal eyes with vertically elliptical pupils. The shape of the pupil varies from a narrow line-like slit in bright light to a broad oval in dim light. The color of the iris approximates that of the pelage; at the time the eyes open (10-14 days) iris color is a dark grayish-brown which matches the pelage; the color of the eye fades during development until a medium brown shade is attained having a slightly more reddish hue than the fur. Though the eyeballs can be moved within the socket, their mobility is limited, and animals rely heavily upon head movement even to maintain visual fixation of objects moving over small distances. Though the eyelids usually blink synchronously it is not uncommon to see a resting animal

blink only one eyelid. DÜCKER (1965), who found that a Genetta tigrina was unable to distinguish between colored cards and brightness-matched gray cards, concluded the species is color blind.

2. Ears. The ear pinnae of Genetta, like those of the other viverrids considered in this study, are of the basic aeluroid type described by POCOCK (1916b) and MOHR (1952). It differs from these other genera, with the exception of Hemigalus, in being covered with a finer layer of hair internally and externally, and in being slightly larger, but lighter in build. The mobility of the pinnae and the relationship between ear motion and the reception of different sounds merits special study. Suffice it to say that the orbits can be moved through a horizontal arc of about 80° from a frontal to a lateral position; they can also be deflected in a vertical plane to approximately the same extent. In addition, the position of the pinnae can be changed within slight limits irrespective or orbital orientation. The orientation of the pinna confers only slight changes in the size and shape of the orbit when the ear is erect. However, the size of the orbit is greatly reduced when the pinna is folded backwards, a position achieved when the posterior edge of the of the pinna is folded immediately above the tragus and the anterior edge is bent at the base. Two types of ear movement are easily discerned. An ear may be twitched once or several times in rapid succession in response to loud sounds and tactile stimuli of the pinna or surrounding hair. Alternating ear motions, on the other hand, consist of asynchronous horizontal deflections of the pinnae accompanied by visual orientation toward a source of sound and/or

movement (PREYER's reflex: NUBOER 1959).

In the absence of a visual target, the head is often scanned from side to side in the direction of the sound, with gradually decreasing amplitude. A decrease in the extent of the ear movements accompanies this scanning until the head becomes motionless at which time the ears are often jerked alternately and sporadically with minimal amplitude. This movement appears to be important means of localizing unknown sources of sound, but the exact mechanism remains to be elucidated. The behavior certainly is not as distinctive in the other species as it is in the genet.

3. Nose. The nose is important for both olfactory and tactile perception. The thin mucous film of the rhinarium (Figure 16f) probably facilitates olfaction by providing a continuous solvent interphase from the external to internal nares. Possibly wind direction can also be detected by differential evaporation and/or cooling of the rhinarial surfaces. Scent perception requires air passage across the nasal epithelium, and as far as is known this is almost always accomplished by an accelerated, low amplitude respiratory rhythm. Though smelling (or sniffing) is often a distinctive activity, it can be difficult to discern because respiration is influenced by general activity, body temperature, and social conditions. In newborn genets the respiratory rhythm is often sporadic, with bouts of rapid and shallow breathing alternating with slow, deep breathing. For example, at the age of 6 days, as an animal (K) slept after feeding, the number of respiratory cycles varied from 27 to 41/minute ($\bar{x} = 34.6$, N = 8).[1] Audible sniffing was first

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[1] Based on visual detection of rib-cage movement; 1 to 3 minutes interrupted each successive observation/minute.

noticed at the age of 2 weeks (K, O, E) (N = 3). In its mildest form it involves rapid low-amplitude expansion and contraction of the belly and rib cage and slight changes in nostril shape; intense sniffing, in addition, is audible and manifests extension and retraction of the mystacial vibrissae in apparent synchrony with inspiration and expiration. Sniffing is frequently accompanied by slight head-bobbing motions. The animal, while smelling, maintains a stationary body position with the head elevated but lacking a specific orientation to a scent source (_testing the air_). Alternatively the nose may be specifically oriented to an object as the animal smells. Such close-range and oriented smelling often involves contact and usually occurs as the animal walks.

B. Locomotion

1. _Body Form._ _Genetta_'s lithe and versatile movement in trees and on the ground is a function of its coordination and the mechanical properties of its skeleton and muscles. Its attenuated axial skeleton conforms to the usual carnivore pattern of 20 thoraco-lumbar vertebrae (FLOWER 1966) but the 29 caudal vertebrae are excessive and by comparative standards contribute to the tail's considerable length (Table 3). Though the tail has apparent function in modifying the body's center of gravity, its relative importance to different species for arboreal locomotion is not apparent from inferences of climbing proclivity based on habitat selection. It can be seen in Table 3, for example, that the body proportions of the arboreal _Nandinia_ and _Poiana_ are more closely approximated by those of _G. genetta_ and _villiersi_, both of which

Table 3. Some Mean Body Measurements and Proportions of Several Species of <u>Genetta</u> and Allied Genera.

Species	Sex and Number	Head and Body	Tail	Hind Foot	% of Head & Body Length		Specimens	
					Tail	Hind Foot	Source	Origin
G. villiersi	♂ 16	427.6	413.8	79.7	96.1	18.6	U.S.N.M.[1]	Senegal,
	♀ 19	409.2	400.3	77.8	97.8	19.0	"	Upper Volta
	♂♀ 35	417.6	406.5	78.7	97.3	18.8	"	
G. genetta	♂ 10	474.7	471.2	88.0	99.2	18.5	U.S.N.M.	Nigeria,
	♀ 13	474.1	459.3	86.3	96.2	18.3	and	Kenya,
	♂♀ 23	474.3	463.5	87.1	97.7	18.3	HOLLISTER, 1918	Senegal,
								Upper Volta
G. tigrina	♂ 24	463.5	418.4	81.4	90.2	17.5	U.S.N.M.	Kenya,
	♀ 11	446.2	401.6	78.5	90.0	17.5	and	Uganda
	♂♀ 35	458.3	413.1	80.5	90.1	17.5	HOLLISTER, 1918	
G. pardina	♂ 4	510.0	418.7	91.5	82.9	17.8	U.S.N.M.	Ghana,
	♀ 6	507.3	416.8	91.8	82.1	18.9	"	Ivory Coast
	♂♀ 10	508.7	417.6	91.6	82.1	18.0	"	
	♂ 9	455.0	470.0[2]	86.0	103.5	18.9	ALLEN, 1924	Congo
	♀ 4	457.0	406.0	85.0	88.9	18.6	"	
G. servalina	♂ 8	489.0	475.0	92.5	97.1	18.9	ALLEN, 1924	Congo
	♀ 10	485.0	446.0	88.7	91.9	18.3	"	
G. victoriae	♂ 13	573.0	444.0	101.0	77.4	17.6	ALLEN, 1924	Congo
	♀ 5	573.0	448.0	100.0	78.1	17.4	"	

Table 3 (continued).

Species	Sex and Number	Head and Body	Tail	Hind Foot	% of Head & Body length		Specimens	
					Tail	Hind Foot	Source	Origin
<u>Nandinia binotata</u>	♂ 11	467.3	498.9	88.7	106.7	18.9	U.S.N.M.	Ivory Coast,
	♀ 7	464.5	529.2	88.8	113.9	19.1	"	Togo
	♂♀ 18	466.2	510.7	88.7	109.5	19.2	"	
	♂ 7	510.0	570.0	92.0	111.7	18.3	ALLEN, 1924	Congo
	♀ 11	480.0	544.0	88.0	113.3	18.3	"	
<u>Poiana richardsoni</u>	♂ 1	332.0	380.0	64.0	114.4	19.2	ALLEN, 1924	Congo

[1] Measurements taken from specimen labels at the U. S. National Museum, Smithsonian Institution.

[2] This figure appears to be an error: if the value was a misprint of 407.0, the corrected tail: head and body proportion of 89.4 would be in accordance with the other values. Furthermore, the ♂ <u>servalina</u> specimen pictured in ALLEN (1924, Plate XIV, Figure 1) appears to have a tail shorter than its head and body.

usually inhabit savanna. Of the latter 4 woodland and forest-dwelling species, all but servalina are relatively short-tailed, and G. victoriae, by far the largest species of genet, has the smallest feet. Assuming the measurements to be reliable and the differences between species adaptive, it appears that as a presumptive arboreal adaptation greater relative tail length is not necessarily indicative of species inhabiting more woody habitats. Additional biogeographic factors may be operative; indeed, longer tails may be thermally adaptive in warmer low rainfall areas (ALLEN's rule: MAYR 1963).

As the legs are moderately short, the resulting body carriage and center of gravity is low. An ample degree of limb abduction is possible, particularly in the hindlegs. The manus and pes have retractile claws and are capable of relatively unrestricted powers of pronation and supination. As noted by TAYLOR (1970), Genetta's manus is palmigrade and its pes semi-digitigrade. Foot pads are smooth and somewhat edematous; in addition to apical and interdigital pads, the metacarpus and metatarsus are covered with medium-sized bipartite pads. Genetta's foot pads are less extensive in surface area than Nandinia's, but moreso than Civettictis (Figure 3). The extent of foot-pad development is commensurate with what is known of climbing ability: Figure 3 depicts a series of feet with decreasing arboreal specialization.

2. Ontogeny of Locomotion. Though voluntary movement following birth is minimal, infants are usually capable of crawling by the age of one or two days. The distinctive pattern of movement at this

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Figure 3. Pad Structure of the Manus (Upper Row) and Pes in 4 Viverrids.

A) The African palm civet (*Nandinia binotata*).

B) the large-spotted genet (*Genetta tigrina*),

C) the giant forest genet (*Genetta victoriae*), and

D) the African civet (*Civettictis civetta*).

Not to scale.

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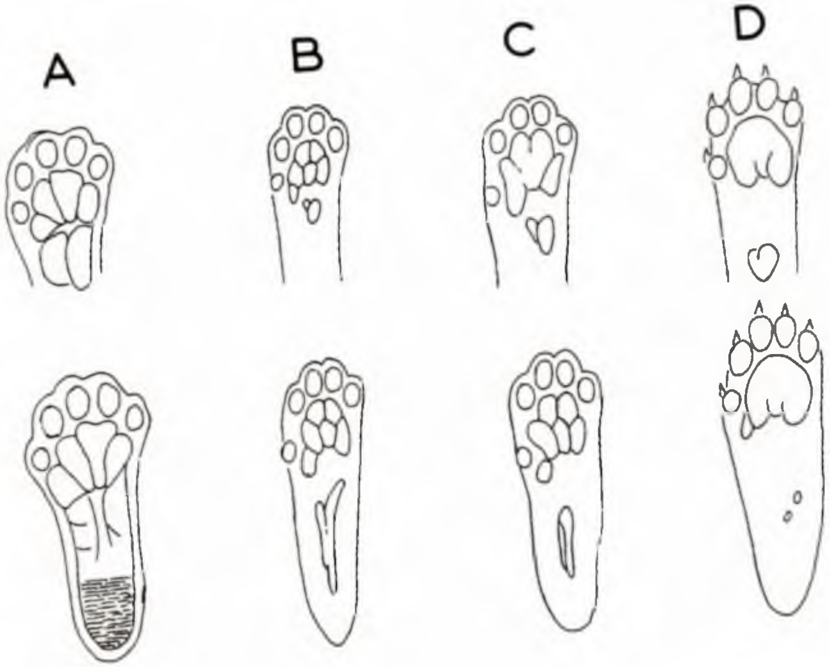

time consists of a slow and rhythmic, alternating lateral flexion of the neck and anterior trunk. As the head sweeps from side to side the philtrum and chin region maintain continuous contact with the substrate. The legs, which are unable to support the body are extended to the side with the soles down, and forward progression is achieved by pulling movements of the forelimbs. Until 4 or 5 days of age the result of head-sweeping is a curving or circular path of movement. As animals begin to support their forebodies when walking, the course of movement straightens, and head-sweeping becomes both less frequent and stereotyped. The movement of the head and forebody, appropriately termed "Kreisbogenschlagen" by FRANK (in DÜCKER 1965) apparently enhances tactile localization of the nipple, the mother, and siblings.

At about the age of one week, young genets are capable of supporting themselves and walking on the fore- and hindlegs for brief periods, though the latter tend to drag. On successive days, as the legs assume a more adducted position under the body, coordination improves and the time required for each stride decreases. The claws apparently cannot be retracted on the first 8-14 days and easily snag on irregularities. Progression across a smooth woolen blanket, for example, is greatly encumbered, but on sloping and vertical surfaces the claws clearly assist clinging ability (Figure 16a).

Even before infant genets are able to walk, they manifest a pronounced faculty to maintain partially suspended and precarious positions on objects while repeatedly uttering squealing vocalizations. When suspended by the head or neck, the tail and hindquarters execute a twirling motion common to young of many species of mammals (HORWICH 1971). If suspended by the tail, the forelimbs are extended, but the hindlimbs often flex with one clasping the other against the belly. The latter behavior was not seen on the week following birth, but was performed regularly until the animals had developed the strength and coordination to flex their torsos sharply and climb up their tails at about 3 to 4 months of age.

Once walking becomes steady, the first occurrence of other locomotor patterns is sometimes observed to be clustered; it seems that the capacity to perform various gaits develops over a brief period and that the occasion of the first performance is subject to circumstances. Trotting, running, galloping, and jumping were observed for the first time in all individuals between the ages of 20-30 days, the unsupported upright posture between 30-40 days, and vertical looping up and down steeply inclined surfaces from 32-40 days. As noted by DÜCKER (1965), the first climbing experiences were characterized by an unwillingness to descend without assistance. Animals displayed a marked following response to the writer when introduced to unfamiliar rooms from the ages of 35-38 days (N = 2); it was impossible to evoke the response thereafter, possibly because the surroundings were familiar.

3. Gaits.

a. Walking (Figure 4a): Although walking velocity varies greatly, the footfall sequence during a walking stride is the hindfoot and forefoot of one side, followed by the same order of movement on the opposite side. The durations (based on 8 mm ciné film, 18 fps) of three consecutive strides or a moderately fast walking animal (O) were .45, .45, .54 sec. The relatively slow strides of another animal (K) as it rubbed its back against the wall of the cage were 1.8, 3.3, and 2.0 sec. When it finished rubbing and walked away, four strides measured .77, .83, .66 and .72 sec. in duration. The mechanical characteristics of the phases of limb elevation and contact are the same in G. tigrina as in the mongooses described by TAYLOR (1970).

b. Trotting: One brief ciné sequence of this gait reveals a resemblance to that described in the white-tailed mongoose (TAYLOR 1970); the footfall sequence is left hind, right fore followed by right hind, left fore; however, the hindfoot-forefoot sequence is not inflexible according to MUYBRIDGE (1957). In this film there is no contact-free suspension phase. At times though, the trot appears to be sufficiently fast that two support-free transit phases do occur per stride. The duration of one trotting stride was .23 sec. (O).

c. Running: Running and rapid trotting are identical, as both involve diagonal limb extension with two support-free transit phases. Though no film of running is available, it appears that as a gait it is secondary in importance to galloping and may occur most frequently as a transitional gait between walking or slow trotting and galloping.

Figure 4. Two Locomotory Gaits of the Genet.

A) Walking in a year-old animal (0; 24 fps). The head is depressed in frames 8-12 as the animal smelled the substrate.

B) Galloping in the same animal at the age of 10 weeks (64 fps).


A
1
3
6
8
11
12
B
1
3
5
6
8
10

d. Galloping (Figure 4b): In this gait, thrust is provided alternately by the forelimbs and hindlimbs with the latter supplying the greatest propulsion. The interval between forelimb elevation and footfall of the hindlimbs is extremely brief. During any one galloping bout, one foreleg usually predominates as the leading limb; but occasionally apparent simultaneous footfalls occur, as do transitions to an opposite leading limb. Of 77 galloping strides (from 11 incompletely recorded bouts), 60 strides were led by the left forelimb, 12 by the right, and in 5 both forelimbs appeared to strike the ground simultaneously.

4. Climbing. Genets are adroit climbers able to traverse horizontal surfaces in an inverted position and to ascend and descend surfaces inclined up to and greater than 90° from the horizontal. All gaits can probably be used in ascending and descending gently inclined planes; however, only two gaits are employed in climbing up and down plane or contoured surfaces inclined at greater than 45° with the horizontal.

A walking gait can be efficiently used on any vertical surface permitting a secure purchase with the claws or toes. Vertical and steeply inclined wire mesh as well as suspended lengths of burlap are easily ascended in this way. Walking descent however requires an irregular surface on which the pads of the manus can partially support the hanging weight of the body. Consequently, in descending smoothly contoured objects and burlap sacks, an alternating anteroposterior limb extension is employed termed vertical looping by

TAYLOR (1970). By arching the spinal column and alternately sliding the fore- and hindfeet forward the animal is able to descend while maintaining quadrupedal contact with the substrate during most of each stride. The same method can be used in climbing upwards with or without the assistance of the claws. When a genet climbs a smooth and narrow vertical surface, such as a house door, the limits of its skill are tested. In such a situation the majority of the body weight is supported by the forelimbs which are adducted with the forefeet opposed and exerting a compressing force. The feet of the hindlimbs prop the hindbody out so that the force vector acting on the forelimbs is at a tangent with the vertical. As the hindlegs extend, the forefeet release their grip and rapidly seize an elevated purchase. Flexion of the spine and hindlegs then permit the hindfeet to assume an elevated grasp. Vertical looping under these curcumstances is considerably strained for, unlike a branch, the smooth parallel surfaces of a door do not permit the use of the claws or an embracing type of purchase. As climbing in an inverted horizontal position requires three feet in contact at all times, only the walking gait can be used.

5. Jumping. Jumping may be divided into four successive phases and usually involves a limb coordination similar to that of the gallop. The jump is often preceded by a quadrupedal stationary phase characterized by retracted mystacial vibrissae, visual fixation of the landing target, and intention movements consisting of alternating up and down motions of the forebody and adjustment of foot position.

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Figure 5. Phases during Jumping in the Genet.

A) Quadrupedal stationary phase (take-off position), *B*) propulsion phase, *C*) suspension free transit, *D*) landing (simultaneous touchdown of the feet, *E*) landing (forward swinging of the torso and flexing of the spine).

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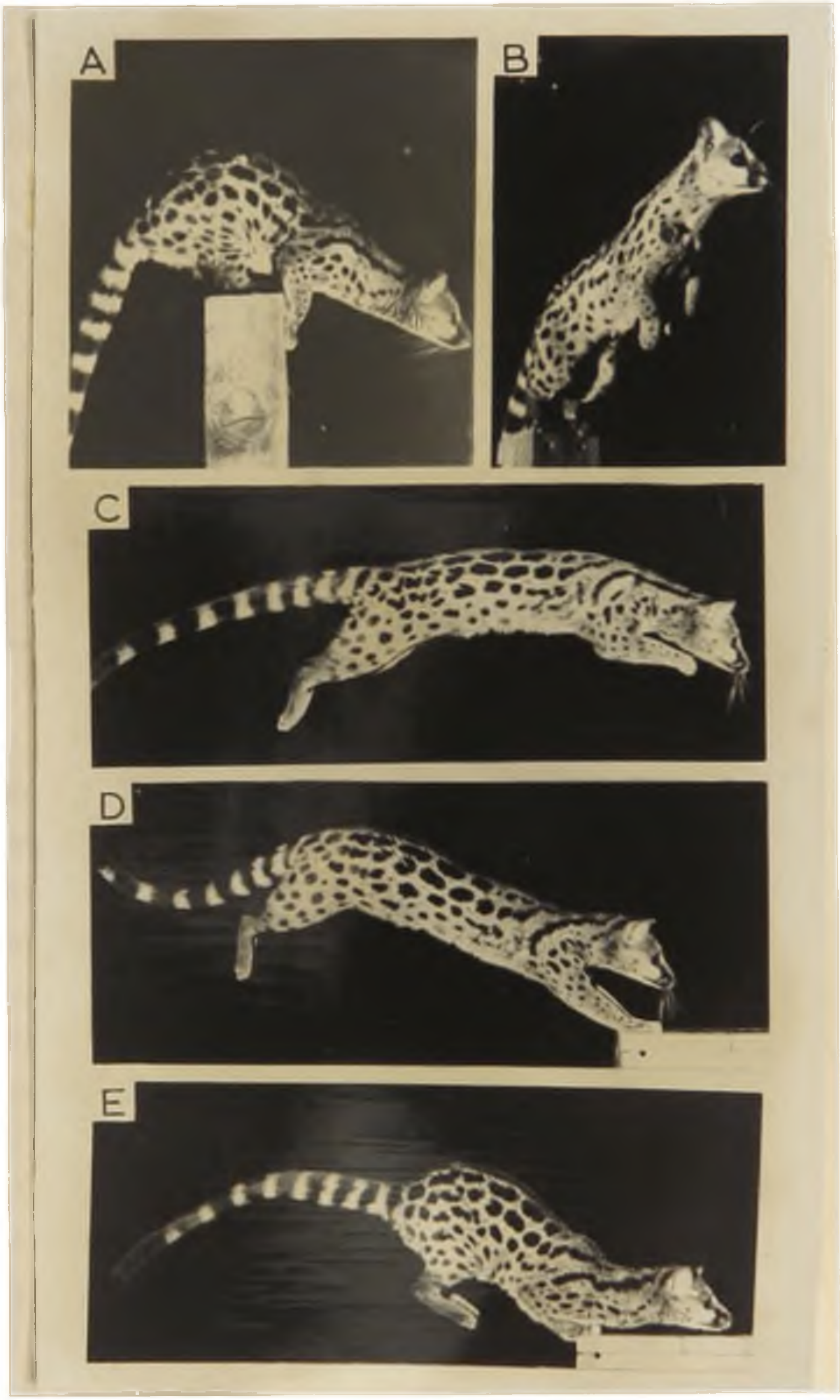

The length of the metatarsus touches the ground and the hindlegs are strongly flexed (Figure 5a). The propulsion phase begins with a push-off of the forelegs, which apparently guides the torso into a position where the hindlegs can be straightened with maximum effectiveness (Figure 5b). The vibrissae are extended foreward, and as the hindlegs propel the body up and forward the forelimbs are again swung into an anteriorly extended position. During suspension-free transit the hindlegs partially flex beneath the body (Figure 5c). In landing the forefeet strike first, but unlike galloping they usually hit simultaneously (Figure 5d). Landing impact forces the forebody down and at this time the vibrissae often contact the substrate. Contact of the hindlegs is preceded by a strong flexion of the upper forelimb segments, a forward swinging of the torso, and a flexing of the spine (Figure 5e). The entire metatarsus makes contact during landing, and momentum forces the body forward several steps.

In jumping both long horizontal and vertical distances the forelegs usually land on the top of the object, but the hindlegs often strike against the side of the object and then with a bipedal walking motion propel the hindquarters up. In short jumps, none of the limbs may land simultaneously (TAYLOR 1970). Occasionally, especially during intense social interaction, genets jump upward from a bipedal stance and land on the fore- and then the hindfeet, or with a variable footfall sequence. They can also jump backward.

HALL-CRAGGS (1965) states that Galago senegalensis maintains a gaze fixed on the landing target at least until the animal leaves the ground. During the photographing of Figure 5, the electronic flash was once positioned in front of the jump path and discharged several times when the genet was in mid-air. The animal often over- and undershot its landings, suggesting visual feedback is important during the jump.

6. Gait-associated postures. Though gaits can be described in terms of the phase relationships of the limbs and the duration of the stride and its components, posture is often overlooked unless it is an inherent property of the gait. The ability to maintain a more or less constant spinal contour is inversely related to the speed of the gait. While fast gaits involve rapid, extensive and recurrent changes in the spatial configuration of the vertebral and limb segments, slow gaits confer few constraints on the spinal column, and the phase relations of the limbs are relatively unaltered over a broad range of limb flexion and extension. A graded continuum of walking postures exists from a low crouched posture to a strong arched-back posture (Figure 6b-e).

Figure 6, based on still and ciné photographs, depicts four variants in walking posture and the immobile extremes at either end of the series. In crouched walking the head and neck are depressed, the humerus and femur strongly flexed, and the elbow and knee act as the primary moment arms (Figure 6b). During moderate flexure of the back there is minimal bending of the leg joints, and the heads of the humerus and femur appear to be the main moment arms (Figure 6e). Though a few short steps may be taken in the extreme postures (Figures 6a, f) slow sustained locomotion does not appear to be

Figure 6. Postural Variation Associated with Stationary Body Positions and the Walking Gait in the Genet.

A) Retracted-limb ventral reclining position; *B*) crouched fore- and hindquarters, minimal spinal curvature); *C*) normal walking and standing; *D*) semi-crouched forequarters and semi-raised hindquarters, moderate spinal curvature; *E*) semi-raised fore- and hindquarters, moderate spinal curvature; *F*) maximally raised fore- and hindquarters, maximum spinal curvature. A and F are stationary body positions; B-F can also be tri- or quadrupedal stances; B-E are also assumed during walking. (Drawings based on sketches from still photos and cinefilm.)

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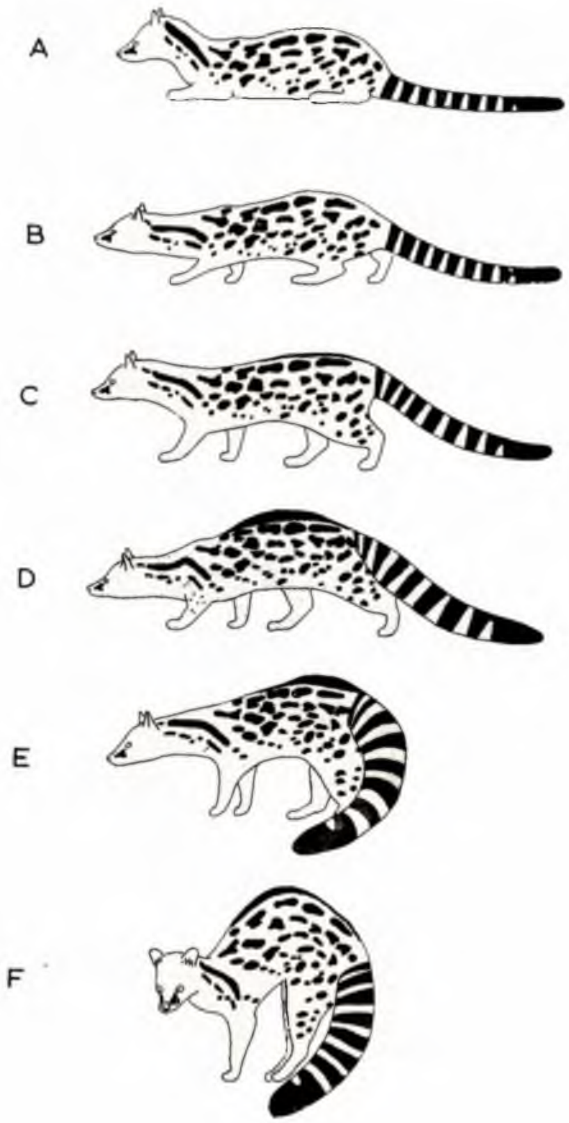

possible unless the stances are modified to approximate the next most similar postures.

In addition to these gait-associated postures which often occur in a social context, a crouched elongation posture is assumed during an irregular walking approach toward novel objects. Once an object is approached, the animal shifts the trunk forward between the limb girdles and leans toward it. During the approach and leaning phases, the direction of movement often vacillates, but usually no more than several steps are taken in the reversed direction.

Startling, a sudden change in body position followed by flight or immobility, is often followed by a crouched stance in which the legs are spread and the ventrum may touch the ground (Figure 7).

C. Shaking and Twitching Movements

1. Head and body shaking (Sichschütteln). Like many other patterns, shaking is a complicated motion of graded intensity. It is apparently accomplished by rapid and alternate partial rotation and lateral bending of the vertebral column with a resultant abrupt tossing of the overlying skin and hair. The head and neck; head, neck, and shoulders; or the torso can be shaken independently; or the whole body is shaken with an antero-posterior wave of emphasis (Schütteln des granzen Körpers).

When head shaking accompanies or precedes shaking of the neck and shoulders, its motion is primarily rotatory because the angle between the head and neck is small. When only the head is shaken, its movement is pendulous because the occipital angle roughly

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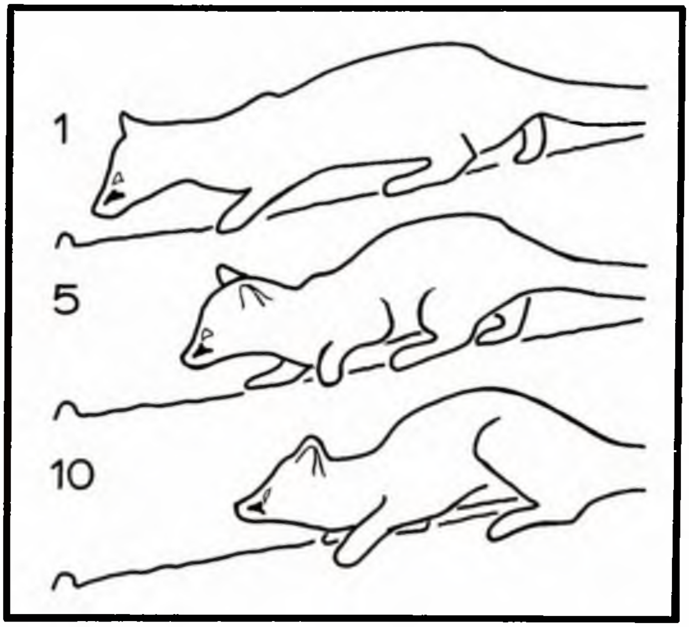
Figure 7. A Startle or Sudden Change in Body Position in the Genet (E; 24 fps).

Within less than a half second animal E made half of a reversed walking stride and became motionless in a crouched quadrupedal stance.


1
5
10

approximates 30 or more degrees. Shaking of the torso seems to be facilitated by a simultaneous circular motion of the vertebral axis which is sufficiently forceful to cause the hindlegs to take one or two steps in place. Slow motion ciné study would greatly enhance an understanding of these involved movements.

Shaking movements of the head and body appear to be responses to direct tactile sensation of the skin and perhaps indirect dermal stimulation mediated by disturbance to the nap of the hair. The patterns are sometimes seen after an animal has rolled and rubbed on the ground, and are almost always seen when the pelage is saturated with water. Thus it serves the removal of water and particulate matter, and may also create a uniform nap in the pelage (LEYHAUSEN 1956). In addition, head shaking is evoked by presumably painful stimuli to the face, ears, and mouth, and may be considered as a component of the facial protective response described by ANDREW (1963). It has been seen, for example, after an animal has struck a hard object with its open mouth, after receiving a bite on the face, and after having a mystacial vibrissa pulled out by another animal. It is elicited by repeated mild tactile stimulation to the ear (see Ontogeny of Shaking, Stretching, and Self-directed Behaviors in Genetta) and once as a bolus of regurgitated food passed from the esophagus into the mouth.

2. Limb twitching. Both the fore- and hindfeet are twitched and shaken. The movement, which often occurs in bi- and tripedal stances or during walking involves a slight flexion of the limb followed by a rapid snapping extension and retraction (Figure 8).

Figure 9. Twitching of the Forelimb in the Genet (E; 24 fps). In frames 1 and 2 the wrist is flexed; in frame 3 it is rapidly extended and in the 4th frame it snaps back into a flexed position. The twitching of this leg occurred as it moved in a forward step.

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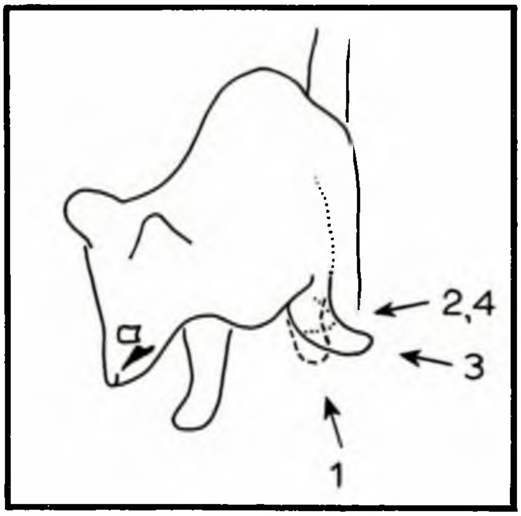

The result is a complete but momentary straightening of the wrist or ankle and a partial extension of the elbow and knee. If the motion is repeated in rapid succession, the limb has the appearance of being shaken.

Animals are often seen to twitch their hindlimbs when their feet become wet from the puddle created during urination. When the body is completely wet, often each foot is raised and shaken. Animal K shook and twitched its forefoot repeatedly after a rat it had attempted to catch bit it once between the toes. In addition, the forefeet and to a lesser extent the hindfeet are sometimes twitched spontaneously as an animal lies asleep or resting. Forelimb twitching has also been seen in a variety of social situations which may be interpreted as containing subjective elements such as surprise, apprehension, or conflict.

D. Stationary Body Positions

Stationary body positions may occur as relatively short-termed interruptions of locomotion, or often as protracted periods of rest. The term stance, in accordance with dictionary definition, refers to the basic types of foot position assumed by immobile standing animals. Posture is the term generally used for motionless body attitudes, but as posture means the "relative arrangement of the different parts" and the "state and condition at a given time,"[1] it will herewith be used to define configurations of the spine and limbs, and positions of the soft anatomy and hair at any time irrespective of locomotion. The term reclining position is self explanatory. The descriptions

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[1] Webster's Seventh New Collegiate Dictionary.

under these categories are not equally complete, as the attitude of the entire body is considered in reclining position, while only foot position is necessary to define a stance. Suffice it to say that a range of spinal curvatures is possible during quadrupedal and tripedal stances. The list of reclining positions includes those most commonly seen and does not take into account postures that result from spatially confining circumstances.

1. Stances

a. Quadrupedal stances: The animal stands with the four legs providing the main means of body support. In an upright quadrupedal stance, the forelegs rest against an elevated surface and the trunk of the body is inclined upwards.

b. Tripedal stances ("indecision-alert" posture: EWER 1968): When the body is supported by three legs, it is usually one of the forelegs that is partially flexed and elevated. A hindleg is rarely elevated for any length of time. The stance occurs most frequently during pauses in slow walking, and essentially constitutes an arrested walking stride.

c. Bipedal stances (Männchenmachen): Three variations of bipedal body support are seen. Support may be provided by the toes and interdigital pads (high-sit: EWER 1963), by the entire metatarsus (semi-bipedal: EWER 1968), or by the metatarsus, the rump and the tail base (low-sit: EWER 1963), (Figure 8a,b). All variations can be maintained for up to several minutes.

2. Reclining Positions

a. Sitting: This posture is characterized by three zones of

Figure 8. Stationary Body Positions and Stretching Movements in the Genet and the African Palm Civet (Nandinia).

A, B) Bipedal stance with the metatarsus touching the substrate, and with only the toes touching the substrate, C) the sitting position, D) the ventral retracted limb reclining position, E) the semi-lateral semi-extended reclining position, F) the extended lateral body reclining position, G) arched-back stretching, H) sitting stretch, I) yawning.

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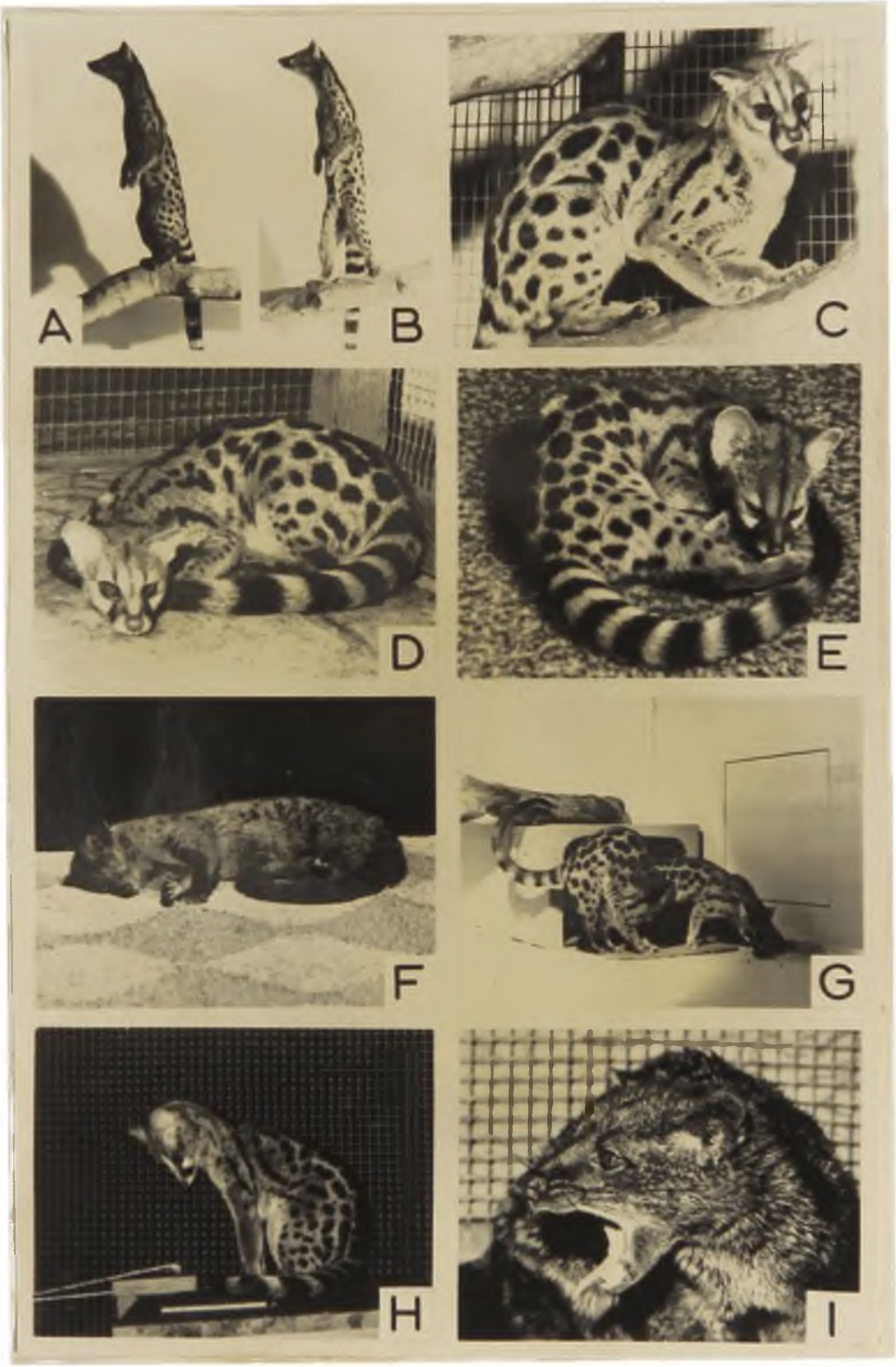

body-substrate contact, the length of the tail, the length of the metatarsus, and the forefeet; the contact zones can be maintained with considerable variation in forelimb flexion. Occasionally one foreleg may be elevated (Figure 8c).

b. Ventral retracted-limb reclining position (aufrechten liegen mit Vorderpfoten nach innen: LEYHAUSEN 1956): In addition to the three zones of contact that characterize sitting, in this position the chest and belly and often the radio-ulna also touch the ground. The head may be elevated or may rest on the forelegs or the substrate beside them (Figure 8d).

c. Semi-lateral semi-extended reclining position: This position differs from the retracted limbs reclining position in that the hindlegs are usually extended and the lateral surface of one leg contacts the ground broadly (Figure 8e).

d. Extended body reclining positions (ausgestreckte Ruhelage: GOETHE 1964): In these positions, the legs are more or less extended, at least not flexed against the body. Usually the animal reclines with either the ventrum or one side of the body contacting the substrate (Figure 8f). Dorsal extended body reclining is less frequently seen and cannot be maintained without lateral support.

e. Lateral curled reclining position: The torso is flexed, limbs are usually partially flexed, and one side of the body broadly contacts the ground. The head usually rests on or between the hindlegs and is covered by the tail which is wrapped about the body contour.

3. Assumption of reclining positions. The bodies of viverrids, unlike those of ungulates have low centers of gravities and versatile limb mechanics which impose few restrictions on the method of reclining or standing (see ZANNIER-TANNER 1965). Retracted-limbs reclining, for example, can be assumed by simultaneous lowering of fore- and hindquarters, or by lowering the forequarters from a sitting position. Sitting is often the transition attitude between reclining and standing. Circling in place, characteristic of canids, often precedes the assumption of reclining postures in which the hip and thigh contact the substrate. In these positions the animal first depresses the rear-end and then sits on the side of the hip.

E. Stretching Movements

1. Walk-stretch (Schreitstrecken: EIBL-EIBESFELDT 1951). This protracted and exaggerated form of walking varies considerably in both duration and complexity. In its most complete form it involves (1) a usually unequal anterior extension of the forelegs, extension of the neck, and a slight concave arching of the back; (2) extension of the hindlegs, depression of the hindquarters, and a concomitant forward shifting of the pectoral girdle; loss of the spinal concavity and the onset of a ventral tailbase flexion; and (3) continued tail flexion as the feet make several short stiff-jointed steps. In partial versions of this stretching movement either the first or the latter two phases are lacking. When initiated from a sitting position, the stretch may involve only the first phase but in the absence of the spinal concavity, or may continue in a standing position to completion (Figure 10).

Figure 10. A Walk Stretch in the Genet Initiated from a Sitting Position on a Log (C; 18 fps).

Frames 1-7: stretching of the fore-quarters (notice unequal extension of the forelimbs); frames 21-30: stretching of the hindquarters (typically the hindlegs are unequally extended); frame 36: a hindleg is moved forward. The tail is hanging on the side opposite the camera.

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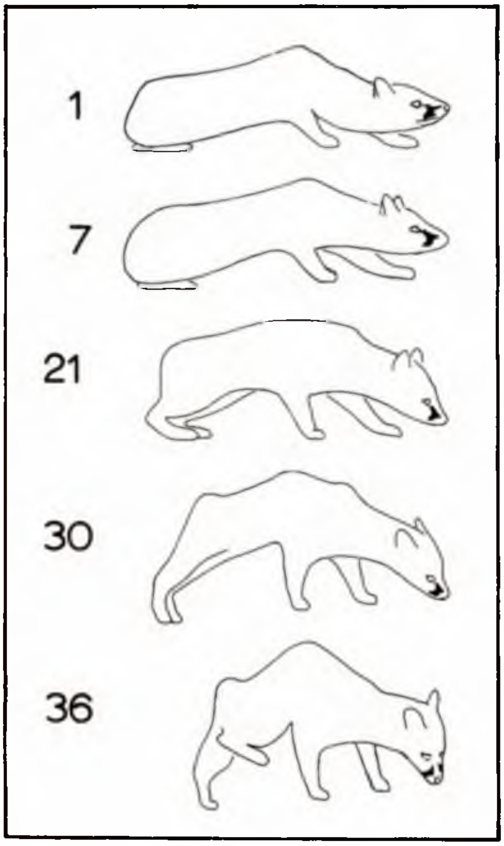

2. Upright stretch. The animal assumes a quadrupedal upright position, extends the forelegs upwards, and stretches the head and neck up and back. The claws are possibly unsheathed during this movement.

3. Arched-back stretch (Streckbuckel: LEYHAUSEN 1956) (Figure 8g). This movement, performed in a motionless standing position, involves extension of the fore- and hindlimbs, a pronounced flexion of the back, and often a dorsal curling of the tail. It is possible that arched-back rubbing (see Object-oriented Contact Patterns) is also a modified type of arched-back stretch.

4. Sitting stretch (Figure 8h). The forelimbs are extended and the scapulae elevated while the neck is ventrally flexed and the head pointed down and backwards.

5. Tail stretch. The base of the tail flexes ventrally while the distal one-half to two-thirds extends posteriorly. Tail stretching is usually performed concurrently with the walk stretch.

6. Yawn (Gähnen). In its most complete form the jaws are gaped maximally to about 80 degrees, the head tilted upward, the vibrissae extended, the eyes closed, and the tip of the tongue curled. In its weakest expression, the jaw gapes to about 30 degrees and the other components are absent (Figure 8i).

F. Object-oriented Contact Patterns.

1. Metatarsus scuffing (Figure 11). In a posture similar to sitting (with the metatarsus but not the tailbase contacting the substrate), the hindfeet are alternately stroked backwards with the pads scuffing the surface. The claws are not extended, and the feet

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Figure 11. Metatarsus Scuffing in the Genet (K; 24 fps). Frames 1-6: the visible leg is thrust posteriorly and the metatarsus dragged on the substrate; frame 9: the leg is returned to its initial position.

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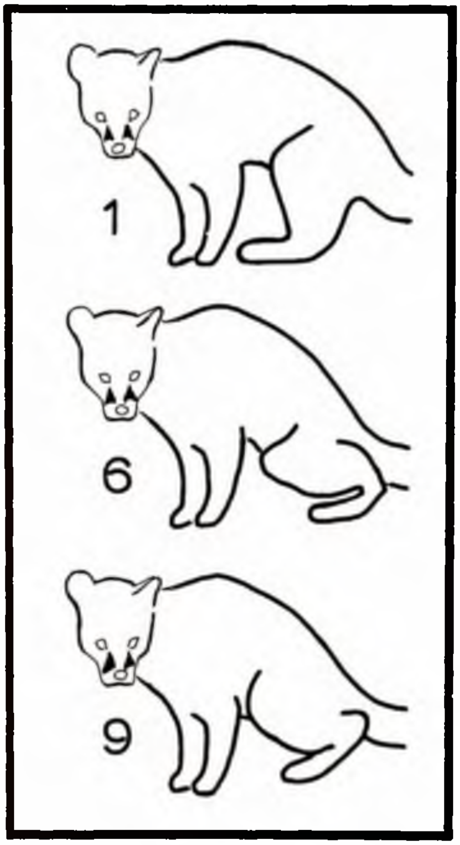

may or may not be lifted when brought forward again to their original position. During this movement the body may be stationary or may be slowly propelled forward by small steps. An animal was once seen to scuff with one hindfoot in an elevated position upon a horizontal log. Scuffing was most frequently seen performed within and on top of plywood and cardboard boxes. Occasionally a rough-surfaced log was used.

2. Substrate-clawing (Krallenschärfen: LEYHAUSEN 1956). The claws are extended and hooked into the substrate as the legs are tensed and slightly retracted in an often sporadic, but alternating rhythm. Clawing is usually performed in a crouched posture on horizontal and diagonal branches, and involves either the forelimbs or both pairs of limbs. Often the claws are not dragged across the surface, but appear to experience tension as the limbs are flexed.

As differential growth of the dorsal and ventral surface of the claw account for its recurved and pointed structure, it seems unlikely that this behavior actually sharpens the claw. Being retracted most of the time, it furthermore experiences relatively little wear. Rather, it appears that substrate clawing removes loose fragments of keratin, and claw sheaths, and also keeps the claw worn. It is well known to zoo keepers that a civet or cat that lacks a suitable clawing substrate will develop long claws which can penetrate the toe pads and become ingrown.

3. Arched-back rubbing (Figure 12). Though this behavior resembles the arched-back stretch posturally, it differs from it in that the animal leans against a vertical or diagonal surface

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Figure 12. Arched-back Rubbing in the Genet (K; 18 fps). Notice the change in the extent and center of spinal curvature. In frame 21 the animal is beginning to lick its breast.

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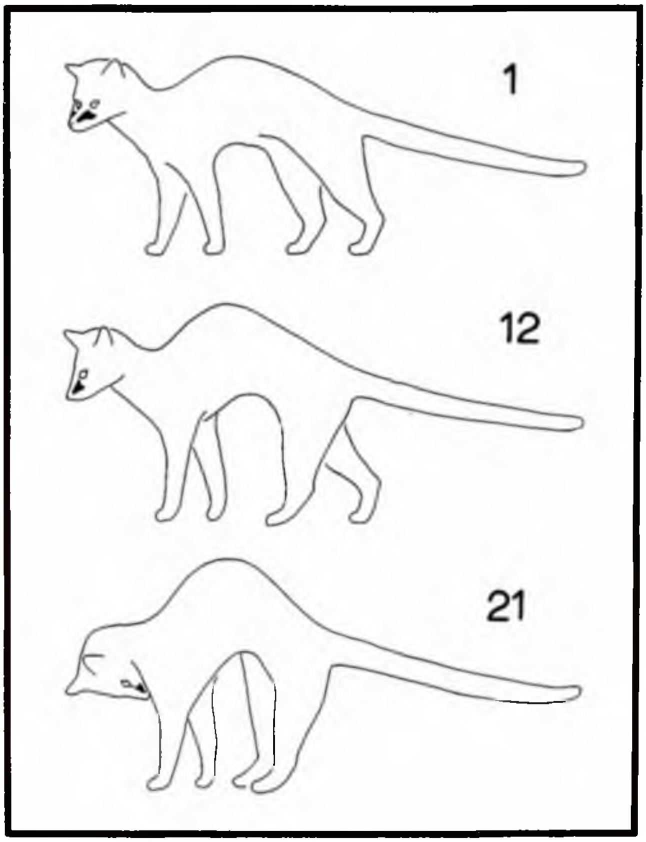


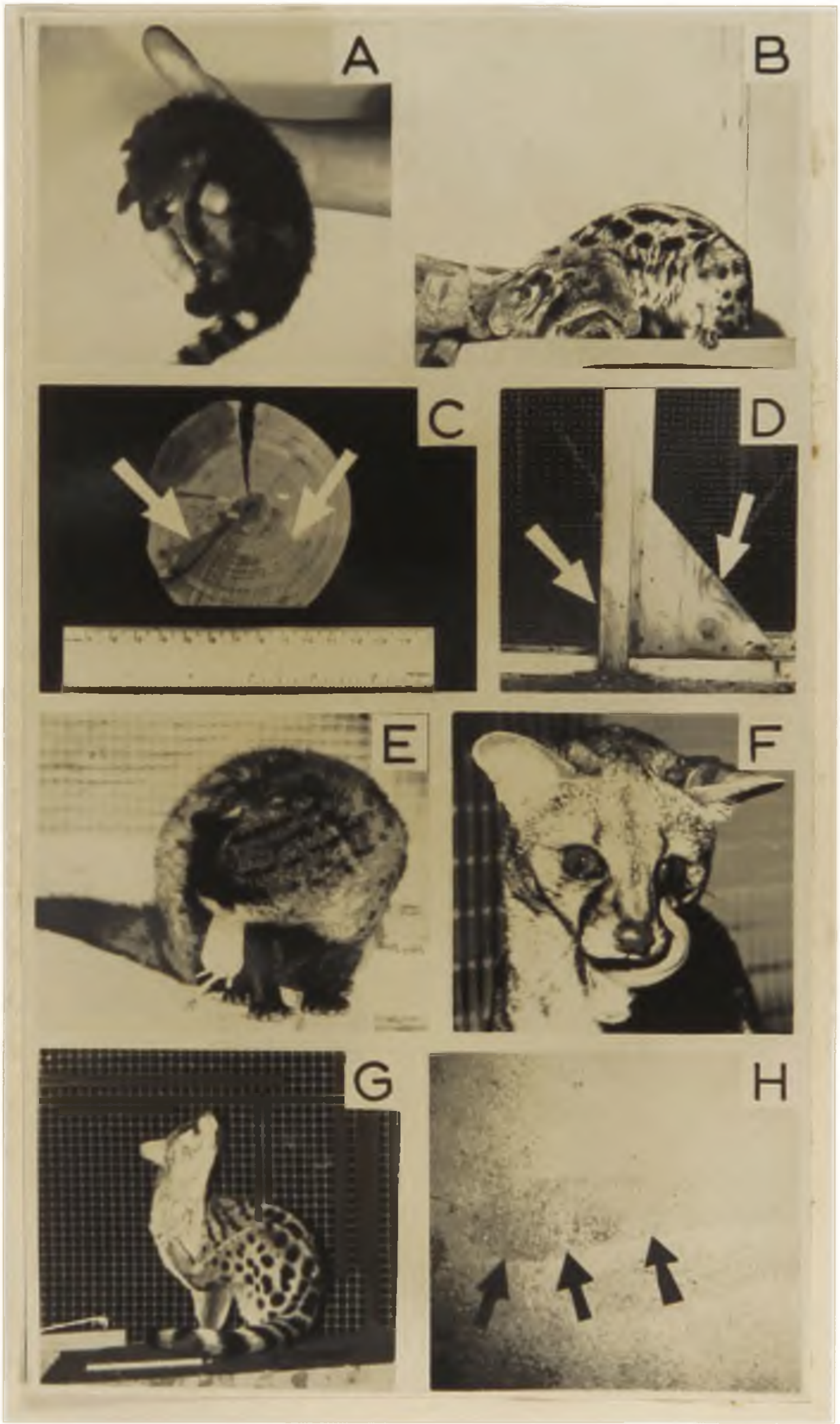
while slowly walking forwards. The movement typically begins with a strong central flexion of the back; as the animal steps forward, the posterior half of the trunk attenuates, and the flexion shifts anteriorly. When the hindquarters are brought forward again the arch assumes a more central position. The areas rubbed are the hip, side, shoulder, and neck, and occasionally the side of the head.

4. Head and neck rubbing (Figure 16b). The variety of stationary body positions assumed during head and neck rubbing depend upon the location of the object being rubbed. When directed to the horizontal or diagonal surface on which the animal rests, a sitting or flexed-limb reclining position is adopted, but upright objects are rubbed in a quadrupedal upright position. Rubbing of the head and neck is achieved by a combination of rotating, extending and flexing movements directed usually to the substrate and to targets on the animal's own body (forelegs and tail). Though the sequence and form of the movements are highly variable, a fairly distinct component of head and neck rubbing is a stroke-like head extension in which the lips on one side of the rostrum maintain contact with the substrate.

Certain aromatic substances are especially effective in eliciting this behavior. Subject O would consistently rub his head and neck against my hair after a fresh application of hair oil. On these occasions the animal maintained a supported quadrupedal stance on my shoulders, clasped my head with the forepaws, and interspersed the rubbing with Flehmen and licking of the hair.

Figure 16. Locomotion and Object- and Self-oriented Contact Patterns in the Genet and the Asian Palm Civet (*Paradoxurus*).

A) Clinging with the everted claws in an infant genet (1 week old); *B*) head and neck rubbing in a genet; *C*) the penetration of the genet's perineal gland scent about 5 cm. into hardwood; *D*) scent and urine deposition within a cage: left arrow: urine encrustation on a vertical cage support; right arrow: perineal gland scent deposit on the edge of a diagonal plywood support; *E*) flank-wiping with a partially masticated mouse in a ♀ *Paradoxurus hermaphroditus*; *F*) lip-licking in a genet; *G*) neck scratching in a genet (notice how posture facilitates contact); *H*) a perineal gland scent-mark made by the ♂ *Civettictis*; the arrows point to 1 of 2 streaks made by the glandular lips.


A
B
C
D
E
F
G
H

5. Reclining-body rubbing and rolling. Though genets occasionally lie down and rub and roll with sinuous movements of the spine in the manner of a dog, the behavior is performed most frequently if the animal's fur becomes saturated with water. In addition, a wet animal often propels its body forward with the hindlegs while sliding the side of the head, neck, and shoulder on the substrate.

6. Perineal-gland marking. Of the several postures employed during the apposition of the perineal scent gland to a substrate, all are characterized by strong flexion of the hindlimbs. When the gland is pressed against a low-lying object, the squatting position may be quadrupedal or tripedal. In four-legged squatting the hindlegs are level or one is placed on an elevated object; in three-legged squatting the elevated leg is flexed. A reversed upright quadrupedal position is used in marking elevated vertical objects or the undersides of elevated horizontal and diagonal surfaces. In all positions the appression of the perineal gland to the object may be accompanied by a rhythmic lateral pelvic oscillation. Though both sexes presumably have the ability to mark by all methods, only males have been seen to use the "hand-stand" position; and, with one exception, only females have been seen to mark in a squat position. Nevertheless, the presence of elevated scent marks in cages occupied only by females suggests the hand-stand position is not sex-specific. The gland is everted shortly before or as it is apposed to the object. Eversion also occurs when animals are manually restrained or held by the tail and, at least in females, eversion

accompanied by a lordotic posture can be evoked by rubbing a finger between the labia of the relaxed gland.

The gland is a longitudinally-folded muscular pad having the appearance of two well-furred labia situated between the anus and vulva or the scrotum and penile aperture. Muscular contraction of the gland results in a parting of the labia and an eversion of the inner surface to form a firm raised oval-shaped pad covered with a fine layer of white hair (Figure 13). The median sulcus, a shallow longitudinal depression corresponding to the floor of the folded gland, is bordered anteriorly by a deeper Y-shaped crease, and centrally and posteriorly by transverse creases. According to POCOCK (1915c) each crease on either side of the median sulcus forms a crypt into which scent, produced by underlying glandular tissue, is secreted via "... a pair of laterally placed clusters of minute orifices." Apparently some species exhibit sexual differences in the number of secretory crypts (POCOCK 1915c).

A clear oily emulsion covers the inner surface of the relaxed and folded pad, but the exudate within the crypts often has a denser pomade-like consistency and a yellowish color. Although the entire pad may secrete scent, it seems likely that passive motion of the folded labia and capillary action distribute the contents of the crypts as an oily film within the folded pad. With repeated deposition on wood or metal the exudate becomes a dark brown coagulum. This color change is also true of the perineal secretion of the African civet (Civettictis civetta) (KINGSTON 1964). Repeatedly deposited scent can penetrate wood to a depth of several centimeters (Figure 16c) and retains its redolence for at least 4 years. The odor is a mildly sweet musk which according to D. MÜLLER-SCHWARZE (pers. comm.) resembles civetone from which odorous impurities such as skatole have been removed.

On three occasions when ♀♀ displayed signs of sexual receptivity, an increased frequency of scent marking was observed and the rooms in which they were caged manifested a heightened scent of urine. Over a 19-day period in which 90-minute observations were made, on alternate evenings, one ♀ (C) exhibited an erratic pattern of intense marking (Figure 14). This pattern does not seem to reflect a relationship to the gradual hormone changes characterizing the estrous cycle. Furthermore the peak in marking occurred after the apparent height of estrus. More significant perhaps is the observation that the majority of scent mark sniffing did not occur in the immediate context of scent marking. This suggests that in this situation the odor of scent perceived at close range is not important in releasing or orienting the marking act. Augmented secretory rate during estrus probably also contributes to the heavy scent accumulation at marking sites. These sites become encrusted with urine and it is my impression that both urine and vaginal secretions are deposited as the perineal gland is rubbed. A drainage of fluid from the vagina into the perineal fold would seem to be a natural consequence of the contiguity of these two structures. Estrous females were also seen dribbling urine on scent marks independent of rubbing the perineal gland.

Figure 15. Perineal scent marking and scent sniffing in a ♀ genet (C) on days before, during and after sexual receptivity. Bars = scent-marking frequency; open circles = scent-mark sniffing independent of scent-marking; circles containing dots = scent-mark sniffing following scent-marking (each circle represents one sniffing event); a = ♀ observed *in copulo* (presumed day of peak estrus); b = ♀ observed mounting her ♀ cagemate (I).

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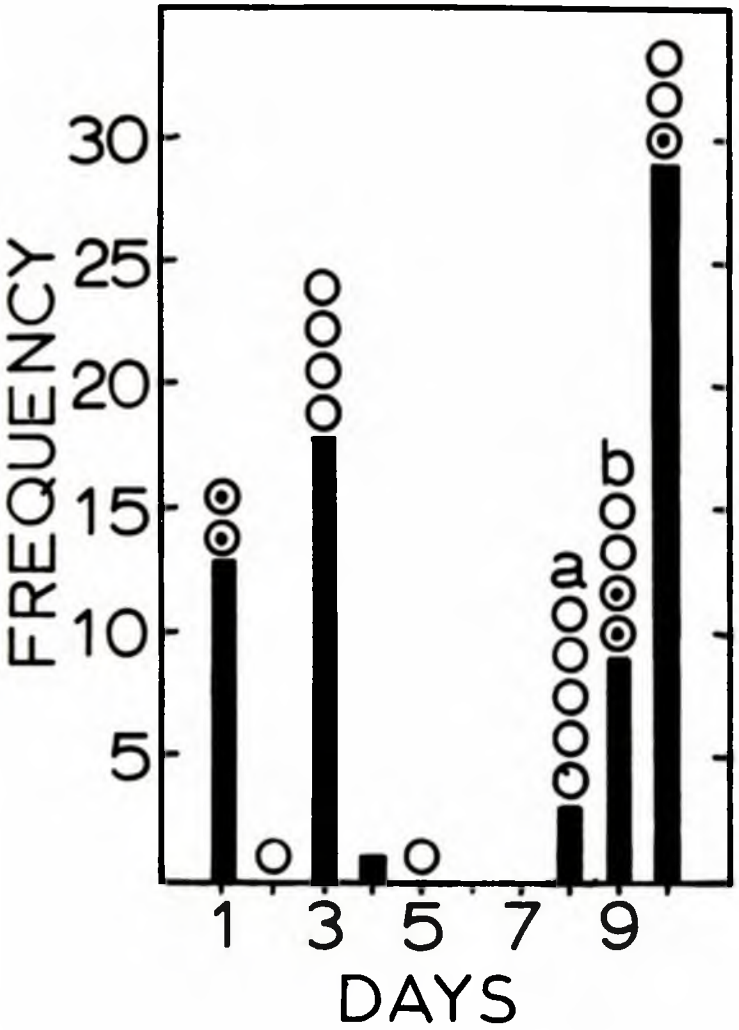

7. Anal drag. The animal assumes a sitting posture with partially spread hindlegs and walks forward with small steps as the anus is dragged on the ground. Though dragging of the perineum in a similar manner has not been seen, genets seem to be physically capable of modifying the emphasis of the drag.

8. The feet. The forefeet are used in several ways to contact and manipulate inanimate objects depending on the object's situation. An animal may touch an object while standing, sitting, or reclining on its side or back by extending a foreleg and contacting the object with the pads of the pronated or semi-supinated forepaw. The object may be drawn in toward the body by hooking the paw slightly and sometimes extending the claws while retracting the limb. A combination of adduction and retraction of the extended limb may result in weakly pushing an object aside. This is seen for instance when an animal enlarges the space between a large cardboard box and a wall. The limb being used always moves the object toward the opposite side of the body. Though usually seen as a companion-oriented contact pattern, clasping with the fore- and hindfeet occasionally involves inanimate objects. When the forelegs are used to clasp, the paws are almost always semi-supinated. The attitude of the hindlegs in clasping an object is the same as when an animal climbs down a narrow vertical log; the pads are completely or semi-supinated with the object held between or pressed against the belly.

9. The nose. The rhinarium often lightly touches the surface an animal is smelling to leave a trace of watery mucous. The ventral-

anterior portion of the rhinarium together with the upper lip on either side of the philtrum and possibly the tip of the lower jaw form an important tactile-receptive zone. This area is used to lightly touch objects being smelled, or may be used to playfully push a small object along the floor. On a few occasions an animal was seen to forcefully push the rhinarium against a novel object it was sniffing; such behavior is far more prevalent in Civettictis.

10. Other genera.

a. Scent-gland marking: A normal quadrupedal stance is employed by ♂ and ♀ Civettictis to mark surfaces at the level of the perineal gland. The gland is usually everted shortly before or as the rear-end is turned toward the marking object; one or two steps are taken in reverse; the tail is elevated and/or deflected laterally, and the gland is pressed against the surface for 2 seconds or less and usually without accompanying pelvic motion. The ♀ however was once seen to execute a weak lateral oscillation against a 1 cm mesh wire, and sometimes dipped the rear-end slightly as she ended the glandular contact. The gland usually closes immediately as the animal terminates contact. Though Civettictis have not been seen to mark low-lying objects in a squatted stance, scent marks on a cement floor (Figure 16h) may have been deposited in this way. They may also have been laid down passively as the animal was sitting.

The perineal gland in Civettictis displays a number of distinct differences from that of Genetta. It is proportionately larger and occupies a slightly more posterior position; like the gland of

Viverra zibetha described by POCOCK (1915c), the lips are confluent and partially fused anteriorly and divergent posteriorly. The gland's pouch-like character prevents its complete evacuation during scent-marking, and consequently some of the contained civetone becomes dark prior to marking. The strong mildly fetid odor of the scent disappears after several days of exposure. Wood shavings from the cage floor occasionally became lodged within the ♀'s pouch where they remained for at least several hours before being deposited with a scent-mark.

Nandinia and Paradoxurus have been seen to both drag and wipe (sans locomotion) their scent glands on inclined and horizontal logs. While these methods of scent deposition differ from one another in duration, they both show only minor differences in posture from dragging and wiping of the anus. Unlike Genetta and Civettictis the glands in these genera are thin-walled, hairless and devoid of secretory accumulation. Nandinia's gland is pregenital in position, and is freely opened into a flat, elongate oval area as the animal climbs about. This sporadic opening and closing is not associated with scent-marking, but may be a passive response to incidental skin movement. On a few occasions when the ♂ became excited a sweet-smelling odor was detected, but it is unknown whether the gland was the source. In Paradoxurus and Paguma, the gland has a circumgenital position with the penis and vulva opening centrally and the labia folding posteriorly.

Male and ♀ Hemigalus and the 3 ♀ Galidia were seen occasionally to wipe the hindquarters both spontaneously and after urination, but

I am uncertain whether these movements resulted in the deposition of specialized dermal gland exudates. GREGORY and HELLMAN briefly mention the existence of small perineal glands within the Hemigalinae, but precise information on their occurrence and structure is apparently lacking. Likewise, little is known concerning the perineal glands of the Galidiinae.

b. Neck sliding (Figure 15): Civettictis, Nandinia, and Paguma exhibit this behavior with only minor differences. It is always preceded by sniffing of the object or area to which the body contact is directed. Typically the animal stands with the head over the object and simultaneously depresses the forebody, partially rotates and turns the head, and slides the posterior cheek region or neck over the scent target until the shoulder is approached or touched. If the animal slides onto the shoulder, foreleg support of the body is relinquished. The neck and forebody is then raised, the head repositioned over the target which may again be sniffed briefly, and the motion is repeated often on the opposite side of the neck.

The main differences between the pattern in Nandinia and Paguma on the one hand, and Civettictis on the other, involve the stance and the extent of the forebody that contacts the target. While the palm civets often depress the hindquarters during neck-sliding, the rear-end in Civettictis is held almost as high as in normal standing. A consequence of Civettictis' higher center of gravity is that it tends to sometimes lose its balance once it slides onto its shoulders; rhather than rolling over, however, the animal usually

Figure 15. Neck-sliding in the African civet (Civettictis). A, B) Frontal views of alternate sides of the neck sliding over a sponge soaked in a lemon-scented detergent; C) sliding onto one shoulder: 3 feet and the neck-shoulder are supporting the body; D) sliding without foreleg support.

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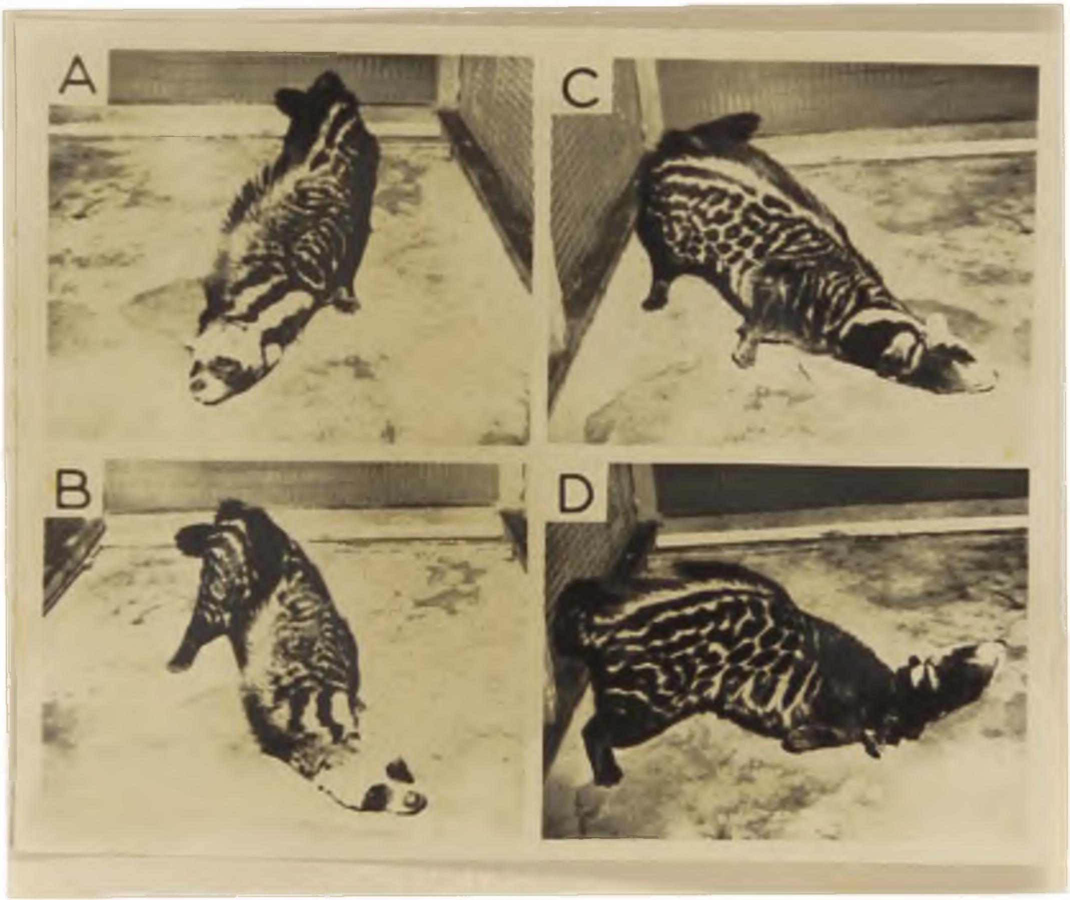

quickly regains a quadrupedal stance. Sliding onto the shoulder is less frequent in the two palm civets and when it does occur contortion of the torso is less exaggerated. In addition, Civettictis occasionally initiates neck-sliding by anointing the length of the throat with a few anterior directed and unrotated extensions of the neck. Thus the sides of the neck, the shoulder region, and to a lesser extent the throat are the chief anointing targets in Civettictis, while primarily the posterior cheek region and the sides of the neck are marked in Nandinia and Paguma.

The movement seems to be both released by and oriented to certain odors, but the odor source need not be embodied in a tactily or visually discernable object. The high degree of target specific accuracy results from the initial sniffing orientation, and also, but not necessarily, from tactile feedback from the object. Both Nandinia and Paguma neck-slid upon dead rats and mice, and in their own and other animal's (civet, genet) urine and feces. DÜCKER's (1971) ♂ and ♀ Nandinia would slide the chin, neck, and sides of the head, as well as the breast for up to 15 minutes on a board used for cutting liver. It was also released by solutions of heliotrope (Baldriantinktur) and cologne.

On several occasions after the ♂ Paguma killed large (400 g.) rats it directed its neck-sliding to the prey's lower abdomen and genitalia which had the effect of forcing a flow of urine. In these instances the movement was clearly released by and oriented to the smell of the ano-genital region, for the crushed heads of the prey were left alone, though they certainly provided a distinct alternative scent. In Civettictis, dead smelt, mice and rats, live mouse pups, genet urine, and a lemon-scented dish detergent were highly effective elicitors of this behavior; occasionally a piece of horsemeat was used. All species sometimes lick the neck-sliding target, and if the target is food it is ingester afterwards.

The effect of the neck motion on the scent source varies. Soft materials and liquids impregnate the hair as they are spread upon the substrate. The bodies of mice, rats, and fish sometimes remain stationary as the neck slides over them, but more often they slide or roll upon the ground depending upon whether the axis of the body is parallel or perpendicular to the direction of the neck movement. The pressure exerted by the neck upon the scent target must be considerable. Smelt are sometimes broken into several pieces and mouse carcasses are noticeably distorted. Mouse pups are crushed by neck-sliding and their blood stains Civettictis' white neck stripes pink. After an animal neck-slides on animal carcasses, they are usually eaten.

c. Upright quadrupedal ventrum rubbing (Abreiben in hochaufgerichteter Stellung: VOSSELER 1929): Cryptoprocta assumes an upright quadrupedal stance in order to rub the ventrum (from the sternum to the pelvis) upon vertical surfaces. The sides of objects such as vertical tree trunks are grasped with the forefeet, while the hindfeet rest on the floor on either side of the trunk; the up and down rubbing motion is generated by alternate extension and flexion of the hindlegs. The inguinal region received the majority of the rubbing in the ♂ animal I observed, while VOSSELER (1929) observed

2 ♂♂ and a ♀ to rub the breast to the inguinal region on cage projections such as metal bars, and the edges of planks and walls. An abundant and easily removeable fatty secretion on the ♂'s rust-red colored ventrum fur suggested to VOSSELER the existence of a diffuse dermal scent gland, but no macroscopic or histological investigations have been made.

Ventrum rubbing in the ♂ Cryptoprocta I observed was almost always preceded by several sequential or simultaneous activities. Most commonly the tree trunk was clawed with the forefeet and the cheeks and lips were rubbed back and forth on alternate sides of the head. At times chewing of the trunk and branches interrupted head rubbing, and at least under some circumstances, as when a new branch is placed in the cage, chewing may be intense (J. F. EISENBERG, pers. comm.). Urine is also sometimes dribbled during these activities, and on one occasion clawing, face rubbing and urination occurred simultaneously. The upright quadrupedal stance assumed during these activities differed from that during ventrum rubbing in that the hind-feet are placed several decimeters away from the trunk, and the back is bowed.

d. Side rubbing: The ♀ Nandinia was often seen to rub one side of its back by leaning against a screen wall in its cage and extending and flexing the legs, particularly the hindlegs. Besides massaging the skin, the movement also removed loose hair which accumulated at each rubbing site.

11. Communicative Function of Object-oriented Contact Patterns in Genetta. The tendency for animal companions to smell the often specific sites where body contacts are repeatedly oriented suggests that chemical communication may be an incipient or definitive function of certain object-oriented behaviors (EISENBERG 1963, 1967). Consideration of the spatial and chemical properties of the odorous substances deposited during these activities provides a convenient though subjective method of evaluating the communicative potential. Table 4 outlines and ranks some of the features of the deposits which result from object-oriented patterns.

The residue of the perineal gland (presumably civetone) is subjectively the most potent source of chemical information, for it is long-lived and is deposited in combination with other substances. At least in caged animals, scent deposits display a bimodal and sometimes discontinuous vertical distribution. This is undoubtedly favored by cage structure and limited availability of suitable objects, but the difference is also a partial function of the two basic stances assumed during marking. In the reversed upright quadrupedal stance, scent is usually deposited at an elevated position on vertical and diagonal planks, and on the undersides of raised diagonal and horizontal logs. The mean central heights of scent marks in cages at the National Zoo, for example, were 22.5 cm on vertical posts (N = 11), and 30.0 cm on diagonal logs (N = 3). Marks that were presumably made in a quadrupedal squat averaged 21.2 cm on 45° plywood edges (N = 9) (Figure 16d), or were limited to a height of 4.5 cm on the base boards of the cage (N = 6). The length of the scent mark is likewise a function of the angle of the object, though marks are also enlarged by absorption into the wood fiber. The longest marks occurred on horizontal base boards ($\bar{x}$ = 23.8 cm), medium length marks on undersides of diagonal logs ($\bar{x}$ = 14.3 cm), and on 45° plywood edges (11.8cm), and the shortest marks on vertical posts ($\bar{x}$ = 9.9 cm). If the quadrupedal squat position was used to mark the upper surfaces of elevated branches, scent marks could appear on all the branches in the cage. This, however, is not the case, as scent-marking is a strictly terrestrial activity.

There obviously has been a strong selection for elevated scent marks as a reversed upright quadrupedal stance has evolved independently in members of three carnivore lineages. In the absence of detailed information on carnivore pheromone chemistry and sensory physiology, two alternative speculations can be advanced regarding function. On the basis of BOSSERT and WILSON's (1963) findings, it seems possible that under similar atmospheric conditions the active space emanating from an elevated mark would encompass a greater volume of air than that from a lower mark. On the other hand, the diffusion properties and receiver's sensitivity may be such that elevated marks increase the probability of detection by sympatric species. This is suggested by the following observations: (1) the level of Civettictis' marks coincides and is broadly overlapped by the elevated marks of Genetta tigrina (Table 4); (2) close-range sniffing of such marks requires an upright quadrupedal or bipedal stance in Genetta, but is achieved in the

Table 4. Distribution of Scent-marks within Genet and Civet Cages at the National Zoological Park.

Scent-mark Target	Cage Occupants	Number of Scent-marks per Cage	Vertical Distance from from Substrate (in cm.)				Length of Scent-marks	
			Smallest		Greatest			
			Mean	Range	Mean	Range	Mean	Range
Genetta								
Vertical and Diagonal Surfaces	I, Fe	12	16.7	(12.5-23.0)	25.9	(19.0-32.5)	9.2	(3.5-15.5)
	E, O	6	20.3	(15.0-23.0)	33.8	(23.0-44.0)	13.4	(12.5-22.5)
	C, K	4	17.9	(8.0-24.5)	27.1	(26.0-28.5)	9.2	(3.5-18.0)
	Subtotal	22	17.9	(8.0-24.5)	29.6	(19.0-44.0)	11.3	(3.5-22.5)
Undersides of Logs	I, Fe	1	17.5		25.5		8.0	
	C, K	2	25.5	(13.0-38.0)	43.0	(30.5-55.5)	17.5	
	Subtotal	3	22.8	(13.0-38.0)	37.2	(25.5-55.5)	14.3	(8.0-17.5)
	Total	25	17.8	(8.0-38.0)	28.3	(19.0-44.0)	11.3	(3.5-22.5)
Civettictis								
Vertical Surfaces	♀	14	28.0	(21.5-30.5)	31.9	(30.0-34.0)	3.9	(2.5- 8.5)
	♂	1	30.5		33.5		3.5	
	Total	15	28.2	(21.5-30.5)	31.7	(30.0-34.0)	4.8	(2.5- 8.5)

Figure 13. The Perineal Scent-gland of the Genet. A) Closed condition, p.o. = penile opening, g.f. = glandular fold, t. = testes, a. = anus; B) everted condition, m.s. = median sulcus, l.s. = lateral sulcus. Top row: cross-sectional profiles of the closed and everted gland.

usual standing position in the civet; and (3) *Genetta* can assume a bipedal stance and thereby more than double its detection altitude when scenting the air, while *Civettictis* is only able to increase its height by leaning against an object in an upright quadrupedal stance. The latter point may seem superfluous, but MADISON and SCHOOP (1970) recently presented suggestive evidence that displaced terrestrial salamanders facilitate detection of home-area odors by climbing up into vegetation. If the similarities of genet and African civet scent imbue them with similar territorial messages, overlapping scent deposition height may be viewed as a form of character convergence promoting interspecific spacing (CODY 1969).

The deposition of perineal scent in combination with urine and vaginal fluid is probably relevant to the "exalting" effect for which civetone has been commercially exploited. It is doubtful that the chemical capacity to fix and enhance odorous components is an incidental property of civetone or for that matter other animal musks. In nearly all species in which musks have been identified (*Viverra*, *Civettictis*, *Moschus*, *Castor*, *Ondatra*), the glandular source is proximal to the genitalia and anus, thereby increasing the chance for occasional mixing of exudate and metabolites. In this connection, the relation of the gland's proximity to the genitalia and the nature of the sensation generated during scent-marking merits attention. In nearly all viverrine and paradoxurine carnivores (*Nandinia* and ♀ *Arctogalidia* excepted), the vagina and penis lie directly beneath the floor of the perineal fold, and as marking undoubtedly compresses these structures, the stimulus of scent-marking may well have a sexual manifestation during parts of the year. In estrous females the compulsive and spontaneous character of scent-marking appears to be more of a response to fluid accumulation within the fold and perhaps heightened genital sensitivity than to specific olfactory stimuli.

The characteristics of rubbing movements do not appear to be sufficiently specialized to have well-defined chemical communicative functions. As rubbing removes loose hair, massages the skin, and often has an intuitively complacent manifestation, both grooming and comfort functions seem warranted. Nevertheless, rubbing sites are important foci for sniffing, and the interpretation that different patterns may produce scent traces with differing odors is supported by (1) the finding that considerable diversity exists in the glandular composition of mammalian skin (MONTAGNA et al 1959, 1964), and (2) the observation that the circumstances associated with the three rubbing movements differ. Though sniffing is associated with the performance of all the patterns listed in Table 5, experimental evidence is required to ascertain whether it has a causative or directive function or is an incidental activity. Probably relevant to the role of sniffing is the action of the movement and the chemical natures of the body and object borne substances. Though an exchange of odorous substances undoubtedly occurs during any object-body contact, the action may be one of reciprocal exchange or may have a primarily anointing or marking effect depending upon the chemical character of the involved substances and the

Table 5. Some Characteristics of Scent Deposits Resulting from Elimination and Some Object-oriented Contact Behaviors in *Genetta tigrina*.

Behavior Pattern	Olfactory Trace[1]	Visible Deposit	Volatile Longevity[2]	Locus Specificity	Distribution of Scent	Volatile Components	Associated Activities
Metatarsus scuffing	-	-	1	?	Diffuse	Sebum, sweat	Arched-back rubbing
Arched-back rubbing	+	-	2	+	Diffuse	Sebum, sweat	Metatarsus scuffing
Head and neck rubbing	+	-	2	-	Localized	Sebum, saliva, food, and mucous traces	Feeding, self-directed movements
Perineal gland marking	+	+	5	+	Localized	Civetone, vaginal secretions, traces of sebum, urine, and saliva	Locomotion olfactory testing
Urination	+	+	3	+	Localized	Urine, vaginal secretions	Trauma, diverse associations
Defecation	+	+	4	+	Localized	Feces, trace anal scent (unknown)	Diverse associations
Anal drag	+	+	3	-	Localized	Feces, trace sebum	Defecation, diverse associations

[1] Detectable to the human nose.

[2] Ranked in increasing order of probable magnitude.

olfactory sensitivity of the message recipient.

Head and neck rubbing, for example, occurs between bouts of self-directed licking, and as responses to water on the fur and to smelling certain aromatic substances. Though the head and neck motions are similar in all three circumstances, in the first two instances it is oriented to both the ground or branch upon which the animal is resting and to the breast, forelegs, and tail. In the third situation, Flehmen is displayed as the animal licks the scent source, and the stance is modified to facilitate contact with the odorant source. Thus, in the first two situations there is probably reciprocal exchange while an anointing function accrues to rubbing in the last situation.

Arched-back rubbing and metatarsus scuffing resemble head and neck rubbing in some circumstances in that a reciprocal exchange of odorous substances occurs and that a diffuse and weak-smelling scent field remains. The causation of these patterns is quite different. Both activities occur in solitary animals either spontaneously or as responses to tactile and/or olfactory properties of the surroundings, and as apparent responses to certain of the companion-oriented behaviors of associated animals.

In view of the fact that all of the patterns listed in Table 5 are regularly exhibited by solitary animals, the communicative potential of the patterns is to an extent dependent upon the quantity of the odorant substance deposited and its volatile longevity. Whereas urine, feces, and perineal scent are durable, the glandular exudates laid down by the three rubbing patterns are probably easily vitiated by climatic conditions. It is possible on the one hand that chemical evanescence conveys recency of physical presence and hence proximity of the message sender. A consideration of the features listed in Table 5 suggests that the chance for a genet to detect an unfamiliar animal's rubbing area would be rather fortuitous. It is possible, however, that optimal rubbing targets may be in sufficiently short supply that the use of rubbing areas may be communal. The collective contribution would magnify the strength of the odor and visitation to rubbing loci would be traditional, thus alleviating total dependence upon olfactory localization.

G. Self-oriented Contact Patterns

1. The mouth. In genets three types of self-directed mouth movements are commonly seen. Two of these, licking and nibbling often occur in alternating bouts during extended grooming sessions. Licking directed to the trunk and limbs involves tongue extension and retraction coordinated usually with an upward motion of the head. The head is thus bobbed·down and up with the respective extrusion and retraction phases of the tongue. In nose licking (Nasenlecken: LEYHAUSEN 1956), the tongue slides out and up over the rhinarium and is retracted over the same path. In licking the rostrum (lips or "chops" (Lippenlecken: LEYHAUSEN 1956), the tongue is extruded anteriorly (often above the canine) and glides posteriorly to wipe the mystacial vibrissae and the upper lip musculature. The length of lip that is wiped varies, but the direction seems always to be posterior and may extend as far as the maxillary spots in front of

the eye (Figure 16f). Nibbling (Beknabbern: LEYHAUSEN 1956), a rapid repetitive biting motion in which the incisors contact the skin or fur, occupies less time than licking. Nibbling of fur may be accompanied by a simultaneous pulling movement of the head (Durch Kämmern: LEYHAUSEN 1956) sometimes apparently in response to particulate matter in the hair. The sides and nape of the neck, the throat, the interscapular region and the most anterior part of the neck are not licked and nibbled because of limited flexibility of the neck. A variety of immobile stances and reclining postures may be assumed during either of these activities.

The third type of self-directed behavior which may be termed bite-pulling involves biting the fore- and hindfoot claws with the incisors or the premolars, and pulling backwards with the head. It appears that irregularities of the claws or possibly the claw's hook provides resistance sufficient to create a distinct popping sound as the claw breaks free from the teeth. The movement undoubtedly removes flakes of keratin from the toe nails, but may also dislodge particles from between the teeth.

2. The head and neck. Rubbing movements of the head and neck are directed to the forefeet and the tail in the same manner as described for inanimate objects. Such activity may be interspersed with other self-directed licking and nibbling movements and often follows bouts of tail licking.

3. The nose. Self-directed nasal contact accompanied by sniffing is most frequently directed to the forefeet, the hindfeet, and the tail, and appears to be the least frequent of all self-directed behaviors.

4. The hindlimbs. Though the hindlegs can clasp the tail and can be pressed against the belly if the animal is suspended by the tail (see Ontogeny of Locomotion), most self-directed movement of the hindlegs involves the rhythmic scratching (SichKratzen) characteristic of most mammals. Scratching is only executed unilaterally in either sitting or standing positions and orientation to various body regions is facilitated by a variety of head, neck, and torso configurations (Figure 16g). All body areas can be scratched with the exception of the forepaws, anterior parts of the forelegs, rump, lower back, belly, and hindlegs, and tail.

5. The forelimbs. The head and the tail are the two body regions most frequently contacted by the forelimbs. The paws may be used to draw the tail closer to the body prior to licking or nibbling, or by standing on the tail. They may secure its position as it is licked, nibbled, or rubbed with the head and neck. An animal lying on its side or back may also clasp its tail with both forelimbs. Most frequently, however, the forelimbs are used in uni- or bilateral wiping of the rostrum, cheeks, eyes, forehead, ears and crown. Unilateral wiping of any part of the head is a relatively simple movement in which a raised forelimb is stroked forward with an attendant head movement facilitating contact.

Bilateral head-wiping, (washing: EISENBERG 1963; Gesichtwäsche: DÜCKER 1965; face and paws: EWER 1967, 1968), on the other hand, involves coordination of head, tongue, eye, and forelimb movements (Figure 17), and, when compared with other self-directed patterns usually follows a relatively rigid temporal program. The movement

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Figure 17. Bilateral Head-wiping in the Genet (C; 18 fps). Frame 1: licking of a forepaw; frame 12: initiation of the bout; frames 13-28: wiping of the rostrum and eyes; frames 224-245: wiping of the ears and crown. Notice the pronated forepaws and the role of head and neck movement during wiping.

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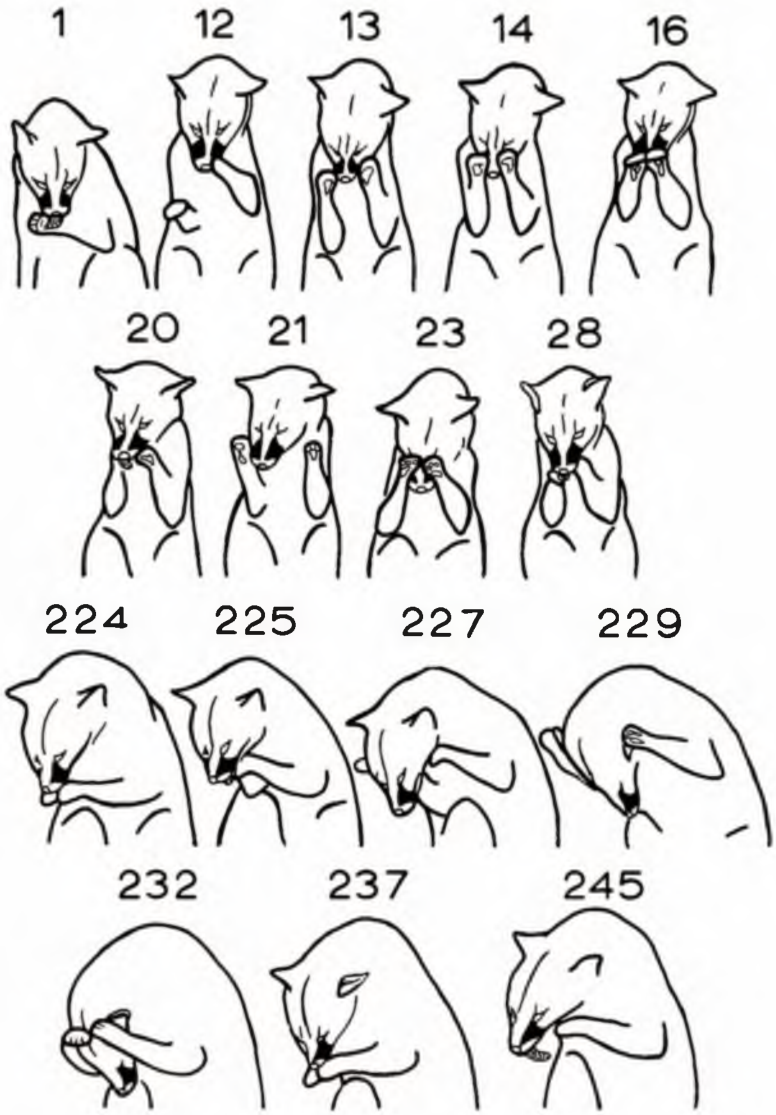

consists of synchronous elliptical motions of the forepaws which are repeated with stepwise increases in amplitude. Each cycle of forelimb motion begins and is completed at the mouth where the pronated medial surfaces of the forepaws come together and are licked at least once before they execute an ascending stroke (Figure 18). During the descending stroke and possibly during ascent, the head is contacted by the medial surfaces of the manus, wrist, and forearm. DÜCKER states that her animals employed both alternate and synchronous strokes of the forelimbs. Although in my animals the descending stroke of one limb sometimes traversed a slightly greater portion of the head, and was hence more emphatic, only occasionally did one limb lead the other by as much as perhaps a centimeter, and never were the limbs seen to be as much as even 30° out of phase during a downstroke.

6. Other genera.

a. Flank-wiping* (Figure 16e): This behavior was frequently seen in the ♀ Paradoxurus shortly after she began to masticate dead mice and young rats. The anterior part of the rodent's body was transferred from the carnassials to the incisors, and the wet bolus and hanging hindquarters of the food was dabbed in several brief posterior strokes on one or sometimes both flanks; mastication was then resumed. Wiping was only seen as long as the rodent's body was still at least half intact, and therefore occurred predominantly

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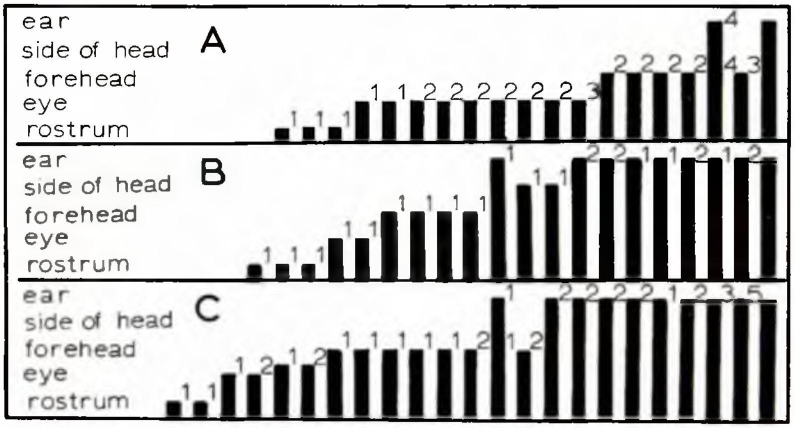
*) I am indebted to GENE MALINIAK for bringing this behavior to my attention.

Figure 18. Sequencing of wiping targets and forepaw licking during bilateral face-wiping in 3 genets, A) C, B) I, C) K (determined from 8 mm film). The height of the bars corresponds to the highest point of the wiping motion designated at the left. The number of licks directed to the forepaws is indicated between bars (wipes).


A
ear
side of head
forehead
eye
rostrum
1 1 1 1 1 2 2 2 2 2 2 3 2 2 2 2 4 4 3
B
ear
side of head
forehead
eye
rostrum
1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 1 2 1 2
C
ear
side of head
forehead
eye
rostrum
1 1 1 2 1 2 1 1 1 1 1 2 1 2 2 2 2 2 2 1 2 3 5

during the early phases of feeding on each carcass. The behavior was usually no longer exhibited after about 3 mice had been swallowed. By this time there is usually a small moist patch of fur overlying either side of the rib cage.

Like neck-sliding, flank-wiping results in the deposition of a foreign scent on a specific region of the pelage. In addition, however, a considerable quantity of the animal's own saliva is spread on the fur. Whether substances other than food are flank-wiped is unknown; hair tonic, though effective in evoking head and neck rubbing in *Genetta*, was not used for flank-wiping when placed on a paper towel.

H. Ontogeny of Shaking, Stretching and Self-directed Behaviors in *Genetta*

Shortly after birth head-shaking and jaw-gaping movements resembling yawning can be evoked by localized tactile stimulation of the head and neck. At this age stretching movements consist of simultaneous extension of both limb pairs and uni- or bilateral extension of the fore- and hindlimbs. The movements are often accompanied by neck extension and a concave back flexion. Stretching during early life is variable and even after animals are able to walk it usually occurs in reclining rather than quadrupedal body positions. The walk-stretch which was first seen at 37 days of age can probably be performed even earlier.

The jaws can execute sustained bites with considerable pressure by 2 or 3 days, and repeated biting movements resembling nibbling are directed at fingers, blankets and other soft materials.

Incipient nibbling of the body, first seen on days 4 and 8 (O and K), was directed to the forefeet; the amplitude of these jaw movements was noticeably greater than in definitive adult nibbling. Licking of the nose and lips was also first seen from 4 to 8 days, and as early as day 8 self-directed licking was seen (O and K).

The earliest ages at which animals were seen to scratch themselves in a sitting position were 9 and 13 days (O and Ma). DÜCKER observed that though the hindfoot was able to execute scratching movements at the age of 10 days, it was still slightly too short to reach the body targets until day 15 when the flank, neck, chin, ear and mouth were successfully scratched. The following protocol from my notes suggests that the apparent inability to scratch with contact is not necessarily a result of the body's mechanical limitations.

> 26 July 1967: Yesterday I was unable to induce baby genets (2 days old) to scratch themselves. Tonight, continued tickling of Clawdina's head and earbase with my finger resulted in the following responses: yawning (3 times), tucking of the head under the chest (twice), more yawning (3 times). She reacted to the sixth stimulation by extending the hindleg...forward toward her head, and there the foot quivered very slightly--seemingly involuntarily.

> After a dozen sessions of tickling Ivy's ear, she finally lifted her hindleg to the side of her head and in a slow ... movement of that foot brushed her ear lightly. The leg remained in a partially extended position with the foot lying on the neck before it recoiled to a flexed resting position.

All animals subsequently reared could be induced with repetitive stimulation to scratch either their head or neck by the age of 4 days. During repeated stimulation of the ear, the leg often initially scratched more distal body regions, such as the side and shoulder, and then approached and finally contacted the stimulation target. The ontogeny of the scratching response is discussed in more detail in the next section.

Bouts of bilateral face-wiping were first seen performed in extended body reclining positions at 29, 34, 36, and 38 days of age (I, K, E and O). The capacity to wipe the side of the face with one forepaw, however, is usually manifested by the 4th day provided there is a sufficient outside stimulus. DÜCKER's animals were first seen to employ the forefoot for self-contact at the age of 22 days.

Hand-reared animals often may have a scruffy appearance because they do not respond as the mother does to presumably unusual or foreign scent traces on their own pelage. Subjectively, it appears that tactile stimuli are more effective in inducing infants to lick and scratch themselves.

The finding that localized tactile stimulation is a simple and effective means of evoking self-directed mouth and limb movements led to the following attempt to quantify behavioral responses during early ontogeny.

1. Materials and Methods. Individuals I and C were tested on 39 and 35 days during a 50-day period beginning at the age of 5 days. All tests were carried out in the evening from 10 to 60 minutes following feeding as the animals were sleeping in their nest box. An effort was made to be consistent in the method of "tickling" the ear during the course of testing; the possibility of human error obviously cannot be dismissed, however. Bouts lasted no longer than 10 seconds and were usually terminated sooner when the animal began to respond. An interval of 2 minutes separated each bout, and each test was comprised of from 32 to 41 successive bouts, with the following exceptions. Animal C was stimulated 11, 20, 26, 24, and 6 times on days 5, 6, 8, 9, and 51; and animal I was stimulated 5, 6, 21, and 26 times on days 5, 6, 8, and 9. If an animal did not respond, it was again stimulated 2 minutes later and the bouts continued until 35 were completed. Animals at times became active in the midst of being tested. Tests were continued if they again became quiescent within 5 minutes. Testing was resumed a half hour later if the animal remained active for longer. As young animals usually sleep after being fed, it was hoped that the effects of hunger could be controlled by testing shortly after feeding. However, toward the end of the experiment both animals frequently played together for up to 40 minutes before going to sleep. Differing

hunger states may have thus affected the level of irritability on different days.

As several different responses could follow a stimulation bout, responses for each bout were chronologically numbered and entered onto a mimeographed sheet divided into 18 labeled response rows and 35 stimulation bout columns.

2. Results and Conclusions. Ear-twitching and head-shaking constituted 66.4% of the combined 3717 responses of both animals. In addition, head jerking movements accounted for 8%, and other motions of the head accounted for 15.8%. Thus, of all responses, movements of the head and ear prevailed (91.2%). Head-shaking and ear-twitching did not occur with equal frequency throughout the course of testing (Figure 19g, h). Head-shaking, which often oscillated over a wide frequency range on different days, became a less numerous response by the end of the fourth week. The decline is less pronounced for animal C because the initial values were not as high. She was also less viable than I because of an apparent inability to digest synthetic milk (Esbilac) and did not receive adequate nourishment from day 15 until day 20 when her diet was successfully changed. Ear twitching, a less variable response, showed a distinct linear increase in frequency of occurrence. The changes in these two behaviors are not reflections of an altering overall level of responsiveness, for Figure 19a shows that the level of the mean number of responses per bout, though oscillating, remained constant throughout the 50-day period. Frequency of occurrence of all behaviors oscillated on different days, probably as a function of a number of uncontrolled internal and external variables. Response diversity also varied between days

Figure 20. Responses to Localized Tactile Stimulation in 2 Infant Genets over a 50-day Period (Ages 5-55 Days). I = hollow circles, C = solid circles. A) Mean number of responses per stimulation bout (total number of responses divided by the number of stimulation bouts completed on that day), B) response diversity (number of response types divided by total number of responses per test), C-H) percentage of (C) scratch side of head, (D) scratch ear, (E) scratch neck, (F) extend hindleg, (G) shake head, and (H) twitch ear, of the total number of responses per test. (As the first 2 values of I are .82, they are not included in order to conserve space.)

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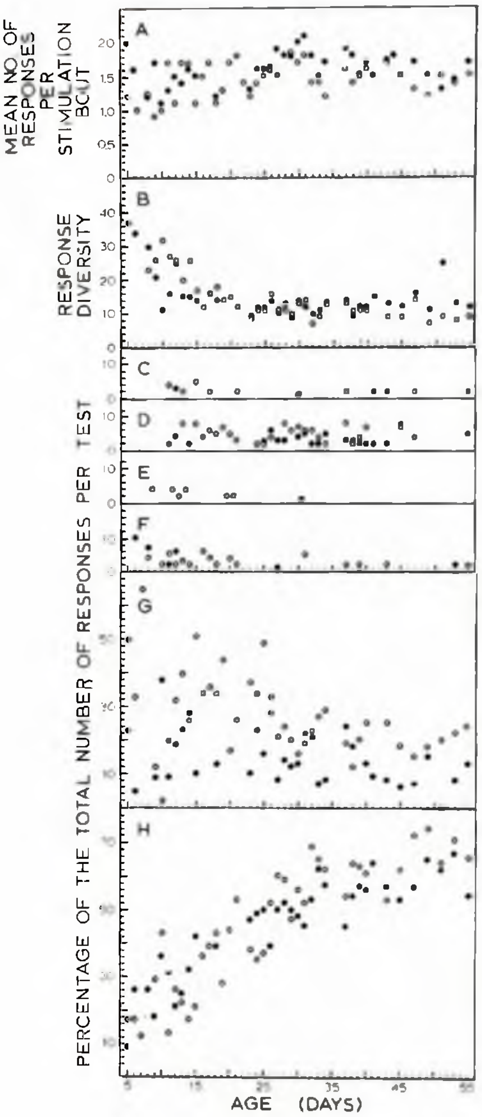

(Figure 19b), but the high values of the first 4 days are probably exaggerated because of the small numbers of stimulation bouts. The elevated figures of the succeeding 4 days suggest that responses to localized tactile stimulation may well be more varied during early infancy.

None of the remaining behaviors evoked contributed more than 1% to the total number of responses. They can be classified into those which were distributed (1) sporadically during the entire 50-day period (change body position, twitch legs, manus to side of head and ear, synchronous forelimb face-wiping, stretching); (2) predominantly during the first 25 days of testing (extend hindleg, pes to neck, yawning); and (3) predominantly during the last 25 days of testing (purring).

Though scratching can be induced by repetitive stimulation as early as 4 days after birth, under these testing conditions it was often manifested in an inaccurate or incomplete form. An anterior extension of the hindlimb, which normally precedes scratching, occurred most frequently during the first 7 to 21 days and only occasionally thereafter (Figure 19f). Scratching of the neck was irregularly performed by I during the first 20 test days, but was an uncommon event in C. While the ear was understandably the most common target of scratching (Figure 19d), the side of the head was occasionally scratched throughout the course of testing (Figure 19c).

Ear-twitching and head-shaking commonly occurred in sequences (Figure 20). Table 4 shows that ear-twitching had a relatively greater overall frequency than head-shaking, was more often a single

Table 4. Circumstances of Occurrence of Ear-twitching and Head-shaking Following Bouts of Localized Tactile Stimulation in Genets I and C from 5 to 55 Days of Age.

Circumstance	Animal I				Animal C			
	Ear twitch		Head shake		Ear twitch		Head shake	
	N	%	N	%	N	%	N	%
Single act	393	42.7	165	32.7	299	34.6	76	28.3
Preceding act	434	47.3	56	11.1	529	61.2	14	5.2
Succeeding act	91	9.9	283	56.2	36	4.2	179	66.5
Total	917		504		864		269	

act, and was more common as a serial precedent. In Figure 20 the following points are apparent: (1) Of those series which began with ear-twitching (A) over a half of animal I's (58.8%) and over a quarter of C's (28.5%) contained head-shaking B as the second serial element. (2) Seven dyads alone accounted for the majority (87.2% in I; 80.5% in C) of all serial combinations which began with ear-twitching A. (3) Though moving the head D was the most common succedent to ear-twitching in animal C, on only a few occasions did this pair of patterns give rise to triads. In both animals, on the other hand, the ear-twitch head-shake (AB) sequence predominantly gave rise to triads terminating with change head position (E) and scratch ear (K). It should also be noted that when head-shaking (B) was a dyadic antecedent (N = 52 in I), the most common second elements were also change head position (C, 26.9%), and scratch ear (K, 21.1%); extend hindleg accounted for an additional 13.4%, and of the remaining 7 dyad types none was more than 5.7% of the total. Animal C displayed only 12 dyads beginning with a head-shake.

The following conclusions may be made. (1) The most common responses were movements of the body region most proximal to that of the stimulated area (the ear); these proximal responses subjectively appeared to require less effort than less common self-directed patterns such as scratching. (2) The two predominating movements displayed somewhat reciprocal frequency changes over the 50-day test period, but they often occurred together in sequences. The most common triad contained a low effort antecedent (ear twitch) and moderate effort succedents (head-shake, scratch ear, or change head position).

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Figure 20. Percentage Occurrence in the Genets I and C of All Behavioral Dyads, Triads, and Tetrads that Began with Ear-twitching as Responses to Localized Tactile Stimulation of the Ear.

Values for I lie below the lines and to the right of the line between A and B; the total of all the figures for each animal equals 100%. The values between A and the inner ring of letters represent the percentage occurrences of dyads between the inner and 2nd ring of letters, triads; and beyond the 2nd ring, tetrads. A = ear twitching, B = head shaking, C = head jerking, D = move head and replace in original position, E = change head position, H = wipe ear with manus, K = scratch ear with pes, O = ALL OTHER PATTERNS (EXCEPT A, B, C, D, E, H, + K)

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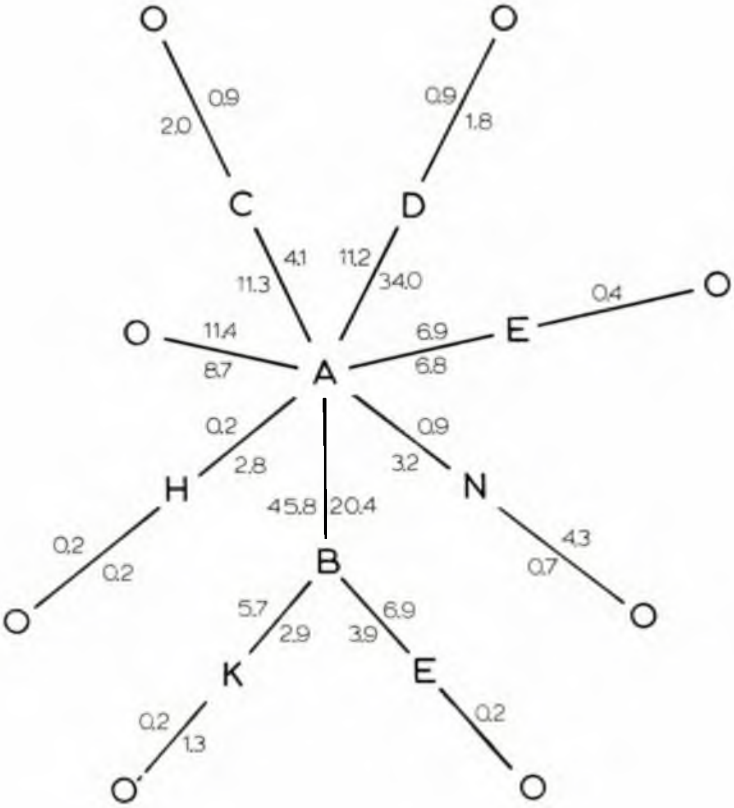

(3) Scratching was the most complicated type of response and, though it was presumably an effective means of alleviating the stimulation, it was far less common than proximal responses (ear-twitch and head-shake). (4) Lastly, the form of the scratching response was sometimes incomplete and inaccurate. It is difficult to say whether inaccuracy is a developmental characteristic, because responses to known sources of tactile stimulation were not observed in adult animals. The intention movement of scratching (anterior extension of the hindleg) however has not in my recollection been seen during grooming sessions in adults. The pattern is probably an ontogenetic peculiarity as it was seen in DÜCKER's young animals and in all of those I hand-reared. However, it more likely results from conditions of the afferent or efferent nervous pathways rather than from mechanical restrictions of body form.

I. Elimination

1. Urination. The three squatting postures assumed during perineal marking are also employed by both sexes during urination, but the crotch does not contact the substrate. Both hindlegs are commonly on the same level, but if the stream of urine is directed to low-lying objects one leg may be cocked over the object or rested upon it. Lateral swaying of the hindquarters sometimes accompanies urination in both sexes. As it is expelled the force and volume of the urine seems to oscillate rhythmically; this suggests that flow is controlled by a muscular contraction rhythm in the urethra. In estrous ♀♀, on the other hand, small amounts of urine are often dribbled upon objects in a steady flow. Urination is usually locus-specific, and animals

can easily be trained when young to urinate in a box of litter. Some genets acquire the habit of urinating in their water bowl. Once mature, however, they tend to direct the urine to the elevated edges of the box and other low-lying objects on the cage floor. The stance is usually stationary, but occasionally, when urinating on a low-lying object, several short steps may be taken forward. Animal Fe was seen to urinate in this manner on elevated branches, but in the other animals it was almost always a terrestrial activity. If frightened or traumatized, however, an animal will void urine wherever it may be, and, of course, this often occurs in the inferior animal during fighting.

2. Defecation. In adult animals of both sexes defecation occurs in a squat position with both legs on the same level. The tail is usually slightly elevated and may be pumped up and down once or twice upon completion. The pelvis is also sometimes jerked forward at the termination of the squat and presumably coincident with closing of the anal sphincter. In infants, both urination and defecation can occur spontaneously or can be evoked in reclining body postures.

3. Other genera. A squatted quadrupedal stance is assumed (with minor variation) during elimination by Civettictis, Nandinia, Paguma, Paradoxurus, Hemigalus and Fossa. Nandinia was frequently seen to urinate while slowly walking forward in a squatted posture. Urination in Nandinia, and to a lesser extent in Paradoxurus and Paguma, occurred in and on top of nest boxes, from elevated branches, and directly on the floor. Nandinia also defecated indiscriminately

about the cage, but Paradoxurus and Paguma often left feces on the tops of boxes and shelves. BARTELS (1964) reports that in Western Java Paradoxurus excrement is found in elevated positions on top of rocks, on fallen logs, and "strung out on slim branches high above the ground as well as in collections on open ground areas." Since "... the tody cat keeps going while relieving itself..." the turds have a characteristic "strung-out" (rather than heaped) appearance. The same often holds true for Nandinia. We were unable to train the hand-reared Fossa to use a litter box, and even when the animal had free run of a large room it did not display what could be considered locus-specific elimination. The two Civettictis urinated and defecated in the end of the cage opposite the nest box; the ♂ frequently urinated and defecated in his water bowl. In South Cameroun and Senegal, Civettictis often defecate along trails in small openings devoid of grass (GAILLARD 1969). Both Hemigalus and Galidia at the National Zoo urinate in the water trough.

Urination in the ♂ Paguma and ♂ Civettictis was sometimes closely associated with hindleg movements. The Paguma, for example, would dribble a small amount of urine on the floor ir its nestbox and then metatarsus scuff in it. During social interaction with the ♀, the ♂ Civettictis was seen on three occasions to urinate while walking and scratch-kicking. The urine was spurted to the rear at about 45°-60° as each hindfoot was alternately scratched backward with a kicking motion. The movement resembles the ground-scratching of dogs except that it occurs during urination as the animal walks, and the kicking stroke is shorter and briefer.

4. Communicative functions of elimination in *Genetta*.

Table 5 shows that when compared with the scent deposits resulting from object-oriented contact patterns, urine and feces rank high in properties making them olfactorily locatable. It is obvious that as odorous chemical mixtures both substances have an intrinsic value as media for information concerning individual identity, and sexual status and condition (HEDIGER 1944). Defecation in the genet is locus specific and presumably communal. Presumably it allows solitary animals in the wild to detect the existence (a chemical symbol) of another animal without confrontation (MYKYTOWYCZ 1969). In captivity both urine and feces are deposited in a single litter box, but when two boxes are provided, feces are usually restricted to one box, while urination usually takes place in both. Anal dragging, a response to voiding unusually soft feces, probably has only incidental signal function as it is infrequent and the remaining olfactory trace is probably prone to rapid fading.

Genet urine is apparently chemically distinct though it has a pungence which characterizes many viverrine and paradoxurine carnivores. CRAWHALL and SEGAL (1965) found that *Genetta tigrina*[1] excretes unusually large amounts of sulfocysteine, and concluded that the substance is neither absorbed from the diet nor results from intestinal microbial metabolism. As amino acids lack the aromatic properties of cyclic hydrocarbons, it is doubtful that the compound

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[1] These specimens were incorrectly identified by the National Zoological Park (cited Washington Zoo) as *Genetta genetta neumanni*.

contributes significantly to the olfactory quality of urine. However, this notable feature does suggest that whatever the odorous components in the urine are, they may likewise be distinct and species typical.

J. Discussion: Some Selected Inter-Generic Comparisons and Derivational Schemes

There can be little doubt that body form is a dominant variable limiting behavioral expression. Inter-taxa behavioral comparisons usually reveal a small number of fundamental patterns whose ubiquity probably results from a similar (possibly primitive) nervous mechanism and a capacity for movement that is relatively uninfluenced by the structural divergence exhibited by terrestrial mammalian orders. Definitive adult patterns which fall into this category are sniffing, licking and nibbling movements, scratching with the hindfoot, head and body shaking, generalized pilo-erection, squatting eliminative stance, the tripedal stance, and the walking gait. Licking movements (nose, lips, and body licking) for example are generalized motions performed by the majority of terrestrial species that have spatulate intra-oral tongues (Type I tongues of DORAN and BAGGETT 1971).

Though coordination of fundamental patterns is usually similar between species, differences which do exist are often clear reflections of structural adaptations for speed or arboreality. Both Fossa and Nandinia, for instance, can touch the pes to the inside of the opposite leg, but this scratching orientation is less commonly displayed by the former than the latter. The lack of an extensive rotatory capacity in Fossa's pelvic appendage may be among the factors accounting for this difference. The dexterity of Nandinia's hind-leg on the other hand probably reflects a primary adaptation for arboreal locomotion, especially head-first vertical descent. As adaptations for climbing and speed imbue differing mechanical properties to the skeleton and muscles, it is not surprising that behavioral differences between species do not always parallel taxonomic distinctions. This contention is supported by Table 7, which compares the distribution of several behavior patterns between members of 4 subfamilies. I have included the first 2 behavioral items in Table 7 (bipedal stance and head-first vertical descent) to give an indirect comparative measure of arboreal specialization. The assumption is that civets unable to descend trunks head-first or stand bipedally, exhibit morphological correlates of at least incipient cursorial specialization, namely digitigrady and suppression of transverse and rotatory limb motion (HOWELL 1965). In the following discussion, which in part is based on Table 7, similarities and differences should be viewed in light of locomotory adaptation as well as systematic status.

Both the long- and the walk-stretch are probably the most common and most frequently performed stretching patterns in carnivores as well as many other mammals. In their complete form, both of these patterns consist of 2 primary and independently performed components, namely stretching of the forequarters and stretching of the hindquarters. The differences between the patterns result from the association of the walk-stretch with forward progression. In the typical walk-stretch the forelegs are sub-equally to unequally extended as

Table 7. Comparisons Between Selected Viverrid Genera of Stationary Stances, Stretching, and Object- and Self-oriented Contact Patterns. (+ = present; - = absent; +? or -? = probably present or absent, but substantiation needed; blank = uncertain.)

			Genetta^1	Prionodon^1	Civettictis^1	Viverricula^1	Arctictis^2	Nandinia^2	Paradoxurus^2	Paguma^2	Fossa^3	Cryptoprocta^4
Stationary Stances		Bipedal stance	+	+	-	+	+	+	+	+	-	+?
		Head-first vertical descent	+	+	-	-	+	+	+	+	-	+
Stretching		Long-stretch	+		+			+	+	+	+	+
		Walk-stretch	+	+		+	+	+	+		+	+
		Arched-back stretch	+	+	+?		-	+				
Object-oriented Contact Patterns		Metatarsus scuffing	+		-			-	+	+	-	
		Head and neck rubbing	+		-			-	+	+	+	
		Neck sliding	-	-?	+	+?		+	-	+	-	
	Scent-marking Patterns	Quadrupedal squat	+	-	+	+?	+	+	+		-	-
		Perineal drag	-	-	+	+?	+	+	-	+	-	-
		Normal quadrupedal	-	-	+	+	-	-	-		-	-
		Reversed upright quadrupedal	+	-	-		-	-	-	-	-	-
		Upright quadrupedal	-	-	-	-			-	+?	-	+
Self-oriented Movements		Bilateral head wiping	+	+	-	+	-	+	-	?	-	-?
		References	a	a	a	b	ac	ad	a	a	ae	afg

1 = Viverrinae; 2 = Paradoxurinae; 3 = Hemigalinae; 4 = Cryptoproctinae.

a = Personal observations; b = DÜCKER 1957; c = HUF 1965; d = DÜCKER 1971; e = ALBIGNAC 1970a; f = LABIGNAC 1970b; g = VOSSELER 1929.

the forequarters are depressed and the hindlegs then take one to several stiff-legged steps. In the typical long-stretch, the forelegs are equally extended in the first phase, and the hindlegs equally extended in the second phase.

The variation of these patterns within a species or individual, however, does not suggest a clear evolutionarily interpretable trend. Genetta, for example, performs walk-stretches with the forelegs equally or subequally extended, and partial walk-stretches in which the 2 forelimb variants are manifested in the absence of the hindquarter stretch (the stiff-legged walk). The same holds for Nandinia and Paradoxurus. Civettictis, on the other hand, stretches like a dog; the forebody is depressed as the forelegs are equally extended forward. Nevertheless, both the civet and domestic dog occasionally terminate such a forequarter stretch with several short steps of the posteriorly extended hindlegs. Quantitative data are clearly needed to establish relative frequencies of the different stretching coordinations.

The categorization of complicated and component coordinations (such as fore- and hindquarter stretches) into walk- and long stretches obscures the possibility that these component coordinations were the precursor elements which combined in time to produce the walk- and long-stretch. Alternatively it is possible that the widespread walk-stretch pattern was the prototype which through fragmentation and changes in form gave rise to fore- and hindquarter stretches, and evolved into the long-stretch through loss of the association with walking. The arched-back stretch is equally enigmatic, occurring in erinaceids (PODUSCHKA 1969) as well as felids and viverrids.

Bilateral face-wiping is an almost identical movement in the Viverrinae and Paradoxurinae exhibiting it (Table 7); Nandinia, which differs slightly from Genetta, holds its forepaws in a semi-protracted position and consequently after each descending stroke they do not meet on their medial surfaces. According to DÜCKER (1965), the pattern in Viverricula also resembles that of Genetta, except that it is performed in a reclining position. Civettictis on the other hand lacks this behavior, though I once saw the ♀ make a strained but synchronous forepaw contact to the nose as she reclined in a lateral extended position. The ability to touch the head simultaneously with the forepaws, however, is widespread within the Carnivora; even domestic dogs will eventually remove a rubber band placed about the snout with simultaneous use of the dew claws. Though bilateral face wiping has not been seen in paradoxurines, other than Nandinia, the forelimbs appear to have ample dexterity. Unilateral face wiping on the other hand was uncommonly seen in Paradoxurus, Paguma, and Arctictis, and rarely seen in Civettictis and Fossa.

With the exception of BURGER's study (1959), bilateral face-wiping has been overlooked as one of the most complex and stereotyped of mammalian behaviors. The resemblance in the coordination and form of this pattern between Insectivores, Tupaiids, rodents, marsupials and carnivores implies either remarkable convergence in neurophysiological evolution, or retention among disjunct lineages of a primitive and formerly widespread pattern. The pattern in the species

I have observed* exhibits the following similarities: (1) bipedal stance, (2) forelimb motions with progressively increasing amplitude, and (3) forepaw licking strongly linked to the completion of each wiping motion (at least initially during the bout). The primary differences between species relate to the posture and action of the manus, the phase relationships of the forelimbs to one another during wiping, and the speed with which the movement is executed. No combination of behavioral, morphological, or ecological criteria can be used to accurately predict which species possess bilateral face wiping within their repertoires, and consequently it has little utility as a taxonomic character.

Subjectively the pattern seems to occur only in species with either (1) lax pelage, or (2) a tactile receptive field on the face composed of long vibrissae and possibly scattered tylotrichs, and (3) a gross body form sufficiently generalized that the limbs have considerable freedom of movement in several planes. This appendicular feature is displayed by non-brachiating arboreal and semi-arboreal species, and those terrestrial species having plantigrade feet. The existence of this pattern in carnivores is highly unusual and suggestive of a more widespread occurrence among the extinct viverrines which presumably gave rise to modern forms. This is confirmed by the occurrence of unilateral face-wiping in many felids (LEYHAUSEN 1956)

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*/ Viverridae: Nandinia, Genetta, Prionodon; Didelphidae: Didelphis virginianus, Marmosa robinsoni, Caluromysiops irrupta, Caluromys lanatus, Chironectes minimus; Phalangeridae: Phalanger gymnotus, P. orientalis, Petaurus breviceps; Dasyuridae: Dasyuroides byrnei, Sminthopsis macrura; Insectivora: Sorex sp., Blarina brevicauda, Microgale talazaci, M. dobsoni, Echinosorex gymnurus.

and its resemblance to bilateral wiping in the form of the motion and the alternating lick and wipe pattern. Furthermore, no movements resembling bilateral face-wiping are known in the most convergently similar arctoid carnivores, such as Potos and Bassaricyon (POGLAYEN-NEUWALL 1962, 1965) and Bassariscus (H. EGOSCUE pers. comm.). On the other hand, this behavior is exhibited by several mustelids (Mustela erminea, M. frenata, Spilogale putorius: EGOSCUE pers. comm.). The bilateral forepaw patting motion that Enhydra lutra directs to its head superficially resembles face wiping. As the movement lacks an association with paw licking and is directed to the entire body, it is probably derived from a behavior pattern other than the one in question.

In the felids and viverrids in which uni- or bilateral face wiping is a regular constituent of the toilet that precedes activity or follows feeding, the pattern's appearance seems to be largely self-generated, or at least more responsive to afferent input from the stomach or the mouth, lips, and vibrissae. EWER (1967) has postulated a scheme which simulates the sequential and repetitive character of grooming sessions based on the interaction of the excitatory levels of the component actions. In those species which only on occasion employ unilateral face wiping, its appearance seems largely governed by external stimuli, and the causal linkage of unilateral wiping to other self-directed patterns seems to be weak or lacking. Fossa fossa, for example, was rarely seen to wipe its snout, but a loose deciduous premolar precipitated a prolonged series of wiping motions that eventually dislodged the tooth.

Head and neck rubbing and neck and shoulder sliding (Table 7) are basically similar in that largely overlapping anterior parts of the body are rubbed. The former pattern, however, is generalized in the sense that it is evoked by a variety of circumstances and its component motions exhibit variable forms, duration, and temporal organization. On the contrary, neck and shoulder sliding seems to be evoked only by certain aromatic substances and consists of one motion repeated with frequently alternating lateral emphasis. Though it is tempting to interpret neck and shoulder sliding as a simplified and exaggerated version of _Genetta_'s rubbing movement, the following observations supply a more logical alternative: (1) Domestic dogs, mustelids (_M. frenata_, _M. erminea_ pers. obs.) and viverrids (_Genetta_, _Nandinia_, _Fossa_) when thoroughly wet sometimes propel themselves forward with the hindlegs while sliding on the side of the head, neck, and to a lesser extent the shoulder. (2) Sliding movements, in which the substrate contact coincides largely with the extension rather than retraction phase of the neck motion, occur in several species as a response to a strong odor field (canids, _Eira barbara_, the 3 viverrids included), and/or in which a dermal scent-producing gland occupies the cheek, throat, neck, or sternal region) (_Trichosurus vulpecula_, _Helogale undulata_: ZANNIER 1965, probably _Herpestes auropunctatus_: D. NELLIS pers. comm.). In dogs neck sliding directed to animal dung may be repeated several times on alternate sides of the neck, or it may occur only as a brief preliminary to rolling about on the sides and back. When in heat ♀ domestic cats apparently spontaneously initiate rolling and rubbing of the body by slowly gliding the neck to the shoulder on the substrate while standing (LEYHAUSEN 1960).

In comparison, neck and shoulder sliding as a prefatory component of body rolling and rubbing appears to be an incipient expression of the definitive pattern seen in civets. According to DÜCKER, neck rubbing (Kinn- und Halsscheuern) in Viverricula is followed by vigorous bouts of body rolling and rubbing. The factors which have selected for the abandonment of body rolling in favor of only neck sliding are obscure; however, the simplification of the movement may be linked to intensification of the sniffing role; brief sniffing bouts are frequently interposed between each sliding motion during the onset of a bout.

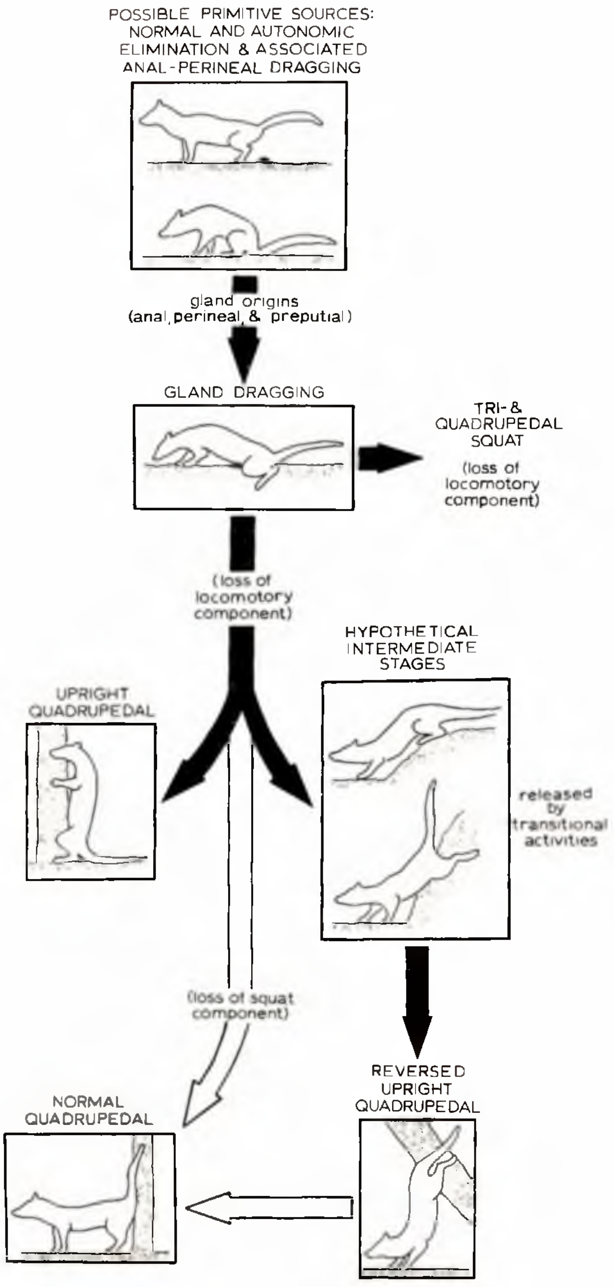
Table 7 attests to the intra- and interspecific variation in the methods by which the selected viverrids appress the pre-genital or perineal gland to inanimate objects. The most common marking methods, namely the perineal drag and quadrupedal squat, have a distinct resemblance to anal dragging and differ from it chiefly in the angle of the pelvis and hence the emphasis of contact. The physical similarity of these 3 movements, and the fact that anal dragging is a prevalent response among morphologically generalized mammals to moisture, feces, or particulate matter on the anus or hindquarters, suggests that both perineal and anal dragging primitively shared common causal features related to elimination. (For the sake of clarity in this discussion, the terms anal drag and perineal drag will be used to designate the presumed primitive cleaning movement and the scent deposition movement assumed herewith to be its derivative.)

The hypothesized significance of autonomic elimination for the evolution of many types of ano-genital scent glands is founded on the following observations. In many mammals reflex discharge of urine and feces is most frequently caused by hostile inter- and intraspecific interaction, often results in ano-genital contamination and is consequently followed by anal dragging and self-directed licking and nibbling. Contained within this complex are the preadapted behavioral sources of 2 distinct modes of scent deposition and a potential social referent and/or message receiver. To elucidate, both autonomic defecation and anal gland evaculation share common features of agonistic contexts and protrusion or eversion of the anus. The implication is that anal protrusion was a possible source of anal scent emission. Anal dragging may likewise have served as a behavioral vehicle which potentiated the development of glandular fields in the anal, perineal, and pregenital regions.

The remaining 3 viverrid marking patterns (Table 7, Fig. 21) differ from the perineal drag in that the association with forward progression has been relinquished and glandular deposition is mediated by a simple pressing motion (quadrupedal stance in Civettictis), a uni-directional wipe (reversed upright quadrupedal stance in Genetta), or a rubbing motion (antero-posterior in Cryptoprocta or lateral in Genetta). A fundamental similarity of the 2 upright quadrupedal patterns (reversed and normal) to the perineal drag can be appreciated by visualizing the necessary postural adjustments that would accompany rotation of the marking log to a horizontal plane (Fig. 21). The implication that both patterns arose as concomitant expressions of arboreal locomotory abilities need not be true. The postural properties of the reversed quadrupedal upright, for example, characterize 2 situations which could conceivably have served as transitional activities in the sense of LIND (1959). As an animal steps from an elevated position to a lower level, the effective angle of descent and center of gravity are decreased by depression of the hindquarters and the acquisition of a spinal concavity (Fig. 21). The loss of this hypothetical stepping-down component which would convert the pattern to its definitive form, could have occurred through an increased dependence upon olfactory releasers and an escape from the transitional action. The transitional act hypothesis is supported by the observation that in Cryptoprocta the upright marking stance is frequently preceded by substrate clawing accompanied by a lordotic spinal curvature; this pattern may have likewise undergone similar changes.

Alternatively and perhaps more feasibly, marking in the reversed upright quadrupedal stance may have evolved as an exaggeration of the tendency to place a slightly elevated mark by raising a hindleg over or by resting it upon the marking object (Genetta tigrina, Suricata suricatta, Herpestes edwardsi, EWER 1968). Cricetomys gambianus (EWER 1967) and ♀ Speothos venaticus (KLEIMAN 1966) achieve more elevated marks by walking backwards up inclined surfaces; such a method is feasibly intermediate to the technique used by Genetta, in which the hindquarters are raised up to the marking position via a quick handstand and without climbing up backwards.

Figure 21. A Derivational Scheme of Some Stances Employed by Viverrid Carnivores during Scent-marking. Arrows point to specific stances exhibited by extant species and a hypothetical intermediate stage. Black arrows designate logical evolutionary pathways of stances in which glandular contact with the substrate is mediated by variations on the squatting theme. The white arrows designate 2 possible (but less logical) sources of the normal quadrupedal marking stance from a squatting stance.


POSSIBLE PRIMITIVE SOURCES: NORMAL AND AUTONOMIC ELIMINATION & ASSOCIATED ANAL-PERINEAL DRAGGING
gland origins (anal, perineal, & preputial)
GLAND DRAGGING
TRI- & QUADRUPEDAL SQUAT
(loss of locomotory component)
(loss of locomotory component)
HYPOTHETICAL INTERMEDIATE STAGES
UPRIGHT QUADRUPEDAL
released by transitional activities
(loss of squat component)
REVERSED UPRIGHT QUADRUPEDAL
NORMAL QUADRUPEDAL

The simple pressing glandular contact and the absence of the squat component indicate a minimal resemblance of the quadrupedal marking pattern to the perineal drag. Derivation from the perineal drag or squat presumably involved a concurrent posterior shift in glandular position for, other than a slight spreading of the hind-legs and lifting of the tail, the quadrupedal marking pattern exhibits no other postural adjustments. *De novo* origin of this pattern is only tenable if it is assumed that perineal glands evolved independently in the semi-arboreal and terrestrial viverrines after divergence from the common ancestor. The remote resemblance of marking with the perineal gland in a normal quadrupedal stance is perhaps a manifestation of *Civettictis*' particular subcursorial habitus.

VI. THE BEHAVIOR OF ASSOCIATED ANIMALS

A. Description.

Patterns of behavior that are performed by animals under solitary conditions, also occur in the presence of other animals. A number of behaviors, however, seem to occur predominantly in the presence of conspecifics because their execution requires an animal referent, or because stimuli and contexts associated with interaction are usually absent in solitary situations. The classification of some of these behavior patterns into the solitary or social realm is equivocal. Generalized pilo-erection, for example, is mediated through any or all of the sensory systems; the characteristics of the stimuli are not specific manifestations of social contexts. Under the conditions of this study, however, certain patterns of pilo-erection were seen primarily in social contexts, hence their inclusion in this section.

The descriptions in Part A define types of body motion as they were identified and recorded during social encounters and subsequently analyzed. With the exception of vocalization which is distinguished by broadcast transmission, the other behaviors are classified on the basis of orientational and spatial characteristics of their occurrence. The perceptual effect and presumably the message of each pattern is or may be modified when executed concurrently with other patterns; thus, the behaviors described under each category represent components which may be combined within and between categories and modified by independent variables such as velocity of movement and posture.

Part B analyzes the organization of signals in time and the dynamics of social interaction in Genetta and Civettictis.

1. Companion-oriented Locomotion.

a. Approaching: Technically, any movement of one animal that decreases the distance between it and a companion may be defined as an approach. Such a definition would include movement tangential to, but not oriented specifically to the other animal. As any movement of one or two animals will involve spatial changes which may have no immediate social significance, approach has only been used to describe those cases in which a decreasing distance between two animals is accompanied by at least one animal maintaining a frontal orientation to some part of the other animal's body Fig. 25a).

b. Departure: This term was used to describe the net movement of one or both animals away from the immediate vicinity of the companion. In most cases a departure was defined as the separation of animals engaging in contact, or the movement of one animal out of a one body length perimeter of space surrounding the companion's head and body.

c. Following: An animal was described as following when its locomotion and spatial orientation was closely correlated with and apparently guided by the companion's movements. Following was usually a distinct action because the animals trotted briskly at close proximity, with the follower at the rear or side of the leader.

d. Circling: When the locomotion of each of two animals is oriented toward the side or hindquarters of the partner, the course of movement is circular. This is seen during mutual sniffing of the hindquarters or when both animals attempt nasal contact with the partner's rear end. This definition of mutual orientation to the companion's body excludes following in which the path is circular.

e. Encircling: Occasionally as one animal remained stationary or moved slowly its companion would walk or trot about it in a tight circle.

f. Jumping-over: Though this pattern may involve an approach and departure, it is best described as a separate case in which the body of one animal passes over the companion's body. During bouts of interaction involving extensive body contact, an animal may jump over another without leaving the partner's proximity. It may be executed by an animal traversing a tree limb in order to negotiate the obstacle its resting companion's body presents.

g. Gait and postural variables: Speed of movement and postural variants of the walking gait add additional though somewhat overlapping dimensions to simple spatial changes resulting from the locomotory movement of two animals (see Gait-associated postures). While approaching, following, and departure may involve any gait, circling and encircling are only performed in a walk or trot. The association of postural configurations with types of companion-oriented locomotion has not been consistently pursued, but it appears that nearly all the variants diagrammed in Figure 6 (b-f) are exhibited by approaching animals, while departing animals rarely exhibit postural variants involving crouched forequarters (Fig. 6b, d).

When a directed gait is interrupted by a stance, the postural configuration of the spine is usually retained. As there is no discrete distinction between a slow walk and brief alternating tri- and quadrupedal stances, the stances described in the following section represent the stationary extreme of a graded continuum of non-contact oriented behavior.

2. Companion-oriented stances. Visual fixation of a companion requires only that the head be oriented in the companion's direction, but in a number of circumstances, particularly when a stranger is encountered, relatively long periods of time may be occupied by often protracted bouts of staring. The stances assumed during visual fixation are characterized by (1) rigid-appearing immobility, (2) interruption by brief periods of walking but often unbroken visual contact, and (3) the maintenance of a particular body orientation to the companion irrespective of the companion's movement. Table 8 presents a rough approximation of the way these stationary body positions are associated with the orientation of the torso relative to the companion's body. It is clear that with the exception of the normal quadrupedal stance there is a tendency for the body to be low during frontal orientation and high during lateral or tangential orientation (Fig. 25a). This is in part a result of the association of the low or crouched stances with approach toward the companion whereas the high or arched-back stances are usually seen in a context of avoidance.

The bipedal stance and the elongate quadrupedal crouch are usually maintained for relatively brief periods, the latter being

Table 8. Associations between Certain Stationary Body Positions and the Orientation of the Torso in Companion Oriented Stances Characterized by Protracted Visual Fixation. (++ = most frequent association, + = less frequent association, blank = uncommon association.)

		Torso Orientation Relative to the Companion		
Stance Type	Postural Variant	Frontal	Tangential	Lateral
Tripedal and Quadrupedal	Crouched fore- and hindquarters	++		
	Normal	++	++	+
	Semi-crouch fore-, semi-raised hindquarters	++	+	
	Semi-raised fore- and hindquarters		+	++
	Maximum raised fore- and hindquarters		+	++

associated with approaching a companion and establishing nasal contact.

a. Other genera. Civettictis, Paradoxurus, Paguma, Nandinia, and Fossa are capable of assuming a crouched posture while stationary or walking. Though not all these species display equal facility in maintaining this position, crouching is a fairly widespread civet capacity. With the exception of Paguma, the posture involving semi-crouched forequarters and semi-raised hindquarters (Fig. 6d) is also seen in these species as a companion-oriented stance. This body position can be converted to a low-intensity arched-back posture by straightening of the forelegs and slightly arching the back. This has been seen in Paradoxurus, Nandinia, and Fossa.

In the ♂ Nandinia, this body carriage was associated with slow and deliberate walking on branches accompanied by visual fixation of the observer or the other animal. The ♂ would reverse the direction of its movement by raising "stiff-bodied" into a bipedal position and pivoting on the hindlegs. Eye contact with the other animal during this maneuver usually was not broken. An unusual form of this bipedal pivot was displayed by the ♂ toward the strange ♀ (Fig. 22). The animal would quickly approach the ♀, rise into a high bipedal position and pivot to one side while holding the forelegs up and tightly flexed to the sides of the body. It can be seen in Figure 22 that the animal actually took several steps while standing upright.

Intense arched-back postures have only been seen in Fossa. I am reasonably certain that it does not occur in Civettictis and Nandinia, but neither Paradoxurus nor Paguma was seen under

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Figure 22. The Bipedal Pivot of the African Palm Civet (_Nandinia_). The figure is based on tracings of 16 mm ciné film (24 fps). Notice that the animal actually walked bipedally.

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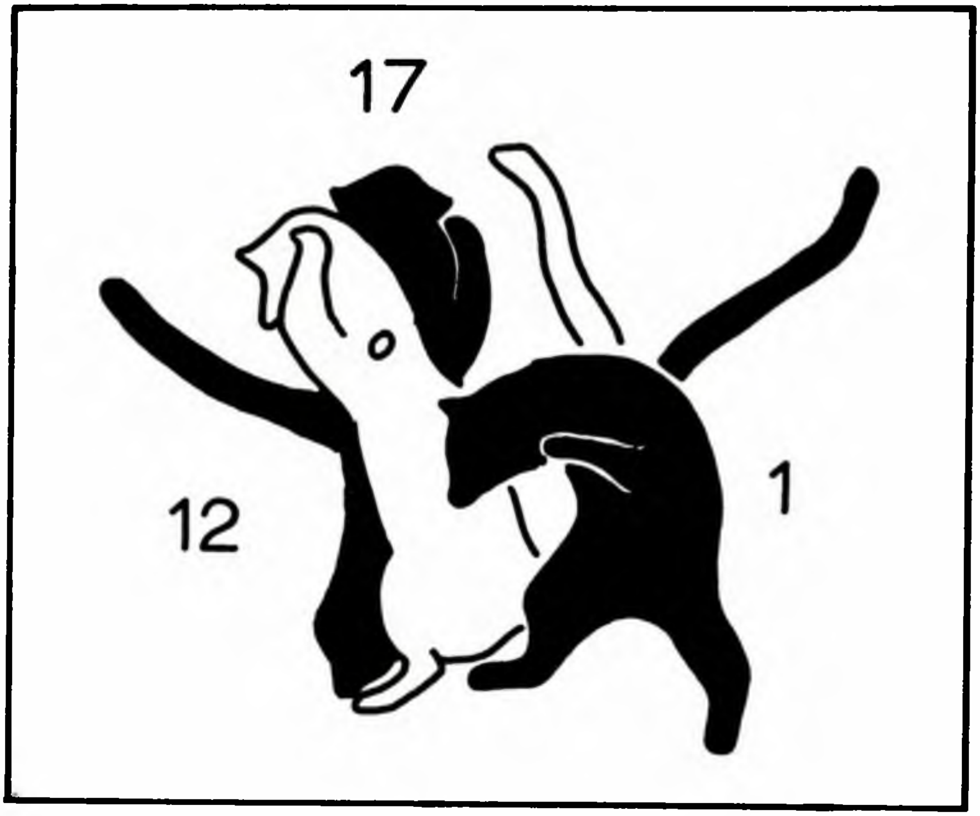


conditions conducive to this behavior (e.g. fighting). Intense arching of the back in Fossa occurs as a laterally oriented stationary stance, and the tail may be held vertically erect.

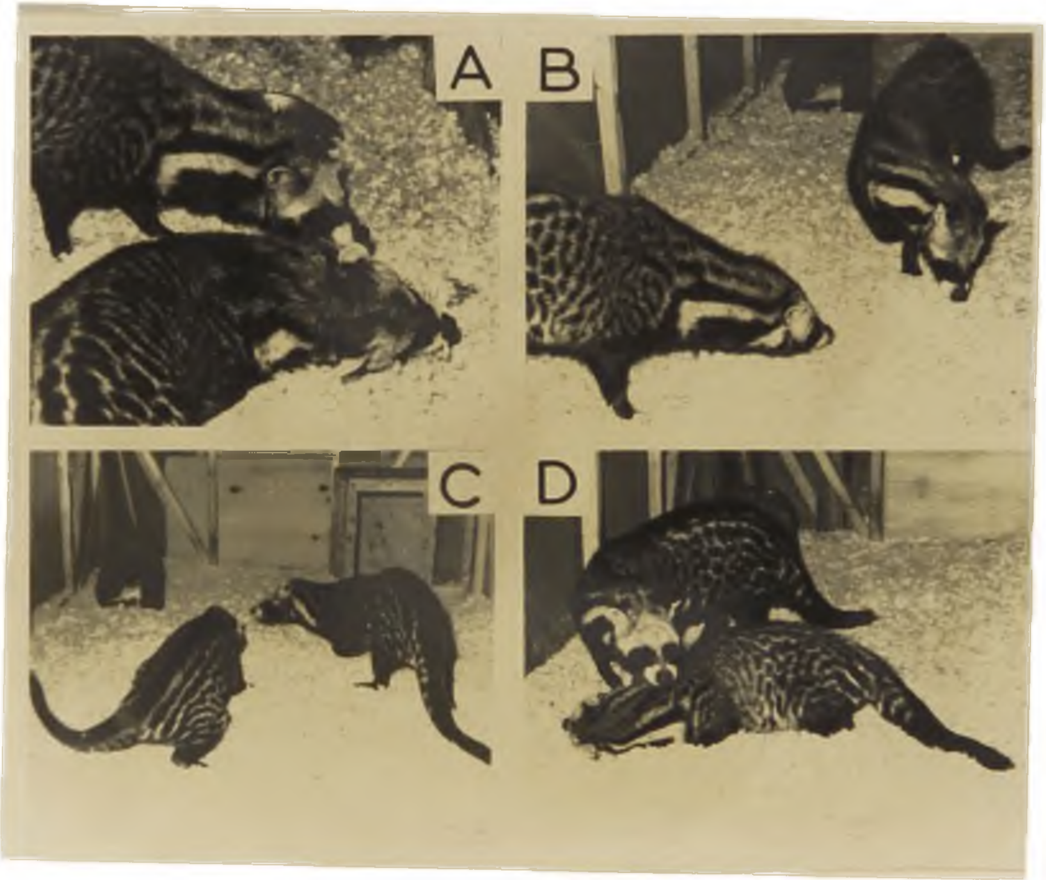
In Civettictis tangential or lateral orientation of the head, neck, and body to the companion is an outstanding aspect of social interaction. There is no simple way this can be described since the position of the head and neck is clearly dependent to a large extent upon the attitude, proximity, and orientation of the companion. In general, the neck is held at the horizontal or slanted downwards while the head is held in the same plane (Fig. 23a) or deflected downwards to as much as 60° (Fig. 23b). The head is usually rotated slightly upwards in the partner's direction (Fig. 23a, d) and may be turned slightly toward or away from and out of the companion's sight. Though it is possible for an animal to display a lateral head and neck orientation to a companion while the trunk has a frontal attitude (Fig. 23b), it is more common for the trunk axis to be tangential or lateral to the companion's head and neck (Fig. 23a, c, d).

Tangential or lateral body or head and neck orientations to a partner occur during slow walking in a normal posture, in a normal or crouched quadrupedal stance (Fig. 23c), or in reclining positions (Fig. 23a, d).

3. Non-contact body movements.

a. Erratic head movements: The simplest form of this movement involves a rapid vertical bobbing motion of the head with the neck contributing minimally. This is most frequently seen as an animal

Figure 23. Lateral and Tangential Orientations of the Head, Neck, and Body in the African Civet (*Civettictis*). *A*) Head and neck deflection in a reclining animal; *B*) lateral head and neck orientation by an approaching animal (♂); *C*) the assumption of a reclining position by an animal receiving head-darts; *D*) head deflection by a recumbent animal towards the superior companion.


A
B
C
D

is approached or followed. Such erratic motions result from rapid twisting of the neck, and lateral, circular and vertical jerking movements of the head, often associated with a brisk trotting gait, or brief bipedal stances.

b. Alternating ear motions: As described under the primary senses, this behavior may be directed toward another animal or to some other region. It is difficult to discern whether the movement itself or the independent perception of sound triggers the same response in companion animals.

c. Turning toward: Any motion of the body or its parts resulting in a frontal orientation of the face toward the companion was defined as turning towards. Facial exposure can be achieved by turning the neck to pivoting the entire body in the companion's direction. This pattern may initiate a long period of visual fixation accompanied by a companion-oriented stance or it may involve only a brief gaze in the other animal's direction.

d. Turning away: Any movement which terminates facial exposure to a companion was defined as turning away.

e. Tail wiggling: An erratic and rapid bending and extension of the tail along its length produces a spasmodic jerking motion which in its most intense form produces a rattling sound against wooden floors or a rustling sound in leaf-litter substrates. In my animals, tail wiggling was always performed in either a ventral retracted limb or an extended body reclining position, but according to LEYHAUSEN (pers. comm.) a violent thrashing motion of the tail accompanies arched-back rubbing in *Genetta rüppelli*.

f. Anal gland scent emission: The emission of anal gland scent is associated with fighting, intense attempts to avoid or escape from another animal or the reception of painful stimuli. Hence, it is not accompanied by any particular stance or movement. On the one occasion I observed scent emission at close range, the anus was briefly opened several millimeters and the fluid ejected as a barrage of about 2 dozen small drops.that traveled about 2 decimeters before striking a surface. The force of the emission is weak, and the associated circumstances such that scent is usually deposited close to the interacting animals. The scent almost always contaminates the fur of the tail and surrounding the anus, as animals usually spend considerable time licking these regions following scent release.

Anal gland scent appears to arise from two spherical structures lying beneath the tail on either side of the anus. The scent is a thin translucent light coffee-colored fluid that is highly volatile and has a slightly noxious musky odor. The odor lingers in the air for several minutes after release; to the human nose it is detectable within a radius of about 3-4 meters in a room with minimal air movement. Even after several weeks the scent residue emits a mild musky but not unpleasant odor which is detectable at close range; a washing with soap and water will not completely remove it from a cloth fabric.

g. Pilo-erection patterns: The longer hair on the head, trunk, upper legs and tail is erected in a variety of circumstances which are not always related to the presence of another animal.

The degree of erection is variable and not necessarily uniform on the body surface. Disturbance of the nap of a pelage often occurs during scratching and object-oriented congact, and uniform erection of the hair seen in resting animals is presumably associated with thermoregulation. In addition, certain patterns of pilo-erection are exhibited in circumstances involving other animals.

(1) Vibrissae. Movement of all the facial vibrissae from depressed to an erect position is presumably under the control of pili-arrectores muscles and superficial facial musculature. Maximal mobility is displayed by the mystacial vibrissae. The anterior movement of these hairs, whether or not associated with gaping of the jaws, always involves a squaring of the rostral contour (Fig. 27). Erection or depression can be gradual and arrested at a certain degree of erection or sudden. Sudden changes in vibrissae position (<1 sec.) seem to be maximal changes involving erection. Depression is usually a gradual process. The mobility of the other facial vibrissae seems to be less developed and less noticeable.

(2) Spinal crest hair. The black hair of the spinal crest, extending from immediately behind the shoulder to the base of the tail, slightly exceeds the length of the surrounding hair (Table 9). Thus, when there is uniform erection of hair on the torso, the crest is slightly elevated (Fig. 24b), but in addition it appears that the spinal crest itself can be raised to a greater extent than surrounding hair. However, maximal and prolonged erection of the crest seems to be linked with a uniform level of erection of the torso hair.

Table 9. Average Hair Lengths in mm. of the Spinal Crest and Tail in a Sample of 18 Genetta tigrina Skins in the Collection of the Division of Mammals, U.S. National Museum.[1]

		Trunk						Tail			
		Shoulder		Midback		Rump		Base		Tip	
		$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
♀♀	dorsum	17.7	16-20	21.7	20-24	25.8	22-30	24.8	21-27	20.4	16-23
N=9	side	17.1	16-19	19.4	19-22	18.8	16-20	24.8	21-27	20.4	16-23
	diff.	0.6	0- 2	2.3	0- 4	7.0	5- 9	0		0	
♂♂	dorsum	19.2	16-22	24.0	20-31	26.1	22-31	25.5	22-29	21.6	16-26
N=9	side	18.8	16-23	18.8	17-24	20.1	17-24	25.5	22-29	21.6	16-26
	diff.	0.4	-2- 4	5.2	0- 9	6.0	2-11	0		0	
♀♀+♂♂	dorsum	18.4	16-22	22.8	20-31	25.9	22-31	25.1	21-29	21.0	16-26
N=18	side	17.9	16-23	19.1	17-24	19.4	16-24	25.1	21-29	21.0	16-26
	diff.	0.5	-2- 4	3.7	0- 9	6.5	2-11	0		0	

[1] Determined by placing a mm rule perpendicular to the skin and then estimating the most common length of the longest guard hairs. The spinal crest constituted hair on the dorsum of the trunk; on the trunk the "side" was located 3 cm to one side of the dorsal midline. On the tail, the side measurement was at right angles to the dorsum measurement; tailbase = level of the third white tail ring; tail tip = a distance from the end equivalent to the tailbase measurement.

When the body hair is depressed, there is no indication of a crest.

(3) Tail hair. Degree of hair erection may be uniform or may vary along the length of the tail. A uniform level of erection seems to be the most common condition (Fig. 24c). Lengthwise pilo-erection gradients are usually unidirectional with either the terminal black segment or the first 2 to 4 white rings being the expanded portions. The velocity of hair erection and compression (hair flux) varies from moderately rapid (<2 sec.) to gradual, but cine film is necessary for accurate description of this aspect. While gradual expansion of the tail hair is more or less continuous, rapid expansion or compression is often, perhaps most frequently, step-wise. That is, rapid flux in erection or compression is followed by a period of very slow change in either direction.

h. Other genera: With the exception of alternating ear motions and tail wiggling, *Civettictis* exhibits all the non-contact body movements described for *Genetta*. The African civet is reputed to expel an anal scent (WALKER 1968) but though my animals fought on several occasions this was not detected. Unlike *Genetta*, the hair on the tail is not erected in step-wise increments. This pattern of hair flux is seen however in the well developed spinal crest. Erection of the crest results in an obvious increase in lateral body dimension and adds a light-colored stripe to the contour of the back above the level of the spine; this is not visible when the crest is relaxed because the light- colored basal segments of the hair are covered by the longer black distal segments.

4. Companion-oriented contact patterns.

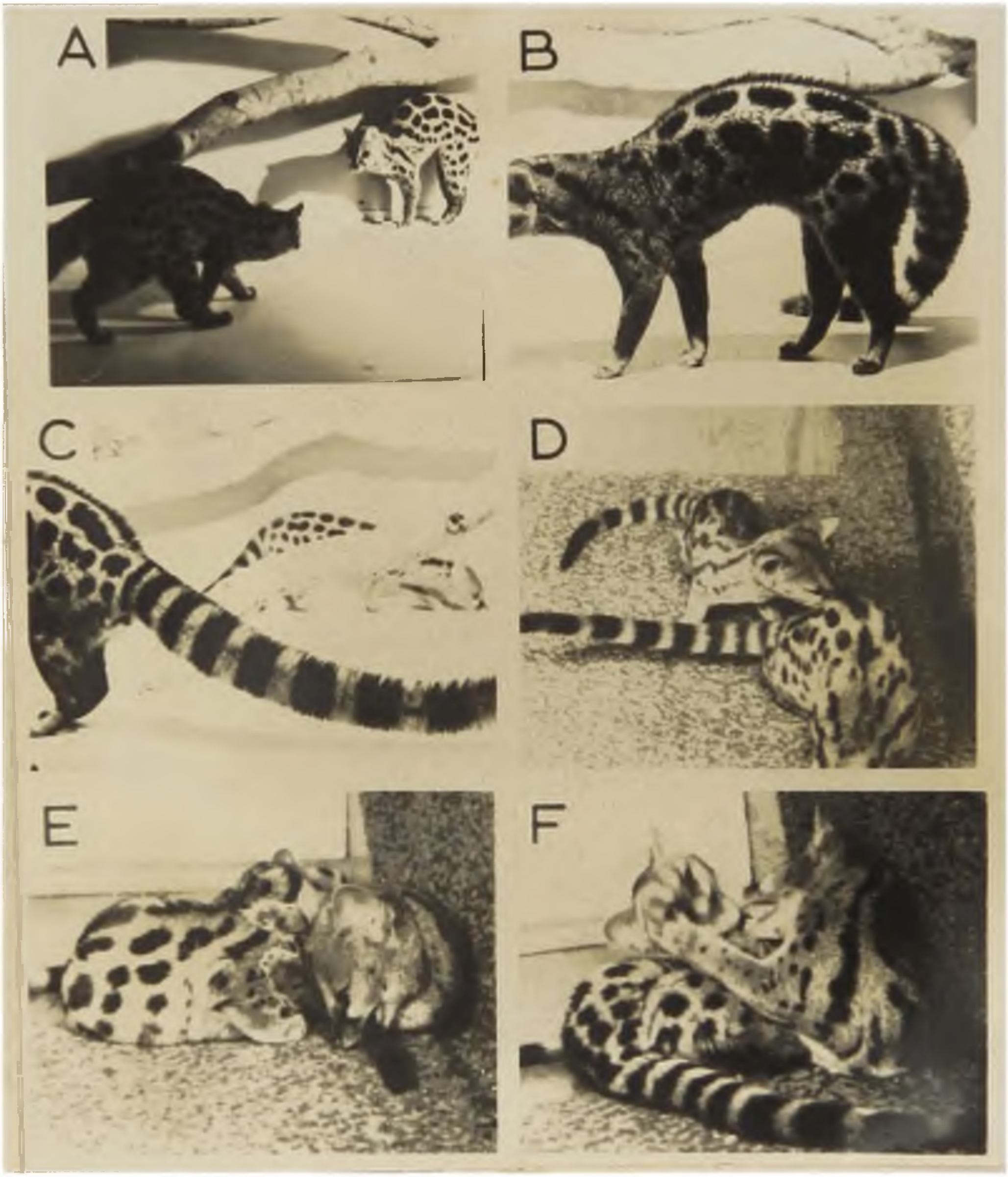
a. The head:

(1) Sniffing (Nasal contact). Sniffing of another animal does not always involve contact, but if not repelled an animal will almost always contact with its nose the fur of its companion. The nose may lightly contact the tips of the companion's hair or may be pushed through the hair to the skin. The rhinarium, lips and the lightly furred zone between them are often rubbed through the underhair and against the skin (Fig. 25d). A variety of facial expressions may be displayed as an animal sniffs and contacts a companion with its nose. When sniffing without contact the eyes are usually wide open and the ears erect and directed forward. If nasal contact is involved, there is a tendency for the eyes to be squinted and the ears oriented laterally (Fig. 23d). When the perineal gland, vagina or urine or an estrous female are smelled and/or licked by a male, the upper lips may be lifted slightly and the corners of the mouth retracted to expose the canines and premolars. This activity, Flehmen, is presumably associated with olfactory and gustatory perception via the Jacobsen's organ. The mouth is usually slightly opened, the eyes squinted, vibrissae retracted, and the orbits of the ears directed laterally in a semi-erect position.

(2) Licking and nibbling. As described for the solitary animal, these patterns may also be oriented to the body of a companion. Both of these types of mouth contact are usually associated with a relaxed facial expression. The eyes may be squinted or closed

Figure 24. Patterns of Companion-oriented Locomotion, Movements, and Contact in the Genet.

A) A crouching animal approaching a companion exhibiting an arched-back stance; B) a low intensity arched-back stance exhibiting general pilo-erection and the spinal crest; C) maximal pilo-erection of the tail; D) a juvenile genet sniffing the spinal crest hair of another animal (notice facial expression); E) a juvenile animal mouthing its companion's tail; F) pawing by an animal engaged in wrestling.


A
B
C
D
E
F

and the ears oriented laterally in a semi-erect position.

(3) Biting. Duration of contact, and force of compression and head movements during contact are three biting parameters which probably form a graded continuum. Engagement of the jaws with another animal's body can be classed as mouthing when the jaws are compressed weakly or not at all (Fig. 24e) or biting if the force is strong. Duration of biting and mouthing is highly variable. Facial characteristics of hard biting include closed eyes, depressed mystacial vibrissae, and laterally directed ear orbits that are folded posteriorly above the notch. During soft biting or mouthing the eyes may be wide open or squinted; the ears are usually held with the orbits oriented laterally, but are not folded above the notch (Fig. 23e).

(4) Head-darting (Fig. 25). This is a highly variable movement involving several levels of integration. It is a rapid form of head extension which may or may not be followed immediately after by head retraction. It may be executed with a closed mouth, with an open mouth, or with an open mouth and an explosive hiss emitted at the end of the extension phase. Figure 26 displays the variability in the duration of extension and retraction phases and the way an open mouth position may be associated with this activity. Thus, head-darting may or may not involve contacting the companion. When head-darting does involve contact, the companion is most commonly struck with the incisors and canines of the partly opened jaws. Brief snapping bites are delivered less often. Associated with such contact is a momentary squinting or closing of the eyes (Fig. 25). A backward

Figure 25. Head-darting in the Genet (E and F; 24 fps). Extension and retraction phases are illustrated in the upper and lower figures; shaded images represent the last frame in the series. Based on 16 mm ciné film of E head-darting at Fr. Notice that the recipient began to respond in less than 1/4 second.

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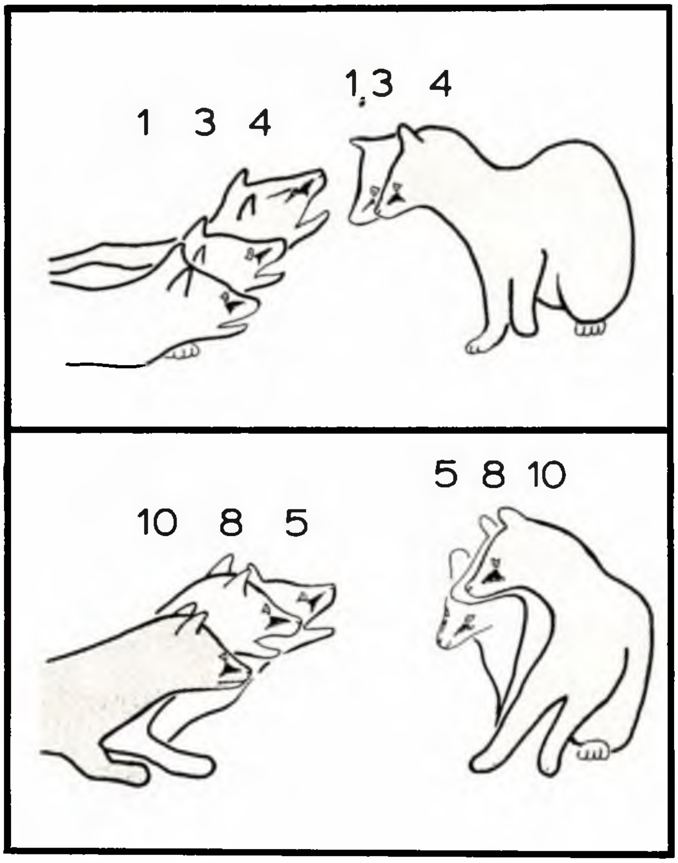

Figure 26. The Duration of the Extension and Retraction Phases in 8 Examples of Head-darting in a Genet.
Black bars = extension and retraction of the head, clear bars = opening of the mouth. The examples were taken from 16 mm ciné film (24 fps) of E head-darting at Fr; no examples involved contact with Fr, and the occurrence of hissing is not indicated.

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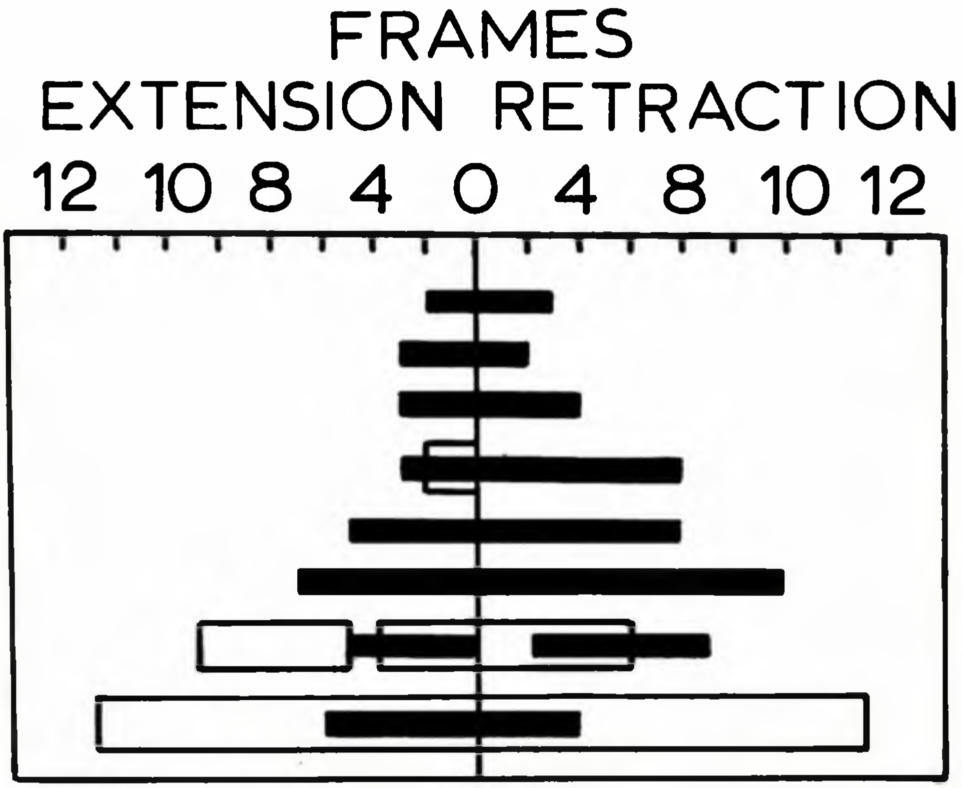


deflection of the ears is a far less frequently associated change. The mystacial vibrissae are often extended anteriorly preceding a head-dart and during the early part of neck extension, but as the subject is approached, they are retracted at least momentarily. The vibrissae may retain an extended position if the velocity of the extension phase is relatively slow.

(5) Jaw-gaping stare. The mouth may be gaped at 20-30° for varying amounts of time as an animal stares at a companion. Extended vibrissae are usually associated with a widely gaping jaw (ca 40°) and a strong tendency to dart the head at the companion. The mouth may be opened briefly and repeatedly while staring as the animal inhales between growling.

(6) Erratic head movements (see Companion-oriented Movements). When executed in the close proximity of another animal virtually any part of the head or neck may touch the companion's body.

b. The limbs: Three kinds of forelimb movement directed toward other animals can be discerned. Whether involving contact or not, pawing motions are usually brief and similar in form to those directed at inanimate objects (see Object-oriented Contact Patterns) (Fig. 24f). Stepping and standing on another animal is distinguished from pawing because the force of the contact is presumably greater and the contacting animal is usually in a superior or elevated position. Clasping of another animal's body occurs as described for inanimate objects (see Object-oriented Contact Patterns). As a partner's body is clasped, the hindlegs may also be pumped back and forth in a rapid motion with the major thrust occurring during the back-stroke. Though both legs may be pumped concurrently in a reciprocal manner, usually only one leg pumps at a time while the other is pressed against the companion's body or held free of contact in a flexed position.

The hindleg analog of pawing, kicking, consists of an often rapid extension of the limbs as the animal reclines on its side or back. When contact occurs it may be forceful and brief or light and of variable duration.

c. The trunk:

(1) Squatting over. Individuals of both sexes are sometimes seen to straddle the body of another animal with the hindlegs, and then depress the pelvic region over some part of the animal's body. This may or may not involve contact; when it does, it is not a forceful pressing movement and there is no indication that the penis is extended or the perineal gland everted. Contact of the inside of the upper legs and genital area seems to be light and intermittent. The position may be retained without movement or the animal may creep forward over the subject with small steps.

(2) Stepping over. When one animal steps over the body of another, it often briefly touches some part of the latter with the ventrum and/or hindlegs. Similar fleeting contacts may also occur when the body of another animal is jumped over.

(3) Brushing against. An animal may briefly brush any part of its body from the head to tail against the body of another animal it is passing.

(4) Somersaulting against. Occasionally as two animals are engaging in long bouts of contact behavior, one may place one side of the head on the ground and perform a lop-sided somersault by rolling over onto the neck, shoulder, and then the side.

d. Compound contact patterns: The behaviors in this category differ from those described heretofore in being composed of several independent but concurrent or simultaneous movements. The movements of the two animals may be alike and reciprocal or different and complimentary. I have used this category for practical reasons because these behaviors are more easily recognized and described at a higher level of organization. The descriptions are simplifications which outline basic elements of complicated dynamic events.

(1) Head-sparring. While frontally oriented, a pair of animals may mutually swing and toss their heads in apparent efforts to avoid mouth striking or biting by the companion. The character of the movement resembles that of erratic head movements except that there is an evident action-reaction relationship between the animals' motions.

(2) Grappling. Each animal stands bipedally upright and paws at and clasps the companion about the head, neck, shoulders or chest, while head-sparring or head-darting and biting the other animal's head, neck, forelimbs and shoulders.

(3) Wrestling. Animals engaged in this activity maintain a braod zone of body contact in a head to head, head to rear, or cross body orientation. One or both animals may clasp the other

with the fore- and/or hindlegs, and paw at, pump, bite at or head-spar with the other. Body contact may be belly to belly, side, or back.

(4) Fighting. Combat between two animals resembles wrestling but it almost always involves a crossed-body or head to head orientation and is usually accompanied by the screaming, urination, and anal scent emission of one animal. Wrestling may grade into fighting, but in fighting movement is more rapid, body contact is usually brief, and usually one animal initiates or repeats the attack. Animals matched in size and fighting in a head to head orientation bite each other primarily on the head, neck, and breast, and usually manage only to pull out each other's hair; wounding did not occur. When a considerable size disparity exists between combatants, the larger one subdues the smaller by clasping and can bite it severely.

(5) Copulation. The ♂ clasps the ♀ from behind about the groin and rests his chest and belly upon her lumbar and sacral region. Intromission is achieved by the ♂'s pelvic thrusting and the assumption of a lordotic spinal curvature in the ♀. In one out of three copulations seen, the ♂ (K) bit the hair on the ♀'s neck (C) during the terminal seconds and pulled backwards apparently counterbalancing the precarious position that accompanied final thrusting. In the other two instances (Fe and I), biting of the ♀'s nape was not seen.

e. Other genera: The two Civettictis were not seen squatting-over, pumping with the hindfeet, or grappling. Clasping with either the fore- or hindlimbs is relatively ineffectual because the wrists and ankles have very limited powers of rotation. Consequently the African civets were unable to effectively restrain one another by clasping during wrestling or fighting. In addition the following contact patterns merit special attention.

(1) Flehmen. In *Civettictis* this is an elaborate and time-consuming pattern usually performed in a quadrupedal stance during and after sniffing and/or licking the ♀'s perineal gland, perineal scent, or urine. The first phase consists of sniffing or licking the scent source; the corners of the mouth may be slightly retracted, the ears directed laterally, and the eyes squinted; this is equivalent to Flehmen seen in *Genetta*. In the second phase, the head is raised away from the scent to approximately a horizontal level and then slowly depressed. If the facial expression was not assumed during sniffing or licking, it is assumed during the non-sniffing phase. Occasionally the eyes are closed and the tip of the tongue extended over the lower incisors. At close range a soft, brief, slowly repeated "puff" is audible, suggesting that the breath is held after sniffing and expired in small amounts at periodic intervals. The non-sniffing phase is terminated with licking of the nose and lips and sometimes a brief shaking of the head. This may be followed by another activity or resumption of sniffing.

(2) Perineal gland scent-marking. On one occasion the ♂ *Civettictis* was seen to evert the perineal gland, back up, and lightly press it against the ♀'s neck as she was sniffing the wall of the cage.

(3) Head and neck wiping. The ♂ *Civettictis* was seen on a number of occasions while walking past the ♀ to extend the head or neck toward her and with a brief extension movement wipe some part of her body.

5. Vocalizations. Table 10 compares the physical characteristics of the various genet vocalizations described in the following pages.

a. Coughing (Muckern: HERTER 1952): The cough, a brief sound pulse having a broad energy distribution and a narrow intensity latitude (Fig. 28a), is similar to and can be mistaken for a sneeze. A true sneeze, however, has a longer duration and is often accompanied by a characteristic head motion. Coughs may be phonetically rendered "üff-üff" (DÜCKER 1957) and are produced singly, in couplets or triplets, or may be repeated in long series with intervals of various duration. It could be evoked in all individuals at the day of birth and is produced throughout life. Production of the sound is preceded by a bump-like expansion of the throat, and is associated with the disappearance of the bump and a jerk-like compression of the rib cage corresponding to expiration of air through the glottis and out the nostrils. Spectrograms were occasionally obtained from individuals O, K, and C in which a weakly harmonic pulse and a wide noise band seem to fit the apparent glottal and nasal events (Fig. 28a).

b. Hissing (Fauchen):

(1) Explosive hiss (Spucken). This vocalization, phonetically rendered as a noisy "hcchhh," is another brief duration

Table 10. Physical Characteristics of Genet Vocalizations. Frequency in kHz, duration in seconds.

Vocalization	N*	Frequency Range		Fundamental Frequency	Duration	
		Total	Dominant		Smallest Discrete Elements	Call
Cough	28(O) 12(K)	.85-8.0	.85-∼7.0	--	<.07	<.07
Explosive hiss	7(O)	.85->8.0	.85->8.0	--	--	N = 7 .13 r = .07-.27
Panting hiss	12(M)	.85-7.5	.85-4.0	∼1.0-2.0	N = 12 .18 r = .11-.27	variable >1.0
Whine	94(O)	1.4->8.0	1.4-∼6.0	∼1.4	--	N = 94 .76 r = .11-3.59
Scream	9(O)	0.5-∼7.0	0.5-∼4.0	∼0.7	--	N = 9 .86 r = .42-1.5
Purr	6(K) 6 (Fr)	.85->8.0	.85-∼3.0	--	<.007	variable >1.0
Growl	6(M) 8(O)	.85-∼1.5	.85-∼1.5	--	<.007	variable >1.0

* Number of evaluated sonograms and animal.

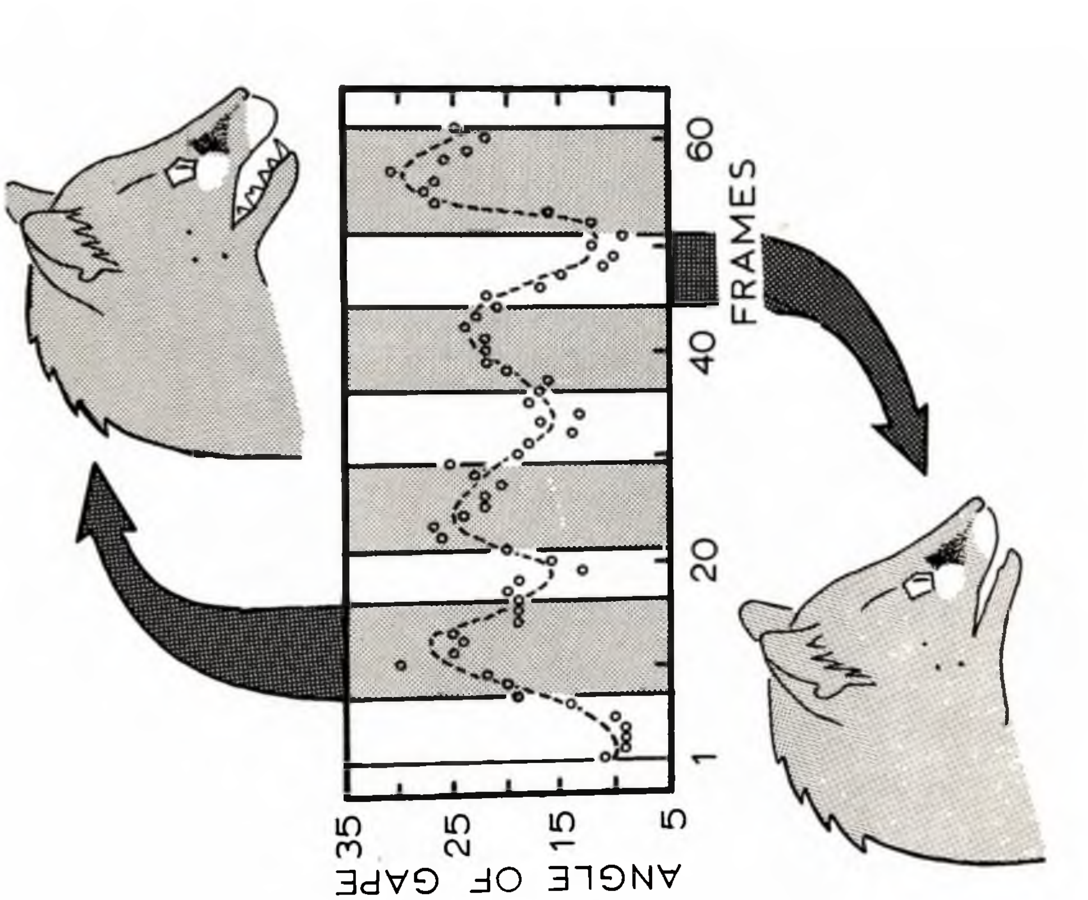
call having a broad energy distribution. It is produced by the rapid expiration of air through the opened mouth, and the extent of the mouth opening seems to be correlated with the intensity of the call. During violent hissing the mouth assumes an angle of about 35-45° and the jet of air from the glottis blows saliva out the mouth. Most of the time explosive hissing is accompanied by head-darting with the glottis opening at or near the end of the extension phase. Eye closure may or may not coincide with the production of this sound but often occurs if the mouth contacts the recipient.

(2) Panting-hiss. This call shares many of the physical characteristics of the explosive hiss, but its temporal organization is a function of accelerated respiration (Fig. 27). The expiration phase of this sound produces a broad frequency range with bands of energy concentration resembling dissapated harmonics, while inspiration produces low frequencies with lower intensity (Fig. 28d). The facial expression of this call is characterized by retracted lips and a jaw gape which varies with respiratory phase. In highly aroused animals the position of the vibrissae during the production of the panting hiss changes the contour of the muzzle (Fig. 27); thus, an intense form of the call has an expiration phase accompanied by a widening of the jaws and an extension of the vibrissae. The retraction of the lips exposes only the lower cheek teeth, canines, and incisors. The call was first observed at the ages of 2 days (F), 5 days (M and E), 13 days (O, I, and C), and 16 days (K).

Both forms of hissing may be associated with growling and screaming.

Figure 27. Facial Expression during the Panting-hiss in the Genet. (E; 24fps).

Shaded and clear columns designate expiratory and inspiratory breathing phases estimated from rib cage movements. Circles represent measurements of the jaw-gape angle made from the film. The curve was fit by eye.


ANGLE OF GAPE
35
25
15
5
1
20
40
60
FRAMES

c. Whining (Nestgezwitscher: GOETHE 1952; Quicken: DÜCKER 1957): This vocalization is highly graded within and between individuals in harmonic, intensity, and duration properties (Fig. 29a-c). The leading and/or trailing segment of a whine may be frequency modulated, and harmonic form which may vary between bouts as a probable function of activity level and general muscle tonus. Calls of moderate duration have the largest number of harmonics while very brief and very long calls have fewer harmonics. Whining is phonetically rendered "wee" or "wew," and is first produced within minutes after birth; it acquires a lower frequency as the animal matures, and is rarely produced after the animal becomes independent. Whining is almost always repetitive and performed with an open mouth, the extent of the gape varying with the intensity of the call.

d. Screaming (Schreien): The scream is essentially a very high intensity whine having a greater number of overtones (Fig. 29e). The distribution of the overtones suggests that 2 or more membrane surfaces are vibrating at different rates. Though the call is produced in situations of high autonomic arousal, the range of intensity subjectively seems to be moderate. Softer calls have fewer harmonics and as a consequence a narrower range of energy distribution (Fig. 29e, left). The sound was infrequently heard but could sometimes be evoked in animals before weaning by rough handling. Young animals seem to be unable to respond to pain or trauma with a sound more forceful than a loud whine. An open mouth, extended mystacial vibrissae, retracted lips and dilated pupils compose the facial expression which

Figure 28. Vocalizations of the Genet, the African Civet (*Civettictis*) and the Lesser Oriental Civet (*Viverricula*).

A) A sequence of 3 coughs and a whine in *Genetta* (O); *B*) a series of 8 coughs in *Viverricula* at the age of 18 days; *C*) a sequence of calls in the ♀ *Civettictis*: a snort (0.2 sec.), growling (0.6-1.0 sec.), and 2 screams (1.0-1.7, 1.9-2.4 sec.); *D*) panting-hisses in *Genetta* (M), high frequency hisses occur during expiration, low frequency hisses during inspiration; 6 respiratory cycles are displayed; *E*)purring in *Genetta* (Fr); the breaks at 0.8 and 1.7 sec. correspond to changes in the flow of glottal air; *F*) a growl grading into a scream and then into a growl again in *Genetta* (O); from 0.7 to 1.1 sec. the scream is marked by the appearance of a 0.5 kHz frequency band; *G*) a growl occurring during a single protracted expiration in *Genetta* (M).

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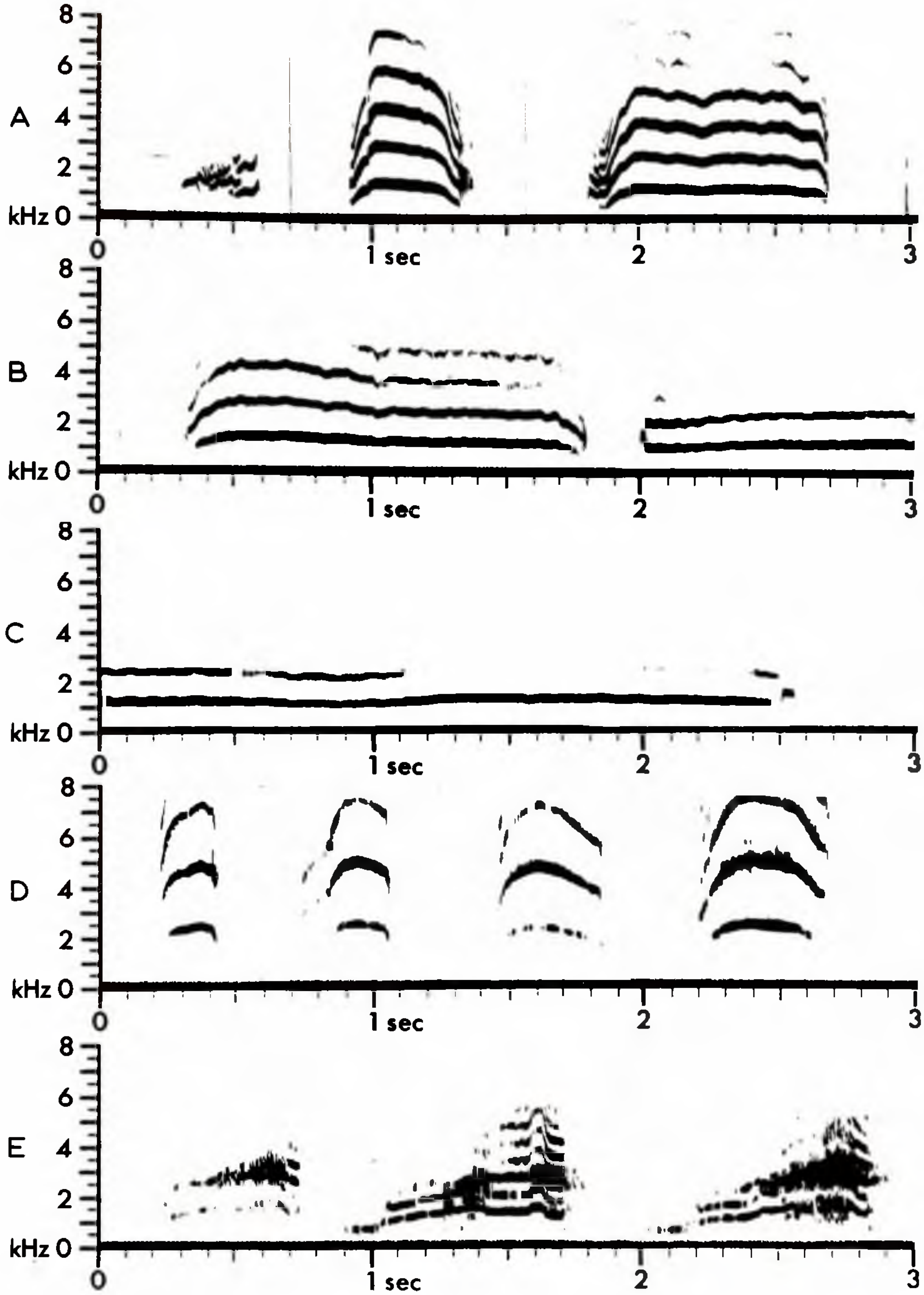

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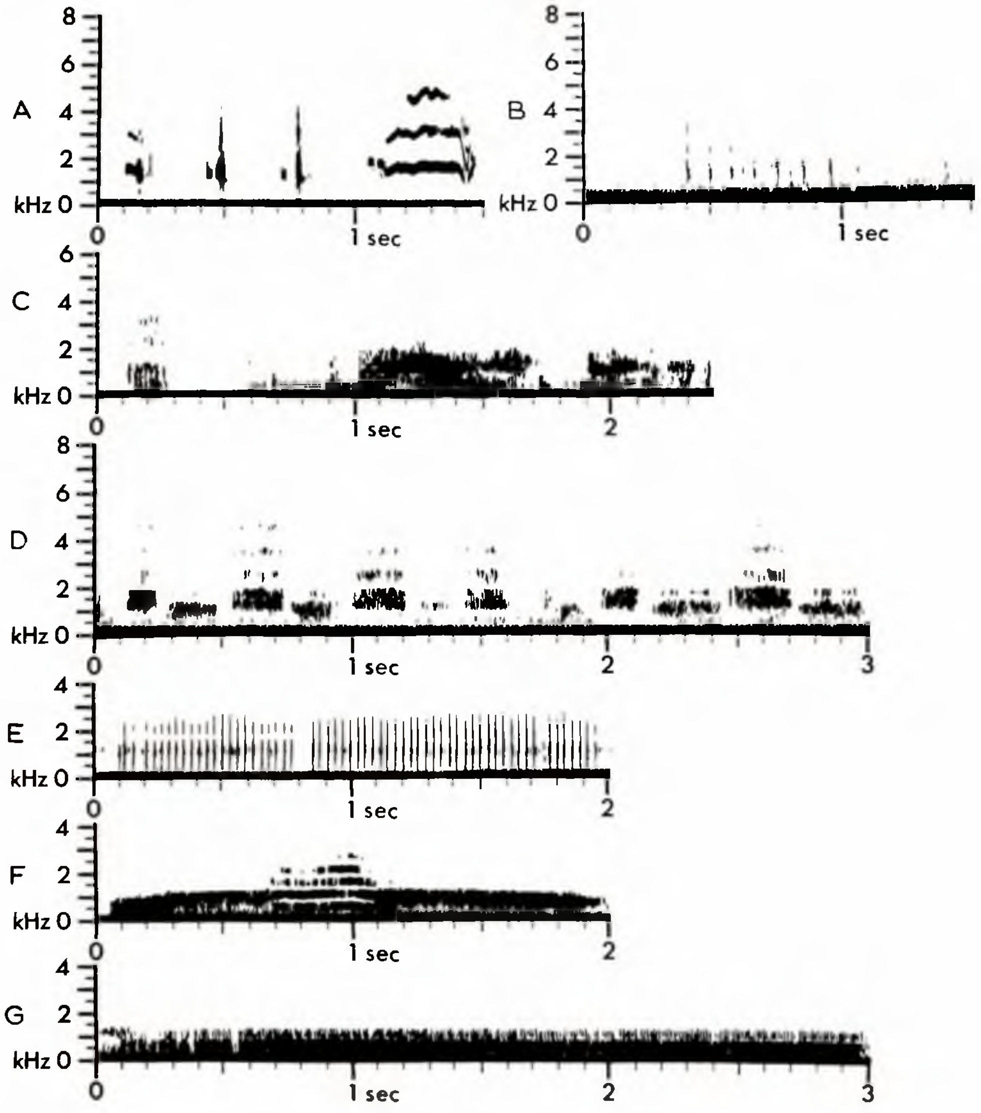
Figure 29. Vocalizations of the Genet and the Lesser Oriental Civet (*Viverricula*).

A-*C*) Variation in the whining call of the genet (K) (not a series); *D*) four examples of whining in *Viverricula* (not a series); *E*) three examples of screaming in the genet (O) (not a series).


A
B
C
D
E
F
G
kHz 0
2
4
6
8
0
1 sec
2
3

accompanies this call. Very high intensity screams display degeneration of harmonic structure and broad noise distribution (Fig. 29e, right). In such cases screams appear to grade into noisy explosive hisses.

e. Purring (Schnurren): Purring is composed of continuous and rapid volleys of low intensity clicks produced during both inspiration and expiration (Fig. 28e). Usually clusters of pulses with similar interval length are separated from other such clusters by longer intervals; these breaks in the sound undoubtedly correspond to the deceleration and direction reversal of glottal air. Purring occurs with the mouth closed or while the animal sucks milk; the eyes may or may not be closed. It was first heard at various ages: 2 days (Fr), 5 days (M, E), 13 days (O, I, C), and 16 days (K); the sound is very quiet during the first week which probably explains why I missed it in my first animals. Some genets continued to purr until they were 6 months old, but these were raised singly and were exceptionally tame. As noted by DÜCKER, purring probably does not occur in adults.

f. Growling (Knurren): Growling is a noisy, usually continuous, moderate intensity vocalization with a repetitive pulse structure. As in purring, the rhythm of growling conforms to the period of the respiratory cycle, but the sound is only produced during expiration. The duration of each uninterrupted period of sound seems to be inversely related to the level of the animal's excitation. Periods of growling in a moderately excited animal may last 10 seconds between breaths, while a greatly agitated animal growls for about 2 seconds before inhaling. Intensity of the sound is similarly related to period. Growling is often, but not always, accompanied by an alert facial contour; the ears are directed anteriorly, the pupils dilated and the mystacial vibrissae extended. It is often associated with hissing and may grade into a scream (Fig. 28f). Though first heard at the age of 80 days (0), it can probably be evoked even earlier.

g. Other genera: The occurrence of call types within selected viverrid genera is summarized in Table 11.

(1) Coughing: Viverricula malaccensis:* Unlike the coughing of Genetta, the call in this species has a click-like quality and is produced in bouts composed of several cough elements (Fig 28b). Of 7 recorded coughing bouts, 2 bouts each were composed of 6 and 7 elements, and 3 bouts contained 8 elements. The intervals separating the cough elements in a bout varied from .03-.46 sec. The majority of intervals (79%) fell within the range of .06-.12 sec. Civettictis civetta: The coughing vocalization in this species, like that of Genetta, is the most common call. It is emitted with the mouth closed and is always a rapid series of sound bursts composed of from 2-12 elements (Fig. 31). The sound is phonetically similar to, but deeper than coughing in Genetta. Fossa fossa: Coughing in the fanaloka has a distinctive quality rendered phonetically as "chuck." The intervals between coughs are variable;

---

* A recording of coughing and whining in an 18 day old ♂ born at the Brookfield Zoo was kindly made available to me by Dr. ROBERT HORWICH.

Table 11. The Occurrence of Call Types within Selected Viverrid Genera. (+ = present; - = absent; +? or -? = probably present or absent, but substantiation needed; blank = uncertain.) Calls are divided by the heavy horizontal lines into 5 major "families" on the basis of overall physical similarity; heavy vertical lines separate the genera into the Viverrinae, Paradoxurinae, and Hemigalinae (from left to right).

	Genetta	Viverricula	Civettictis	Nandinia	Paradoxurus	Paguma[1]	Fossa
Cough	+	+	+	-	-	-	+
Hiss	+	+*	+?	+	+	-	+
Snort	-	-	+	-		+	-
Whine	+	+	+?	-	+?		-
Tremelo groan			-	-	-	-	+
Bleat	-		-	+	-	-	-
Scream	+	+?	+	-?	+?		+
Purr	+			+			-
Growl	+	+*	+	-	-	-	+
Hum	-		-	+	+?	+	-
Hoot	-		-	+?		-	-
Neigh	-		-	-	+?	+	-
Σ	6	5	6	5	5	3	5

* In literature.

[1] *Paguma* was not observed in a social situation.

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Figure 30. Variation in the Number of Elements Composing Coughing Series in the ♂ and ♀ African Civet (*Civettictis*).

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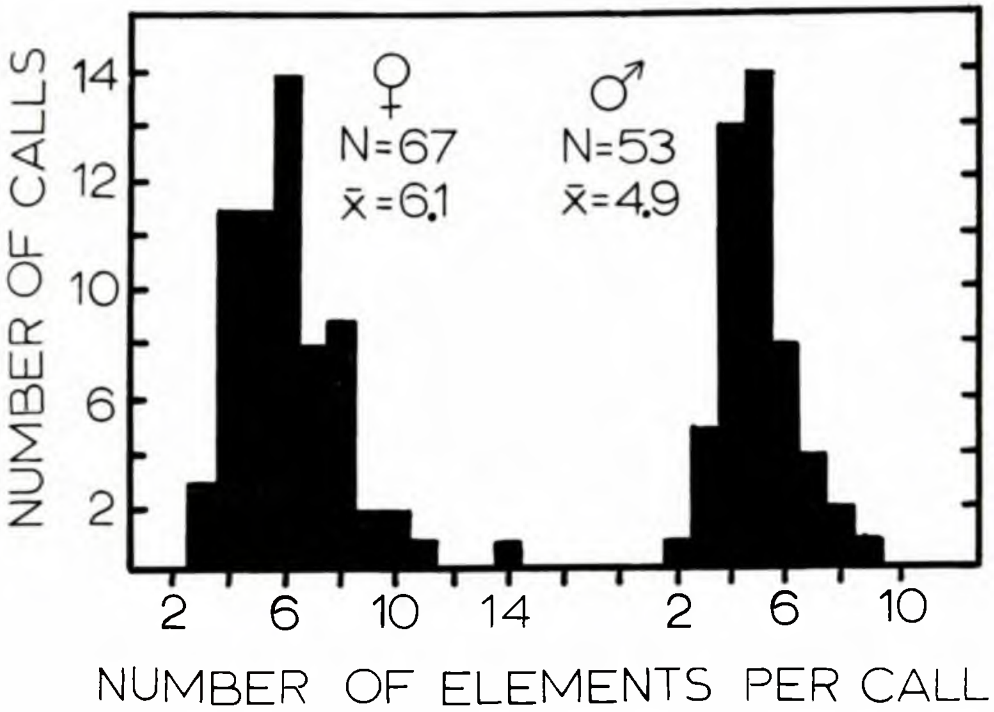

while the sound is most commonly repeated in a rapid series as in Civetticis, it is also emitted singly at longer sporadic intervals.

(2) Hissing (Snorting): Hissing or snorting was heard in all the observed genera with the exception of Viverricula. DÜCKER however recorded "spitting" (Spucken) in this species (Table 10). Snorting constitutes a specialized variant of the hiss in which the dominant lower frequencies probably result from vibration of the soft palate. Unlike hissing, however, snorting always has a loud, brief and explosive character. As infants are often unable to produce the most forceful of adult vocalizations, it is possible that hissing may replace snorting in the early life of Civettictis (Fig. 28c) (Table 10). Paguma: Though snorting or hissing may be associated with head-darting in all the observed species, limited observations on the ♂ Paguma revealed that snorting was always associated with a modified method of head-darting. The snort was produced as the animal extended and raised the neck while swinging the head upwards. At times the animal would quickly rise up off of the forefeet while snorting.

(3) Whining (Groaning, Bleating) and Screaming. Viverricula: Four whining calls out of a recording of 21 are reproduced in Figure 29d. In form these calls resemble those of Genetta except that harmonics are more widely spaced and there is relatively little variation in call duration. The 1 kHz difference in the fundamental frequences between the fanaloka and genet can be attributed to age difference. Civettictis: Whining was not heard but a recording of the ♀ screaming during a fight is presented (Fig 28c).

This sonogram is representative of 6 others. All are characterized by an aharmonic broad frequency scattering of noise. Nandinia: DÜCKER (1971) described a loud drawn-out Fiepen which is apparently heard only in young animals. This was not heard in my young ♂ when he was received at the age of about 2 months. Bleating (Fig. 31d) is a term for a call which may be a variant of whining but which DÜCKER (1971) recognized as distinct. It is produced with the mouth open and was uttered softly but spontaneously by a motionless or slowly moving solitary animal. A louder version occurred as a response to "unexpected, sudden contact of the body" as noted by DÜCKER (1971). Bleating may be rendered phonetically as "Krää" (DÜCKER 1971). Though the ♂ and ♀ Nandinia fought on several occasions, a screaming vocalization was not heard. Fossa fossa: The tremelo groan and the scream in this species usually differ in their physical properties, but both are uttered with an open mouth and sound like extremes of a graded continuum (Fig. 31a, b, c). Though the groan usually differs from the scream in having a more complicated and varied sonic structure, groans can have the discrete harmonic organization that characterizes screams devoid of vocal noise (Fig. 31, compare a, 1 with c, 3). Most sonograms of groaning consist of unbroken series of tightly spaced pulses having broad zones of frequency emphasis (Fig. 31a, calls 2 and 3, b). These pulses may resolve themselves into deep narrow chevrons (Fig. 31a, 2) or thin, broken, superimposed horizontal bands (Fig. 31b). The scream of Fossa physically resembles and sounds like that of Genetta; the fundamental frequency lies in the vicinity of 1 kHz and the harmonics are tightly packed (Fig. 31c, 1-3). Harmonic structure can also be completely disrupted (Fig. 31c, 4).

(4) *Purring*. This call was only heard in the ♂ *Nandinia* at the age of 2-3 months. Unlike DÜCKER's animals it was not heard in the 2 adults.

(5) *Growling and humming*. Figure 32b, c, and d presents growling vocalizations in *Genetta*, *Civettictis* and *Fossa*. Low frequency noise and a repetitive pulse structure are common properties of growling in all 3 species. The trace of higher frequency pulses in *Fossa* (Fig. 32d) and the predominance of these elements in *Genetta* are reflections of the young age when both animals were recorded (Fig. 32 legend). It can be seen that the humming vocalization of *Paguma* (Fig. 32a) has a fine grain pulse structure similar to the growl of the young genet. This common physical property probably accounts for the relatively smooth sound quality of the growl of young animals and the humming call of *Paguma* and *Nandinia* (Table 10). Humming, however, is frequency modulated and has a lower sound intensity than growling. In both *Paguma* and *Nandinia* it usually began at a low frequency (1 kHz) and then rose slowly and steadily to a higher pitch. As no recordings of protracted humming are available, the higher frequency levels of this call are unknown. Humming may last from several seconds to at least a half minute. As noted by DÜCKER (1971) the call resembles a siren and pairs of animals seem to hum together. Duetting was also heard in my pair of *Nandinia*. In addition, the ♂ *Nandinia* was once heard

Figure 31. Vocalizations of the Fanaloka (*Fossa*) and the African Palm Civet (*Nandinia*).

A-*B*) Four examples of the tremelo groan in *Fossa*. Notice variation in frequency and temporal structure. *C*) Four examples of screaming calls in *Fossa*. Notice variation in harmonic detail. *D*) Four examples of bleating in *Nandinia*.

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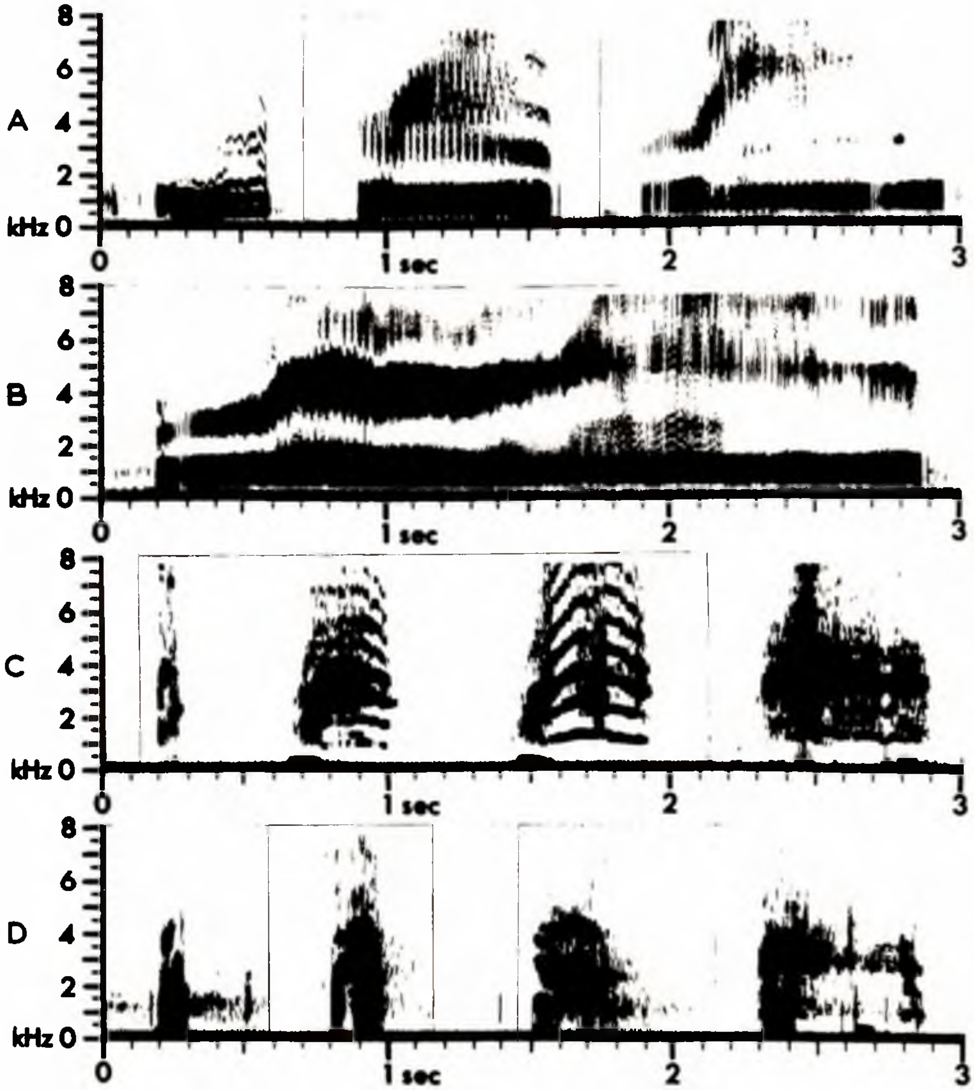

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Figure 32. Growling and Humming Vocalizations of the Genet, the African Civet (*Civettictis*), the Formosan Masked Civet (*Paguma*), and the Fanaloka (*Fossa*).

A) Humming in Paguma.

B) Growling in a juvenile *Genetta* (O).

C) Growling in an adult *Civettictis* (♀).

D) Growling in a juvenile *Fossa*.

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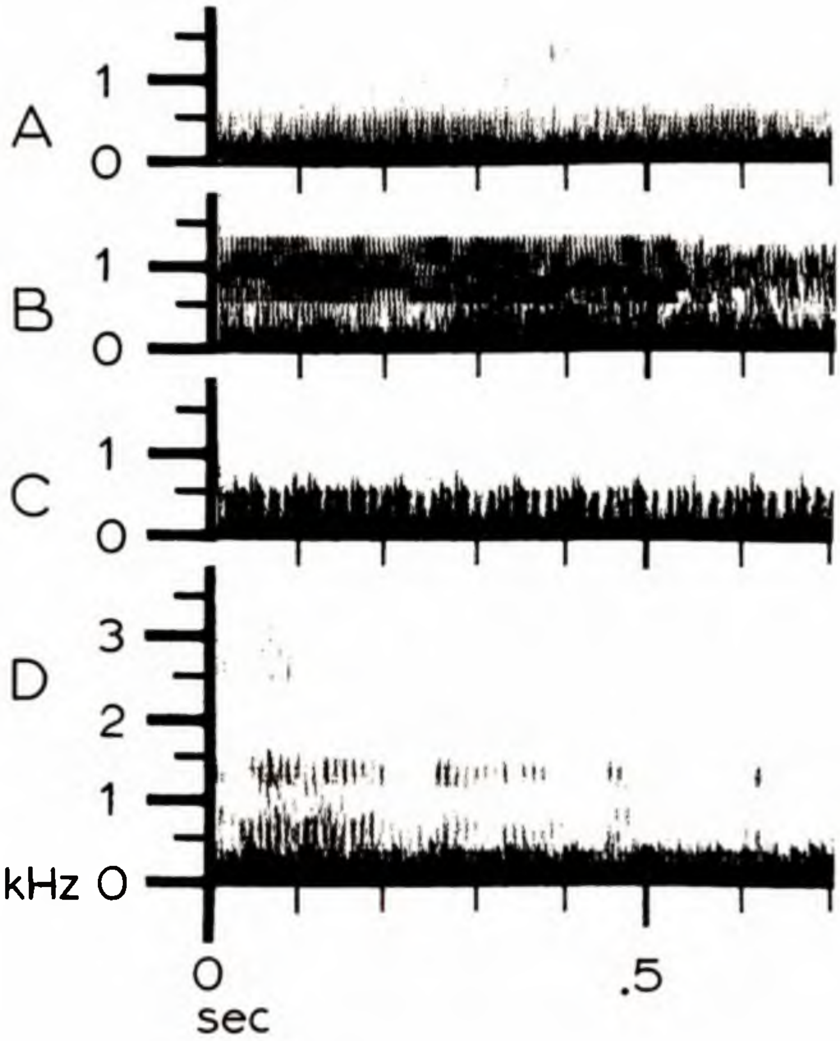

to "answer" a distant fire engine siren by matching the frequency change pattern remarkably.

(6) Hooting and Neighing. These two distinct sounding calls are produced with a partly opened mouth and share the characteristic of high intensity. Hooting was heard in an old ♂ Nandinia at the National Zoological Park. It is repeated at a rate of about 2 calls/sec., has a relatively high unvarying frequency, and can be imitated with an owl-like "hoo-hoo-hoo-hoo..." sound. Neighing in Paguma on the other hand is composed of a rapid series of brief high-pitched sounds which gradually rise and fall within a narrow frequency range; it is best rendered as "yip-yip-yip-yip...". A bout of neighing is uttered with a single drawn-out expiration.

B. Analyses of Interaction.

1. Materials and Methods. Data on social interaction in *Genetta* were collected on a socially stable group of 3 adults, and during encounters between familiar and unfamiliar pairs in a neutral observation cage.

Interactions of 3 adult genets (K, C, I) within the home cage were recorded for 90 minutes on 10 alternate evenings. Animals were fed from 2 hrs. 15 min. to 3 hrs. before observation, which with one exception began at 1900 hours; on the 6th evening observations began at 2150. The animals' activities were dictated into a Uher 1000-L tape recorder as the writer sat 1 m. from the end of the cage. After 30 minutes, a large burlap sack was placed on the floor of the cage. The sack had the effect of a novel object and induced sniffing, manipulation, and finally intense interaction between the animals. The sack was removed after 60 minutes. The recorded notes were transcribed for compilation.

Encounters were staged between familiar and unfamiliar animals in a plywood cage measuring 1.2 x 1.2 x 2.4 m. long (4 x 4 x 8 ft.) having a wire mesh top and a 1.2 x 2.4 m. plate-glass front. Animals were introduced through doors measuring 30 x 30 cm. The cage interior was covered with several coats of blue-green semi-gloss paint. The floor, walls and glass of the cage were always sponged with soapy water between series of encounters or after an encounter in which an animal urinated, defecated, or emitted anal scent. A cardboard box was placed in each rear corner of the cage and a large forked limb was placed lengthwise in the center of the floor.

One branch of this limb rested on the top of the left box. Initially a small entrance was made in each box, but after a pair of animals interacted out of sight, the fronts of boxes were cut away for visibility. Boxes were replaced after each series of encounters.

Each pair of animals was usually placed together every other day until 10 successive encounters were completed. To minimize disturbance during transfer to the encounter cage, a delay of from 1 hr. 15 min. to 6 hrs. 50 min. preceded the introduction of the second animal (Appendix A). Each animal alternated as the first to be transferred. Animals were transferred in cardboard tubes, burlap sacks, or wooden boxes; these were often explored and entered shortly after being placed in the home cage. Animals that did not enter a container were transferred in their nestboxes. Some animals had to be captured ahead of time and held in a small transport cage to reduce excitement before the second introduction could be made. After recording an encounter, each animal was allowed to enter its own nestbox and was transferred and fed. A total of 108 encounters was staged, ranging from 11 min. 40 sec. to 52 min. 50 sec. in duration; 84 (77%) of the encounters lasted 30-40 minutes. Observation time for all encounters amounted to 62 hours, 49 minutes and 32 seconds.

Tape recorded observations began as soon as the second animal entered the cage. The observer sat within an enclosed canvas blind and viewed the animals through a 30 x 60 cm. window ca. 1 m. from the cage. The room was illuminated with white fluorescent lights, but the blind was dark. Most of the time the animals seemed unaware of my presence. The durations and the targets of contact behavior on the companion's body were recorded (Fig. 33). It was not always possible to record whether proximate patterns, such as sniffing and head-darting, involved contact with the companion. Tape recorded accounts were transcribed to Esterline Angus charts at 15 cm./min. (6 in./min.) and behavioral events were numerically coded. A Model F Benson Lehner Corporation Oscar and Decimal Converter linked to an IBM Number 26 Printing Card Punch was used to transpose information on the charts to punch cards. Data were analyzed with the use of a Honeywell 2016 Computer and a CDC 6400 Computer.

The Civettictis were held separately in adjoining cages measuring 1.8 x 1.8 x 3.6 m. long (6 x 6 x 12 ft.). Encounters occurred when a gate was opened and the ♂ entered the ♀'s cage; the duration of 9 recorded encounters staged over a 14-day period ranged from 33 min. 15 sec. to 59 min. 24 sec. (Appendix A) and totaled 6 hours, 29 minutes and 4 seconds. All but the first 2 encounters occurred under infra-red light. The animals experienced an artificial light cycle of 10 hrs. dark, 14 hrs. light with onset of darkness occurring at 1430. Feeding took place at ca. 1330 and encounters began from 15-60 minutes after dark.

The observer sat unconcealed at the narrow end of the cage and notes were dictated into a tape recorder. Data tabulations were based on transcriptions of these recordings. Unless otherwise noted, data were statistically tested with the Wilcoxon matched-pairs signed-ranks test (SIEGEL 1956).

Figure 33. Body Topography Used in Designating the Targets of Sniffing and Head-darting during Encounters between Genets and African Civets (*Civettictis*). The anogenital region lies beneath the tail and between the hindlegs anterior to the penis and vagina. The belly encompasses the ventrum posterior from the chest and anterior of the genitalia.

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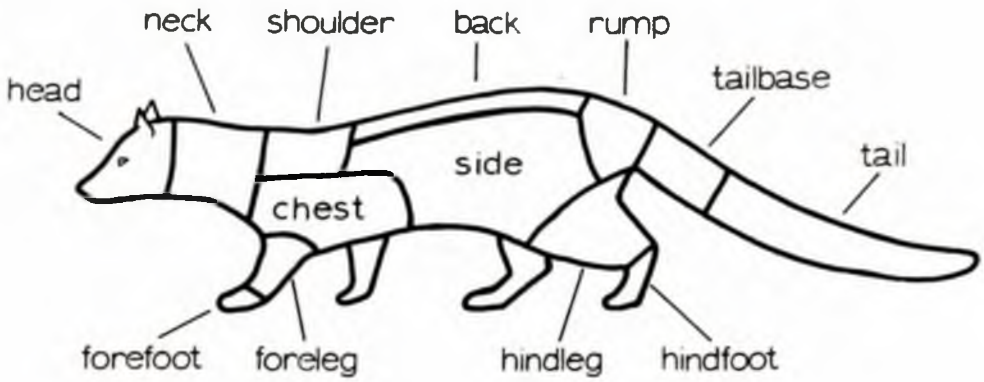

2. Results.

a. Effects of the encounter introduction schedule on behavior in Genetta: The order of introduction of the two animals in a series of encounters could directly or indirectly affect the conduct of the participants and the outcome of the encounter.. Five behaviors were selected to evaluate the effects of introducing an animal into the encounter cage before or after the introduction of its partner. Approaching and sniffing the partner were used to measure social initiative; it was hypothesized that having explored the cage, a resident animal might initiate more social interactions than the recently introduced animal. Alternatively, an animal might become quiescent after exploring an empty cage and exhibit behaviors of a restful state when the partner is introduced; yawning was used as an index of inactivity. Sniffing of the cage and climbing upon the cardboard boxes were used as measures of exploration and activity. Such behavior was hypothesized to predominate in the second animal introduced to the cage.

The frequencies of each behavior were tabulated for each animal whether it was introduced into the encounter cage before or after its partner. The total frequencies under each condition for all encounters in which the 6 animals participated were tested statistically, and only sniffing of the cage exhibited a significant difference ($P = .025$). This suggests that introducing one animal into the encounter cage a considerable time before the partner did not determine the social initiative of the participants.

b. General features of encounters: The types of interaction patterns and their frequency varied greatly between encounters involving different animals, but within any given series of encounters a certain mode of interaction generally prevailed. In this section the general features of encounters are outlined.

(1) Companion-oriented contact. Frequencies of contact between the 3 cagemates (K, I, and C) provide a base for comparison with those in the encounter situation. Social tendencies of these 3 animals are illustrated in the sociograms of Figure 34. The relative frequencies of the 4 classes of contact agree with subjective impressions gained over almost 3 years of daily observation. Contact was most frequently exchanged between the ♂ and ♀♀. This is most evident in sniffing and body contacts (Fig. 34, a, d), but it is also seen in licking and nibbling (Fig. 34 C). Most licking and nibbling was done by the ♂. Head-darting was most frequently exchanged between K and C. Though C seldom darted at I, I directed over 75% of her darts at C, making C the most frequent recipient of this behavior.

Table 12 illustrates that all forms of contact exhibited in the home cage were also displayed in the encounters. As might be expected, the relative frequencies of contact differed under the two conditions. The level of contact exchange seen in cagemates occurred in only 2 out of 9 pairings involving unfamiliar animals (Table 12). Protracted sessions of playful interaction occurred between K and M and between the 2 immature ♂♂ (F and O). Mutual licking and nibbling was exhibited only by K and M and in the 3 series of encounters involving familiar

Figure 34. Sociograms of Selected Contact Patterns between the 3 Genet Cagemates (K, I, and C). A) Sniffing (nasal-contacts); B) head-darting; C) licking and nibbling; and D) body contacts (Paw-at, clasp, stand-on, wrestle). N = the number of times each animal performed a given type of contact. Arrow thickness is proportional to the percentage of occurrence rounded off to the nearest 10%. Actual percentages (in decimals) accompany each arrow.

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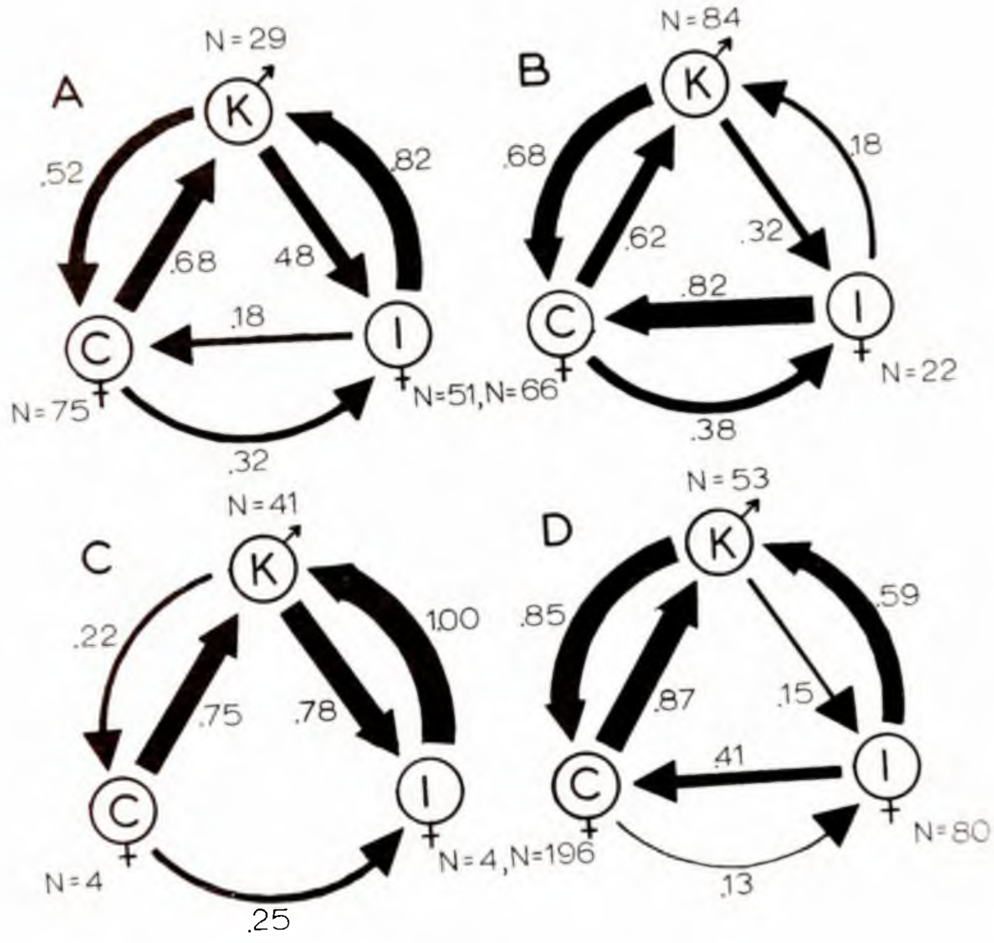

Table 12. Frequencies and Percentages in <u>Genetta tigrina</u> of 5 Contact Behaviors That Occurred Between the Paired Members of Encounters.

Animals and Sex		Sniffing		Head-darting		Licking and Nibbling		Biting and Mounting		Limb Contact		Total
		N	%	N	%	N	%	N	%	N	%	N
F	♂	401	64.8	31	5.2	0		106	17.2	80	12.9	618
O	♂	444	59.8	62	8.3	0		56	7.5	181	24.4	743
C	♀	233	38.7	170	28.2	58	9.6	79	13.1	62	10.3	602
K	♂	161	42.8	42	11.2	27	7.2	71	18.9	75	19.9	376
M	♀	234	78.0	16	5.3	8	2.6	14	4.6	28	9.3	300
K	♂	218	84.5	8	3.1	19	7.4	5	1.7	8	3.1	258
I	♀	160	78.4	24	11.8	7	3.4	6	2.9	7	3.4	204
K	♂	92	79.3	8	6.9	14	12.1	1	0.9	1	0.9	116
I	♀	60	81.1	4	5.4	1	1.4	2	2.7	7	9.5	74
C	♀	58	45.3	49	38.3	5	3.9	9	7.0	7	5.5	128
C	♀	58	77.3	17	22.6	0		0		0		75
M	♀	64	74.4	21	24.4	0		1	1.2	0		86
C	♀	79	100.0	0		0		0		0		79
F	♂	1	1.7	57	98.3	0		0		0		58
I	♀	0		9		0		1		0		10
O	♂	43	53.7	30	37.5	0		7	8.8	0		80
C	♀	5	11.9	33	78.6	0		3	7.1	1	2.4	42
O	♂	38	90.5	4	9.5	0		0		0		42

Table 12. (continued)

Animals and Sex	Sniffing		Head-darting		Licking and Nibbling		Biting and Mounting		Limb Contact		Total
	N	%	N	%	N	%	N	%	N	%	N
I ♀	8		4		0		0		0		12
M ♀	30	75.0	7	17.5	0		3	7.5	0		40
I ♀	1		12		0		1		0		14
F ♂	2		2		0		0		0		4
M ♀	6		0		0		1		1		8
F ♂	1		0		0		0		0		1
Totals	2242	56.5	610	15.4	292	7.4	366	9.2	458	11.5	3968

animals. In all other encounters contact between strange animals predominantly involved sniffing and head-darting. In almost all cases these 2 activities constituted the majority of the contact exchanged between animals.

(2) Fighting. Fights occurred in 5 out of 12 series of encounters, and were initiated by K and M. K initiated a fight with his cagemate (C) and with the unfamiliar ♀ (M). In both instances, the fight was preceded by an extensive bout of playful interaction involving wrestling, biting, mouthing, and limb contact. These activities became progressively more vigorous; the ♂ repeatedly clasped and bit the ♀ and finally attacked her violently. The ♀ screamed and attempted to escape for about a minute before the ♂ desisted. M initiated 3 attacks without prior wrestling.

Adult ♂♂ must be kept separate to avoid possibly fatal hostility. On occasions when either O or F were moving freely about the laboratory, K responded to their presence with unmistakable signs of aggression. When an unrestricted animal approached the cage, K would rush toward it and follow its movements by running along the inner boundary of the cage. On 2 occasions the ♂'s excited demeanor caused the resident ♀♀ to run also. The motion of the 2 ♀ cagemates and the outsider appeared to confuse the ♂ who then chased a cagemate until he caught and attacked her. For this reason, K was never introduced to either of the other ♂ genets.

(3) Non-contact patterns. While sniffing and head-darting are the most frequent forms of contact, they usually occupy a relatively small amount of the time that 2 animals are together. An

animal's non-contact activities are also a potentially important source of information to the companion. In particular, the time-space characteristics of a number of patterns have obvious social significance. The method of data recording, however, did not permit consistent precision in assessing the duration and graded character of these patterns, so the following qualitative description will have to suffice as a rudimentary coverage of this aspect of communication.

Before considering some of the details of interaction characterized by minimal contact, the protocol of an encounter will be summarized. This should not be interpreted as a "typical" encounter, but should illustrate some non-contact features of encounters. Paragraphs are numbered to delineate episodes of activity.

> M (♀) and I (♀); Encounter No. 5; 1930 hrs.
>
> (1) M leaves nestbox; I reclining within her own nestbox and watching M; M approaches I, naso-nasal contact, turns, departs, enters nestbox; M's tail = 3/4 expanded, I's tail = 0.
>
> (2) M leaves nestbox, smells cage; I watching M; M returns to nestbox.
>
> (3) M leaves nestbox, tail = 1/2, approaches I to ca. 30 cm., smells cage, departs; approaches I again, looks at her, moves about cage, tail flares to 2/3, enters nestbox.

(4) M leaves nestbox, tail slightly $<1/2$ expanded; I still watching, assumes crouched stance; M backs up, turns away, flares tail to 2/3, then to 3/4, smells cage, sits, tail = 1/2; I still staring in crouched stance; M stands and enters nestbox; I assumes reclining position; M yawns and sits down.

(5) I leaves nestbox, tail = 0; M looks at I, I stops moving, looks at M, returns to nestbox, sits, then lies down.

(6) M leaves nestbox and smells cage, tail = 0, climbs on top of I's nestbox, smells it, departs, tail flares to 1/2, enters her own nestbox and sits.

(7) I leaves nestbox and smells floor, tail = 0; M watches her; I approaches M, sits down and looks at M, stands and assumes a weak arched-back stance with a tangential orientation to M, flares tail to 3/4, departs, climbs on top of her own nestbox, smells cage, tail = 1/4, steps down from nestbox; M still watching motionlessly; I walks to front center of cage, looks at M, flares tail to 2/3, turns away, returns to top of nestbox, tail = 1/4; M still watching; I yawns and steps to the ground; M turns her head slowly while watching I...gaze is fixed on her; I approaches M to within 30 cm.,

> smells toward her, turns away, departs, tail flares to 3/4, walks to front center and back to nestbox 2 times; M staring intensely; I's tail is 1/2 expanded; M rushes at I, I departs, M chases her about the cage, bites her, they fight, M bites, chases, bites, grabs her on the back and bites her on the neck; I escapes and ricochets off the cage walls; more biting; they stop and both animals assume lateral body orientations and stare at each other in strongly arched-back stances; tails are fully expanded; I runs into her nestbox growling, looks out at M who is smelling urine, anal scent, and tufts of hair on the floor. M enters her own nestbox, smells the inside and then sits, tail = 7/8 expanded; I still maintains an arched-back stance and growls. Termination.

There were several notable features of this encounter: (1) unequal amounts of activity were exhibited by the 2 animals, (2) nestboxes were foci of rest, (3) the active animal was watched intently, and (4) body stances and hair postures were sometimes modified during visual fixation.

Activity of the 2 animals during encounters involving minimal contact is usually non-overlapping and one animal often predominates. This results when one animal becomes active more frequently or for longer periods of time; when the companion becomes active it usually evokes the activity in this dominant animal. The companion then usually retreats and avoids concurrent activity. It is difficult to make general statements regarding non-contact patterns on the basis of frequency alone; undoubtedly a number of other variables determine the appearance of these behaviors.

Three patterns of approaching and departing were observed in the encounters (Table 13). First, the relative numbers of these actions by each animal may be approximately equal, indicating equal activity. In minimal contact encounters (rows 6-12), the activity of the participants is largely out of phase, with neither animal predominating (M and I). Second, both acts may be performed predominantly by one animal; in the minimal-contact situation this simply reflects that one animal predominates activity to the exclusion of the companion (C and O, I and O, C and M). Third, when approaches and departures are most frequent in different animals, they may be supplanting each other. In the minimal-contact encounters (C and F, I and F), the inactive animal almost always departs to curtail contact from the active companion.

A comparison of approaching frequencies (Table 13) with sniffing frequencies (Table 12) reveals that in the case of high-contact encounters (rows 1-5), the animal that approached most often also sniffed most often. In low-contact encounters, with one exception (I and O), the approaching animal sniffed the most. This feature of low-contact encounters appears real because the frequency disparity between animals was large for both sniffing and approaching (Tables 12, 13). Among high-contact encounters, the subequal frequencies of approach and sniffing suggest a fortuitous association.

Table 13. The Occurrence of Companion-oriented Locomotion, Stances, and Movements during Encounters in *Genetta tigrina*.

Animal and sex		Approaches					Departures Total	Deviation from a Proportion of 50:50[2]		Visual Fixation	Jaw Gaping	Arched-back Stance	Tail Flaring
		Crouch[1]		Rush		Total							
		N	% of total	N	% of total	N	N	App.	Dep.				
F	♂	1	0.5	1	0.5	199	235	5.0	2.5	19	0	0	0
O	♂	13	7.9	13	7.9	163	260			36	0	3	0
C	♀	4	3.9	6	5.9	101	137	3.5	4.5	20	33	0	7
K*	♂	10	8.6	7	6.0	116	171			35	3	1	13
M	♀	35	74.5	11	23.4	47	141	29.2	3.4	132	6	1	5
K*	♂	25	14.8	9	5.4	168	123			97	3	2	19
I	♀	0	--	0	--	60	51			5	0	0	2
K	♂	0	--	0	--	38	36	11.2	8.6	12	1	0	1
C	♀	0	--	0	--	28	50	17.4	2.6	7	2	0	1
I	♀	0	--	0	--	58	45			10	0	0	0
C	♀	10	12.9	2	2.6	77	59	16.2	11.2	173	12	9	22
M*	♀	58	38.4	8	52.9	151	93			179	3	0	23
C	♀	6	8.6	0	--	70	16		31.6	64	0	1	8
F	♂	3	42.8	2	28.6	7	71	40.9		78	49	0	1

Table 13 (continued):

Animal and sex	Approaches					Departures Total	Deviation from a Proportion of 50:50[2]		Visual Fixation	Jaw Gaping	Arched-back Stance	Tail Flaring
	Crouch[1]		Rush		Total							
	N	% of total	N	% of total	N	N	App.	Dep.				
I ♀	9	69.2	1	7.7	13	3	45.4	48.2	82	19	2	2
O ♂	33	12.1	39	14.3	272	160			221	1	3	11
C ♀	2	13.3	5	33.3	15	10	47.9	38.6	95	34	1	8
O ♂	25	22.9	0	--	109	78			168	2	0	8
I ♀	11	15.7	3	4.3	70	53	2.6	0.9	147	58	10	20
M* ♀	4	6.3	1	1.6	63	55			105	4	6	27
I ♀	0	--	0	--	2	31	45.9		87	115	9	3
F ♂	6	12.7	3	6.4	47	3		41.2	49	0	1	1
M* ♀	1	20.0	0	--	5	3			7	0	0	1
F ♂	1	50.0	0	--	2	1	71.4	25.0	6	1	0	0

* Encounters in which fighting occurred; the asterisk lies beside the animal that initiated and won the fight.

[1] Includes crouched stances.

[2] Calculated by subtracting from 50.0 the lowest percentage an animal contributed to the approach or departure total for that pair. The value is placed in the row of the low scoring animal. Deviations ≳ 5.0 are placed between rows.

Crouching and rushing appear to be associated with social initiative. That is, animals that most often crouched and rushed also sniffed their companions the most (compare Tables 12 and 13). In the encounters between I and M, I crouched the most but smelled the least; in this case the deviation from a 50:50 approach proportion was 5.0% (Table 13). Because arched-back stances are of long duration, it is difficult to evaluate their relationship to the other patterns by considering frequencies. Suffice it to say that animals which maintain protracted stances crouch and rush less frequently than their companions, and hence usually display low social initiative. Both clearly have an intimidatory function and give the impression that crouching is offensive and back-arching defensive.

Though visual fixation and jaw-gaping are also duration events, they are briefer and more frequent than the arched-back stance, and therefore more easily related to other behaviors. In 9 out of 11 encounter series, the animal that most often stared at its companion also crouched and rushed most often. In instances where this animal also jaw-gaped the most, it had experienced defeat in combat (M and K, M and I).

Visual fixation was generally most common among animals exhibiting minimal contact (Table 13, rows 6-11) and among animals that fought (rows 1-5, C and K, M and K). The lowest frequencies of visual fixation occurred in encounters between the 3 familiar animals, C and I, I and K.

Jaw-gaping was relatively infrequent in familiar animals and in those that interacted physically (C and K and M and K). In the minimal-contact encounters (Table 13, rows 6-11), a marked disparity is evident between the 2 participants varying in magnitude from 4 (C and M) to 14 times (I and M). Among animals that fought, the loser jaw-gaped the most. These were also the animals that approached their companions less frequently (excepting I and M).

Flaring of the tail hair occurred in both minimal- and high-contact encounters (rows 1-5, 6-12). High frequencies of tail-flaring were seen in 4 out of 5 encounter series in which fighting occurred (the exception was the brief discontinued encounter between M and F, row 12). Tail-flaring was infrequent among familiar animals that did not fight (I and K, C and I) and the pair that played (F and O). A comparison of tail-flaring and jaw-gaping (Table 13) reveals that the animal that jaw-gaped the most also tail-flared the most (P = .05, Appendix B-1). Tail-flaring often occurs as an animal maintains an arched-back stance, but this relationship is not shown in the table.

c. Contingencies of Common Non-vocal Interaction Patterns:

(1) Genetta. The simplest form of interaction during encounters consisted of movement toward and away from the companion (Fig. 35, I→M). A large amount of such companion-oriented movement however was associated with (a) sniffing by one or both animals (F→I, C→F, I→M, O→C), and (b) head-darting by the animal being sniffed (F→C, C→M, C→O, I→K). Head-darting may precede sniffing in some instances (K→M, K→I), or may alternate with sniffing (K→M, M→C), and both of these events were frequently repeated in series (e.g., M→K, I→K). This association between sniffing and head-darting (termed the sniff-dart axis) occurred in both maximal and minimal contact encounters and was the most common form of social exchange.

Licking and nibbling was the only other pattern linked predominantly with sniffing, but the strength of this association was not supported by the low frequency of contingencies in Figure 35 (I→K, K→M). Sniffing was a relatively uncommon antecedent of other forms of contact because the rate of interaction involving these contact patterns was usually much more rapid. The majority of limb, mouth, and body contacts (with the exception of erratic head movements) was contingent upon one another and head-darting (Fig. 36, F and O).

The sniff-dart axis and multiple-contact exchanges therefore represent the ends of a complexity continuum involving contact. Though it was possible for any 2 patterns to occur either singly or in repeating and alternating series, sniffing and darting were by far the most common elements composing dyadic interaction. When other

Figure 35. Contingency Webs of Selected Companion-oriented Locomotion, Stances, Movements and Contact Patterns in the Genet.

Each pair of diagrams contains the acts each animal directed to its companion. Numbers represent the frequencies with which each event served as an antecedent or succedent to other patterns performed by the animal in question or its companion. The behaviors and frequencies were taken from a 135^2 contingency table. Abbreviations: A = approach, Ab = arched-back stance, B = bite, mouth, Br = brush against, C = contact (general) but excluding wrestling, Cl = clasp with fore- or hindlegs, Cr = crouched approach or stance, D = depart, Dt = head-dart, E = erratic head movements, F = follow, Ho = hold one leg over or squat over, Jo = Jump on, Ln = lick and/or nibble, P = paw or kick, S = sniff (nasal contact), St = stand on with fore- and/or hindlegs, Tf = tail flare, W = wrestle.

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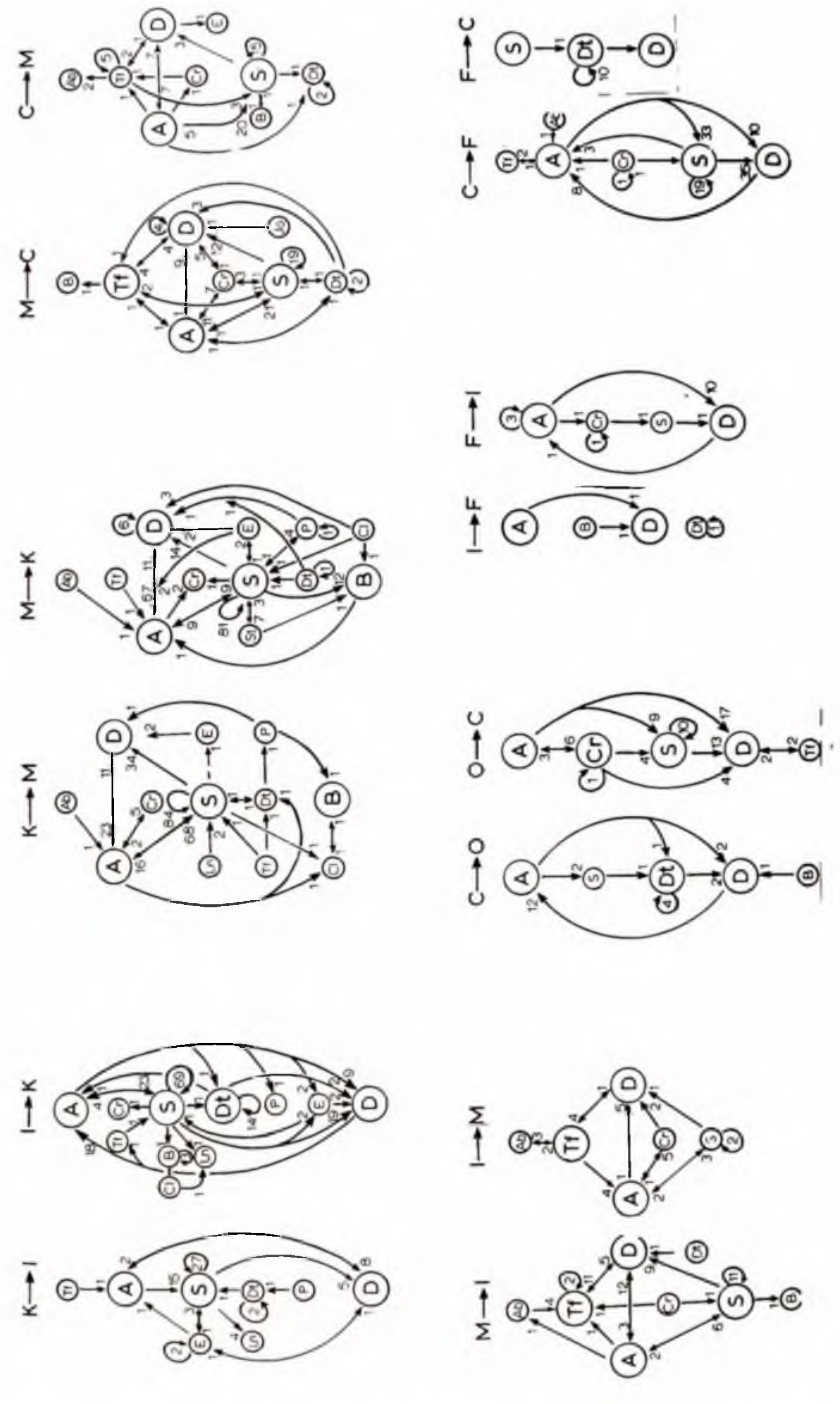

Figure 36. Contingency Webs of Selected Companion-oriented Locomotion, Movements, and Contact Patterns during High Contact Encounters between the Genets O and F. The lower webs lump together all contact patterns (C) except wrestling (W), sniffing (S) and erratic head movements (E). Arrow thickness indicates the percentage of the total number of succedent patterns (in the diagram) that was followed by the event in question (Sniff in F→O = slightly 100%, W→C in O→F = ca. 50%. The number of following events for each animal varied from 120-328 for C, A, E, and S; and from 46-97 for F, D, and W. The upper webs consider the various contact contingencies encompassed in C of the lower webs. Approaching (A) and departing (D) are also considered. Abbreviations of all patterns are presented in the legend of Figure 35.

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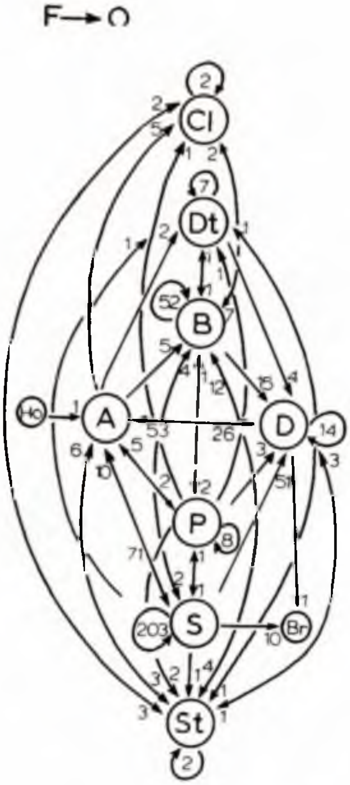
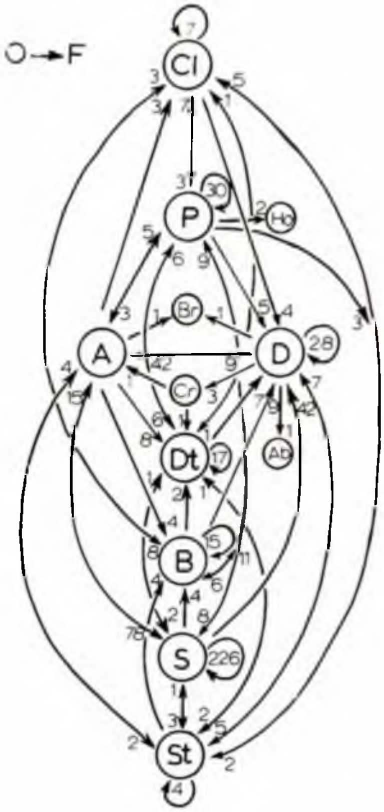
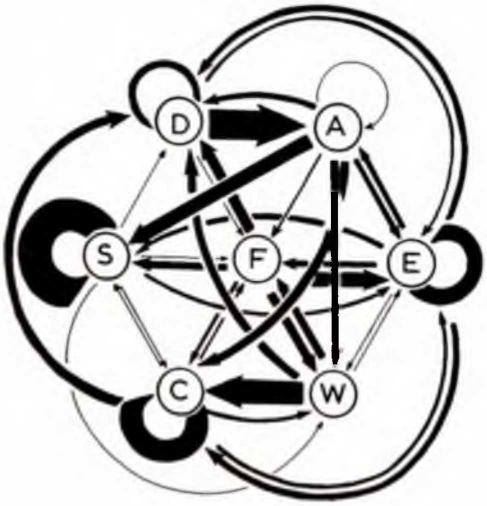
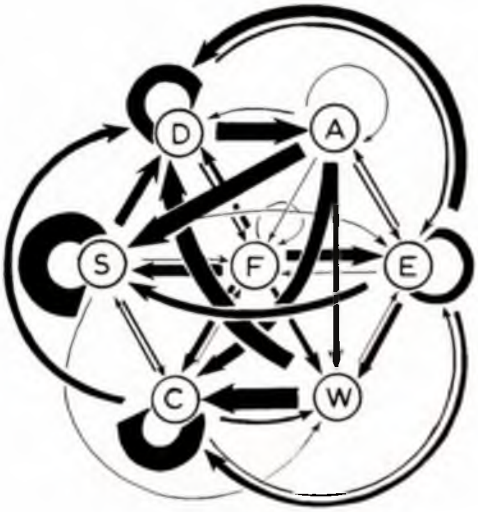








types of contact occurred they lost their dyadic integrity. The difference between the sniff-dart axis and the association between other types of contact can be appreciated by comparing minimal contact encounters (Fig. 35, C and M, O and C) with maximal contact encounters (Fig. 36, O and F; Fig. 35, M and K).

During intensive bouts of contact interaction (Fig. 36, F and O), approaching or wrestling usually preceded chains of contact patterns, but contact rarely led to wrestling. Likewise, sniffing was rarely followed by wrestling or other contacts. This illustrates that the sniff-dart axis primarily characterizes minimal-contact episodes. Erratic head movements were subequally contingent upon contact, sniffing, and companion-oriented locomotion, indicating that the pattern was performed during as well as between episodes of contact.

Non-contact patterns such as back-arching, crouching, and tail-flaring were usually contingent upon companion-oriented locomotion (Fig. 35, I and M, K and M, K and I, M and C). Sniffing and darting were the only forms of contact with which they were associated. Though tail-flaring and back-arching may be precipitated by fighting, they almost always occurred during departure or as one animal stared at its companion. Crouching and sniffing by the companion, on the other hand, evoked tail-flaring and back-arching (Fig. 35, C and M, M⟶I, O⟶C, C⟶F, F⟶I). These 3 non-contact patterns were associated with minimal contact and modified movements toward or away from the companion.

It should be pointed out that both crouching and back-arching are duration events. When tail-flaring followed an arched-back posture in one animal, the 2 acts were concurrent, because arching of the back is a duration event. When crouching preceded tail-flaring, the acts were performed by different animals (Fig. 35, C→M, M→I).

Erratic head movements were contingent upon darting and sniffing (Fig. 35, I and K, M and K) as well as movements to and from the companion (Fig. 36, O and F). It usually occurred during encounters involving maximal contact.

(2) Civettictis. Behavioral contingencies in the 2 Civettictis exhibited similarities to Genetta but differed by the incorporation of several other patterns. As in the genets, sniffing and head-darting were repeated more often than they were followed by other patterns, and departure frequently terminated sniffing (Table 14). Of the 6 most common contact patterns, sniffing was most frequently followed by head-darting. Unlike the genets, however, the recipient of head-darting more commonly reclined than departed from the companion's vicinity. Under these circumstances, recumbancy characteristically involved a lateral or tangential body orientation to the companion. This kind of body orientation was also assumed by standing animals; the pattern was most commonly a response to the head-darting or frontal orientation (T.T.) of a proximate companion. Sparring and clasping were also common antecedents of reclining, but only in the former situation was reclining associated with a lateral body orientation. It was evident that in these 2 animals the assumption of either a standing or reclining lateral orientation precipitated further darting. After the darting animal departed or desisted, the reclining animal would stand and move away. Approaching, turning away, departing,

Table 14. Contingency Matrix of Interaction Patterns in *Civettictis civetta* Based on Nine Encounters. (EHM = erratic head movements, LO = lateral or tangential body orientation, TT = turn towards, TA = turn away.) Values enclosed in heavy lines accounted for 20% or more of the column totals (the total number of following acts).

Precedes

Follows	App	Sniff	Dart	Spar	Bite	Clasp	EHM	Recline	Depart	Follow	Stand	LO	TT	TA	Totals
App								4	**32**		4		3		43
Sniff	**125**	**108**	14	1	1	2	1	40		**8**	4	3	13	5	325
Dart	47	27	**140**	12	4	4	1	**47**		4	13	**21**	**40**	4	364
Spar	6	7	16		2	11	1	8			4	5	13		73
Bite	7	2	4	5	1	6	1	4		1	5				36
Clasp	23	7	7	1	2	1	3	3		3	4				54
EHM	5	6			2	3	2	5		1	3		3		30
Recline	26	24	**78**	**19**	2	**21**	4	11	11	6	7	4	16	6	235
Depart	17	**96**	48	**21**	**13**	8	**10**	26		7	**65**	**18**	12	**12**	353
Follow	2								**39**						41
Stand	4	26	19	8	2	2	3	**42**	13		2	1	3	7	132
LO	13	6	32	4							2		14		71
TT	17	37	10		3	1	2	15	2	7	10	3	1	2	110
TA	3	10	15	1	2	1	1	3				3	5	2	46
Totals	295	356	383	72	34	60	29	208	97	37	123	58	123	38	1913

and following bear a basic similarity to the same patterns in the genet. Erratic head movements were not commonly seen, but occurred most often before an animal moved away from its companion.

In both Genetta and the Civettictis sniffing and head-darting were more commonly contingent upon each other than upon any one other pattern of contact. At this level, interaction in Civettictis appeared to be more complicated by the assumption of postural modifications that permitted further head-darting; proximal interaction was usually terminated when the head-darting animal departed. In Genetta head-darting and sniffing were terminated when either animal departed. Lateral body orientation, assumed during back-arching, was characteristically displayed at a distance rather than in the companion's proximity. In addition, Genetta modified its movement toward and away from the companion with postural adjustments such as crouching and tail-flaring.

d. Contingencies of Vocalizations:

(1) Genetta. As mentioned previously in Genetta, coughing was usually produced in bouts with intervals ranging from 1 to several seconds. It is evident in Table 15 that more than half of all coughs were preceded or followed by other coughs. Locomotory transitions, and movement to and from the companion accounted for nearly 30% of all contingent behaviors; about 15% of the calls occurred either before or after the animal sniffed the cage or its companion. An outstanding feature of this vocalization is that though sometimes a response to another animal's contact, it was most commonly produced during transitions in gaits, stances, reclining positions and sniffing.

Table 15. Behavioral Contingencies of Vocalizations in <u>Genetta</u> <u>tigrina</u>.

Contingent behaviors+	Vocalizations															
	Cough				Hiss				Growl				Scream			
	Preceded by		Followed by		Preceded by		Followed by		Preceded by		Followed by		Preceded by		Followed by	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Sniff cage[1]	45	7.4	56	9.2	7	4.7	0	--	2	3.3	3	5.4	--	--	--	--
Pacing	--	--	--	--	--	--	--	--	13	21.6	6	10.7	--	--	--	--
Locomotion[2]	97	15.9	96	15.8	--	--	--	--	11	18.3	2	3.6	--	--	--	--
Companion-oriented movements	69	11.4	78	12.8	33	22.3	8	5.6	1	1.6	1	1.7	14	36.8	3	9.1
Arched-back stance	--	--	--	--	2	1.4	1	0.7	5	8.3	8	14.3	--	--	--	--
Visual fixation	--	--	--	--	7	4.7	16	11.2	5	8.3	12	21.4	--	--	--	--
Jaw-gaping	--	--	--	--	14	9.5	20	13.9	11	18.3	14	25.0	--	--	--	--
Nasal contact	49	8.1	45	7.4	1	0.7	--	--	--	--	--	--	--	--	--	--
Head-darting	--	--	--	--	25	16.9	45	31.5	2	3.3	2	3.6	3	7.9	2	6.1

Table 15. (Continued)

Contingent behaviors*	Vocalizations															
	Cough				Hiss				Growl				Scream			
	Preceded by		Followed by		Preceded by		Followed by		Preceded by		Followed by		Preceded by		Followed by	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Other contacts	6	0.9	6	0.9	1	0.7	1	0.7	--	--	--	--	18	47.4	25	75.8
Vocalizations	316	52.1	316	52.1	58	39.2	52	36.4	4	6.6	3	5.4	3	7.9	3	9.1
Stretching, shaking, and self-oriented contact	25	4.1	9	1.5	--	--	--	--	6	10.0	5	8.9	--	--	--	--
Total[3]	607		606		148		143		60		56		38		33	

* Each category is exclusive of others.

[1] Includes licking and nibbling the cage or scent-marks.

[2] Including transitions from stances to locomotion.

[3] Estimates of degree of tail-hair erection were occasionally contingent upon vocalizations. The exclusion of these figures results in unequal totals.

Once an animal produced the sound, it was likely to call again before a change occurred in its ongoing behavior.

Hissing also occurred most frequently in series; of the 110 contingent vocalizations, only 10% consisted of another call type (growling) (Table 15). There was a 4-fold difference in the percent of the time that hissing was preceded and followed by companion-oriented locomotion; this is because the call was usually produced as a response to a companion's approach. Darting was almost always performed by the vocalizing animal and was twice as common after the call. About 25% of the time either visual fixation or jaw-gaping followed the delivery of a hiss; both of these acts are displayed predominantly by the caller. It is clear that hissing occurred primarily during proximal interaction in which contact was minimal.

In the encounter situation, growling was only exhibited by animals that had been defeated in fights. Following defeat, animals often growled merely at the sight of the companion indulging in "neutral" activities, such as self-directed licking and nibbling, cage sniffing, or changing body position (Table 15). Defeated animals also growled as they paced in a stereotyped manner at the front of the cage. Animals exhibited growling before as well as after they visually fixated their companions, or assumed an arched-back stance. These 3 behaviors accounted for 35% of all antecedent acts and 60% of the succedent acts (Table 15). Hissing was the only other vocal pattern contingent on this call.

Screaming was the least frequently heard call during encounters. It occurred before or after the reception of head-darts, but was most frequently emitted as animals engaged in wrestling, fighting, biting, and clasping. Contact patterns accounted for 50-75% of all antecedent and succedent behaviors. Approaching was the only form of companion-oriented locomotion that animals responded to by screaming. Screaming then differs from growling and hissing by its association with extensive body contact. The contingencies do not reveal that pain inflicted during biting is probably the most important stimulus evoking this call. Associated patterns such as clasping and wrestling by themselves were never seen to elicit the call. It appears that once an animal received a painful bite, however, more generalized patterns such as approaching became effective stimuli.

(2) *Civettictis*. As in *Genetta*, sniffing the cage and general body movement constituted the vast majority of coughing-associated activities (Figure 37 a). It can be seen in each animal that olfactory and (less commonly) gustatory sampling of the cage was more often an antecedent activity. In both animals less than 95% of all nasal-contacts was contingent upon coughing. Locomotory transitions were relatively more frequent succedents.

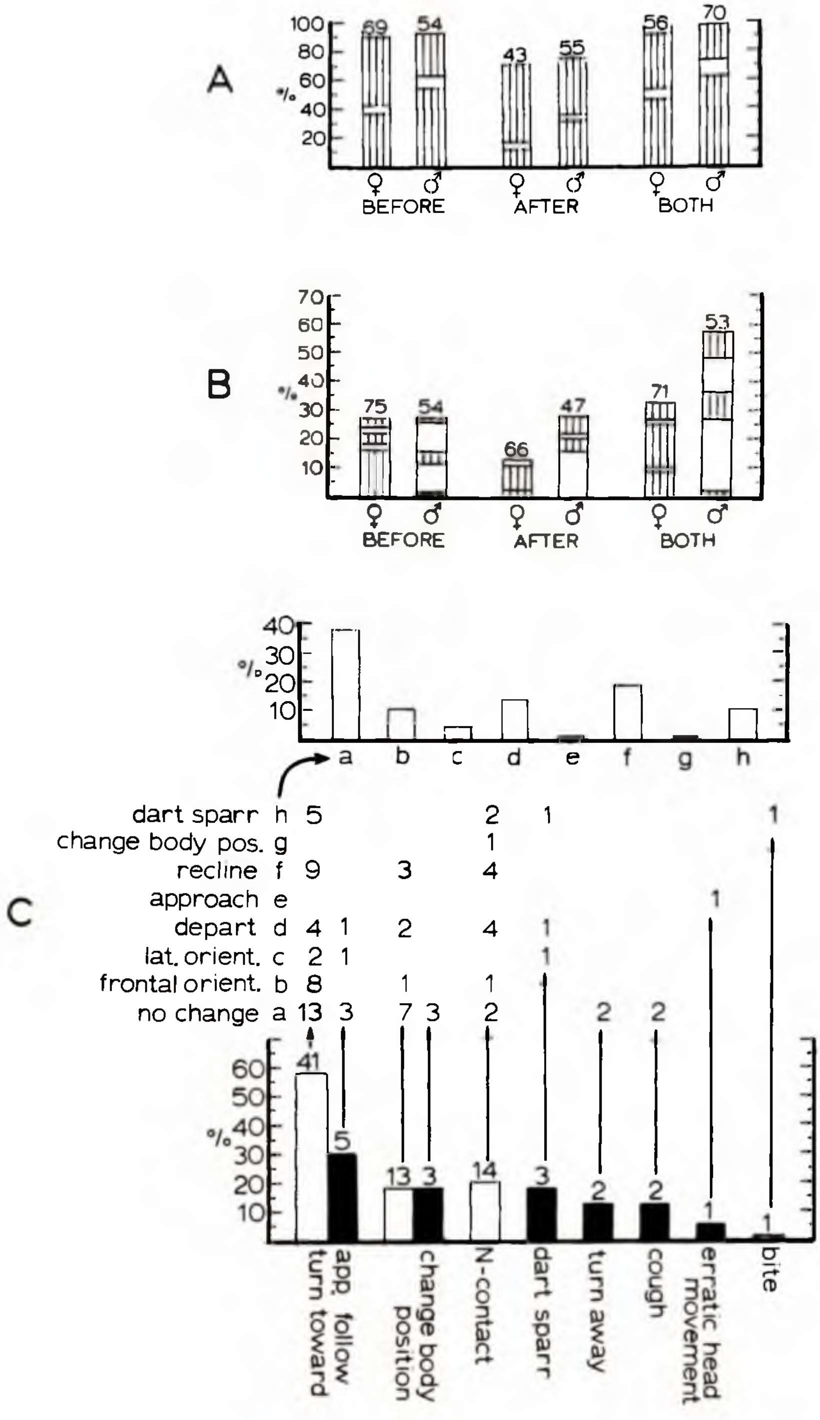
More than 70% of the time after a call was given, there was no overt change recorded in the companion's behavior (Figure 37 b). Antecedent activities of the companion may have evoked the call on some occasions (Figure 37b). It is evident that the ♂ coughed more often after the ♀ contacted him; the ♀ coughed more often after the ♂ moved, or looked towards or away from her. Differences between animals were also exhibited in types of response. The ♀ sniffed the ♂ 3%, approached 9%, departed 2% of the time, and never coughed back.

Figure 37. Behavioral Contingencies of Vocalizations in the African Civet (Civetticictis).

A). The caller's behavior before, after, and before and after (both) coughing. The segments of each bar in the histograms represent different behavior patterns. Bottom segment = sniffing, licking and nibbling of the cage (or scent marks); middle segment = sniffing of the companion; top segment = transitions in locomotion and stances.

B). The companion's behavior before, after, and before and after (both) the caller coughs. Bottom shaded segment = nasal-contacts; lower clear segment = all other companion-oriented contacts (bite, dart, paw, stand on, etc.); middle shaded segment = approach, turn toward, look at; upper clear segment = depart, turn away, look away; top shaded segment = coughing. The numerals above each bar represent the numbers of calls from which percentages were calculated.

C). Growling. The bottom histogram displays patterns of the ♂ (white bars) and ♀ (black bars) that were antecedent to growling by the ♀. Numbers above the bars represent the portion of the totals upon which the percentages were calculated. Arrows above each bar indicate the succedent events in the ♂. The upper histogram presents the relative proportions of those succedent events expressed as percentages of the total number of times the ♀ growled. The lower case letters correspond to the same behavior patterns.


A
%
100
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approach e 1
depart d 4 1 2 4 1
lat. orient. c 2 1 1
frontal orient. b 8 1 1
no change a 13 3 7 3 2 2 2
%
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50
40
30
20
10
41
5
13
3
14
3
2
2
1
1
turn toward
app. follow
change body position
N-contact
dart sparr
turn away
cough
erratic head movement
bite

After the ♀ called, the ♂ contacted her 15% of the time, approached 5%, and coughed 7% of the time.

The contingencies of growling differ considerably from coughing. Of 85 growls by the ♀, 81% were apparent responses to actions of the ♂ (Figure 37 c, bottom graph). Female oriented movements and nasal-contacts accounted for 80% of all the ♂'s actions that evoked growling; she also growled when the ♂ simply moved. When there was no change in the ♂'s behavior, the ♀ most commonly growled when she moved in his direction.

It is evident that nearly 40% of the time after the ♀ growled there was no change in the ♂'s conduct (Figure 37c, top graph). The most common form of response consisted of position or orientation changes (e.g., reclining, lateral and frontal orientation, and departure). Growling led to contact in the form of sparring only 10% of the time.

e. Sensory Characteristics of Some Non-vocal Behaviors: As a nocturnal forest species having an all-rod retina (DÜCKER 1959), Genetta distinguishes only degrees of brightness and probably cannot discern fine visual detail. In view of these limitations, it is important to consider the visual characteristics of non-contact patterns and how they might be perceived by conspecifics. The patterns discussed below can only be recognized visually. Non-contact patterns involving gaits (approach, departure) may also have important visual components, but concurrent environmental sounds produced by footfalls also provide information concerning proximity, and direction and rate of movement.

Staring is a common activity during encounters between strange animals. If visual fixation provides information only to the animal exhibiting it, there would not be selection for behaviors or structures that pronounce this activity to the companion. On the contrary, the patterning of light-colored fields of facial hair fulfills 2 requirements hypothesized to facilitate the companion's recognition of the head and its orientation in dim lighting. (1) The markings present a distinct visual configuration not present elsewhere on the body, and (2) angular deflection of the head from a frontal position is precisely indicated by relative changes in the number and surface area of the markings. Figure 38 indicates the appearance of different head positions and provides measures of the amount of white facial hair exposed through a 180° horizontal arc. It is evident that disruption of pattern symmetry and disparity in spot size are 2 manifestations of only a 30° deflection from a frontal head position. These changes occur with about a 20% decrease of the area of white hair exposed during frontal orientation. As the eye has relatively little mobility (see the Primary Senses), visual fixation of movement is achieved primarily by adjustments of head position. A moving animal being stared at therefore probably receives a constant facial image in which 4 symmetrical light markings are prominent. A similar effect is also produced by an animal with closed eyes if the head is directed toward the companion.

Staring accompanies crouched and arched-back stances, but the visual characteristics of these patterns are distinct. The body axis is frontally oriented during crouching, exposing a relatively small

Figure 38. The Appearance of Different Head Positions in the Genet and Variation in the Relative Proportions of the White Facial Markings through a 180° Horizontal Arc from a Frontal Position.

The gray horizon delimits the area of exposed white hair as a percentage of the amount visible at 0°. The approximate percentages of the muzzle and eyespot markings are indicated by the solid and dotted lines; together they equal the percentage level of the gray horizon. The calculations are based on planimeter measures of enlarged photos taken of the horizontally resting head of a dead genet. Because the head is tilted vertically during staring, these measures are in disagreement with the relative sizes of the muzzle and eyespots depicted in the models.

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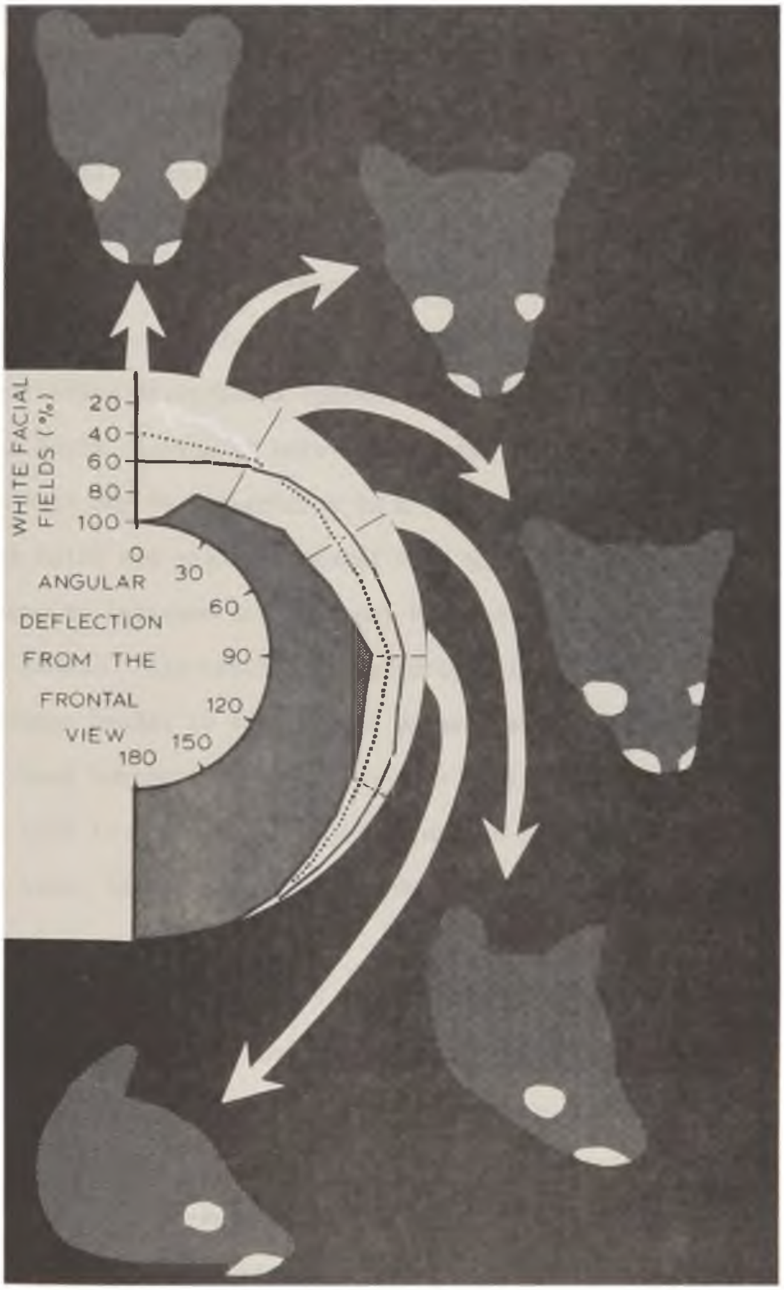

body surface to the companion. The tail is concealed or minimally visible and the above-mentioned facial characters predominate. The arched-back stance, on the other hand, maximizes body exposure with a lateral or tangential position. The light-colored hair on face and tail delimits the animal's dimensions. Differences between these 2 patterns may be considered antithetic (DARWIN 1872) and involve both quantitative (head elevation, degree of body exposure) and qualitative differences (presence or absence of tail).

The rapid flaring of hair on the tail produces several changes that may be perceptible to a companion. Because the bases of light hairs are lighter colored than the tips, erection of the hair seems to increase the contrast between the dark and light colored bands. Pilo-erection also noticeably enhances the demarcation between bands; in the relaxed state overlap of light and dark hair at band boundaries produces a more graded effect. The visual pattern that is produced, a rapid expansion of a series of light-colored bars, in all probability draws attention to the tail and the animal.

The sensory properties of other behavior patterns are more difficult to enumerate. The properties actually transmitted are not necessarily those perceived by the observer and probably vary under different environmental and social circumstances. Head-darting, for example, involves several levels of motor integration. In its simplest form it may be visual or tactile. If the companion is watching the darting animal, the signal can exhibit visual, tactile, and auditory properties. The sensory manifestations of the transmitted signal therefore depend upon the receiver's body orientation and attentiveness. The redundant character of such a pattern probably compensates for interference of one or more sensory channels. Sudden high stimulus contrast characterizes all the sensory properties of this pattern.

It appears that the most obvious properties of certain patterns may not always embody the salient stimuli. Though erratic head movements are usually conspicuous in a lighted room, they are commonly performed in circumstances where visual detection is not possible. The irregular and noisy sequence of footfalls is an outstanding feature of this movement detectable irrespective of orientation to the other animal. In a sense the quality of this sound mimics the visual character of the movement. When the movement is performed during following, the head and neck glance and brush against the rump, hindlegs, and tail of the anterior animal.

f. The Body Targets of Sniffing and Head-darting:

1. *Genetta*. Figure 39 reveals a bimodal distribution of sniffing frequencies to the fore- and hindbody. While the head and neck were the most commonly sniffed forebody targets, the rump, anogenital region and tail (including tailbase) received 45.2% of all nasal contacts; the tail composed 29% of these. These common anterior and posterior targets accounted for exactly two-thirds of all companion-oriented sniffing. The side was the remaining most commonly smelled target region; it also constitutes a relatively large surface area. Forty percent of all sniffs were directed to targets between the head and side, while the remaining parts of the body, composing slightly

Figure 39. The Body Targets of Head-darting and Sniffing in the Genet.

Numerals above the bars in the histograms represent the number of observations for that target. Percentages are based on the total number of all observations for unspecified and specified parts of the body.

Black bars = percentages based on total frequencies.

Gray bars = percentages based on total duration of sniffing in seconds. The top number above each pair of bars indicates the frequency, the bottom number the duration of sniffing to each target.

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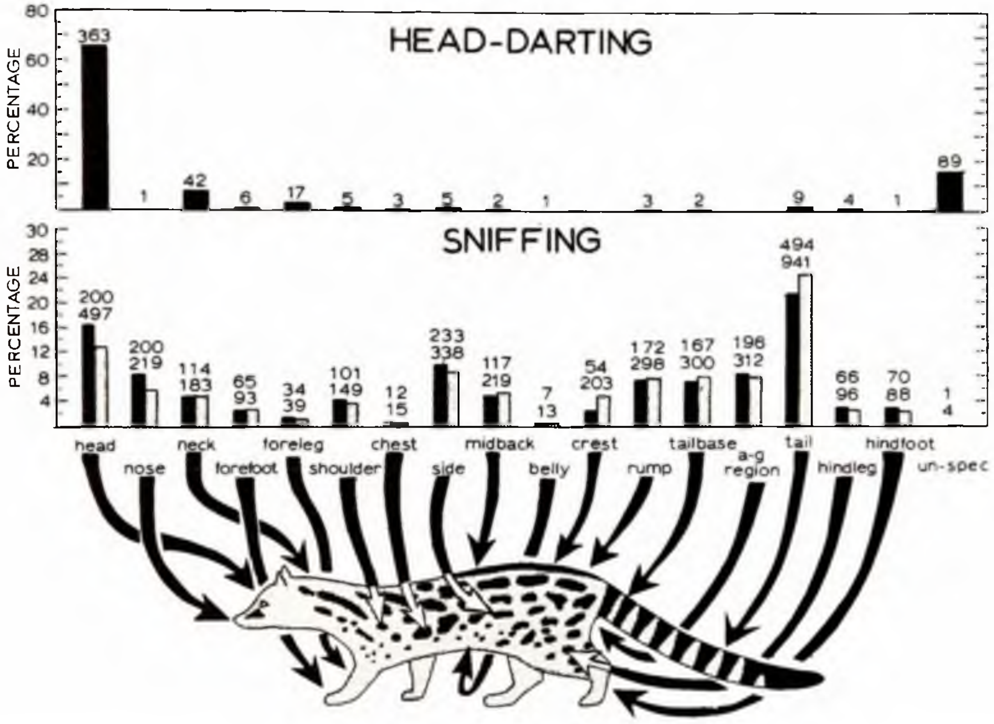


less than half the available body surface, received 60% of the total number of sniffs.

The ratio of the frequency to the total duration of sniffing for any given target varied considerably (Fig. 39). Ratios of ≤1:1.5 were obtained for all targets anterior to and including the side. On the hindbody only the legs and feet had similar ratios. Almost all other posterior body targets had frequency:duration ratios of 1:1.5-1.9. The spinal crest had the exceptional ratio of 1:3.75. This clearly demonstrates that duration and frequency of contact are not equally proportional for all targets. Frequently sniffed targets such as the head were sniffed briefly (Freq.:Dur. = 1:1.3), while relatively long periods were devoted to infrequently sniffed targets such as the spinal crest (Freq.:Dur. = 1:3.75). Spinal crest sniffing exhibited a characteristic pattern. The nose (probably guided by the contour of the underlying vertebrae) was rubbed anteriorly within the confines of the black hair of the crest.

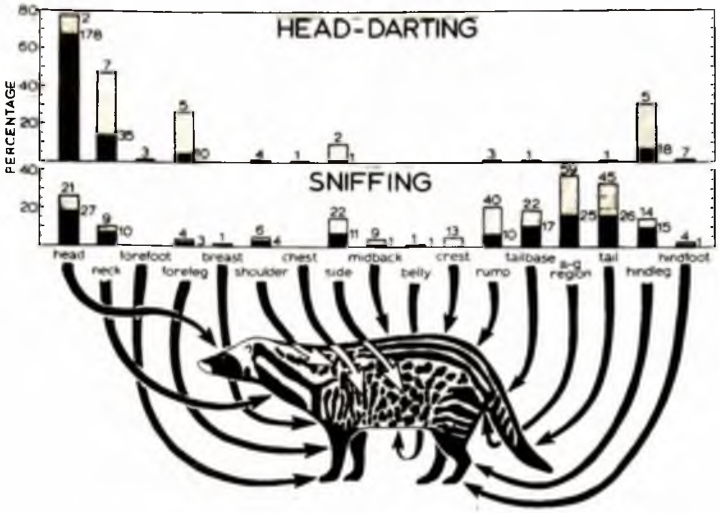
The companion's head was the target of head-darting the vast majority of the time. While the neck, foreleg and tail were sometimes struck at, other areas were infrequent targets (Fig. 39).

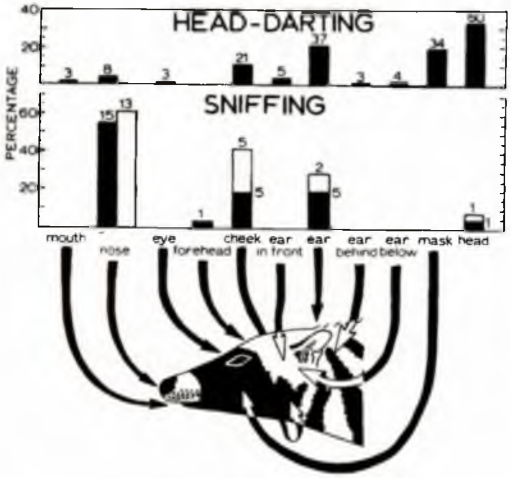
2. *Civettictis*. *Civettictis* provides an interesting comparison with *Genetta*. While the head, neck and side were the most frequently sniffed anterior regions, in both animals the majority of sniffing was directed to posterior body targets. In the ♀ 60% of all N-contacts were directed to the ♂'s hindquarters, while the ♂ oriented 65% to the posterior half of the ♀'s body (Fig. 40a).

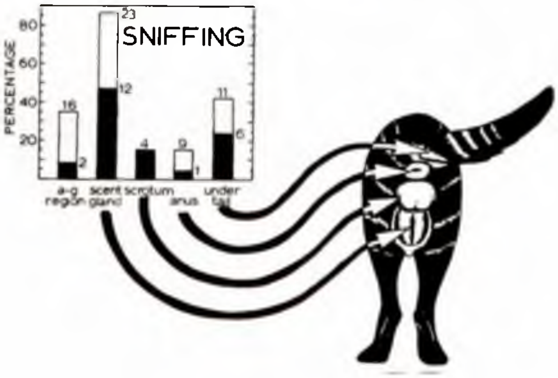
Figure 40. The Body Targets of Head-darting and Sniffing in the ♀ (black bars) and ♂ (gray bars) African Civets (*Civettictis*).

Numerals which accompany each segment of the histograms represent the number of observed instances upon which the percentages are calculated. Each category is exclusive of others.

A) General body targets of head-darting and sniffing in the ♂ and ♀. *B*) Specific targets of head-darting and sniffing on the head of the ♂ and ♀. *C*) Specific targets of sniffing on the anogenital region of the ♂ and ♀ (for convenience only the hindquarters of the ♂ are represented). As body targets were not always noted specifically as an encounter progressed, general targets such as head and anogenital region have been duplicated in *B* and *C*. The under-tail category of *C* was included as part of the anogenital category in *A*.


HEAD-DARTING
SNIFFING
PERCENTAGE
80
60
40
20
40
20
2
178
7
35
3
5
10
4
1
2
1
3
1
1
5
18
7
21
27
9
10
4
3
1
6
4
22
11
9
1
1
1
13
40
10
22
17
52
25
45
26
14
15
4
1
head
neck
forefoot
foreleg
breast
shoulder
chest
side
midback
belly
crest
rump
tailbase
a-g region
tail
hindleg
hindfoot


HEAD-DARTING
SNIFFING
PERCENTAGE
40
20
60
40
20
3
8
3
21
5
37
3
4
34
50
15
13
1
5
5
2
5
1
1
mouth
nose
eye
forehead
cheek
ear in front
ear
ear behind
ear below
mask
head


SNIFFING
PERCENTAGE
80
60
40
20
16
2
23
12
4
9
1
11
6
a-g region
scent gland
scrotum
anus
under tail

In a number of instances it was possible to determine the precise orientation of sniffs to specific body parts (Fig. 40b, c). Based on a limited number of observations, the nose, cheek, and ear received the majority of head-directed nasal-contacts. Sniffing targets of the hindquarters differed only slightly between the 2 subjects. Targets on the ♀ can be ranked in decreasing frequency from scent-gland, under-tail to anus. On the ♂'s body, the order of the first 2 targets was the same; the scrotum was the third, and the anus was sniffed least commonly.

As in Genetta the companion's head was the most common target of head-darting, but in addition the neck, foreleg, and hindleg were also hit. While these targets were also struck in the genets, the relative proportion of darts to these areas was less, particularly in the case of the hindleg (Fig. 39). There is an obvious difference in targets between animals. The ♂ darted primarily at the neck, foreleg and hindleg (totaling 80% of 21 darts) and the head and side were infrequently struck. The 2 directed over 65% of 262 darts to the ♂'s head and struck at the neck less than 15% of the time. The neck, hindleg and foreleg were the next most common targets (Fig. 40a). Thirty percent of the ♀'s head-directed darts struck the ear region, while the mask and cheek were less common targets (Fig. 40b).

In comparison with Genetta several quantitative differences can be cited. Whereas the genets sniffed the tail more often than the anogenital region (71% of all sniffs to both areas), the civets exhibited only a slight bias in favor of the tail (54% and 63% in the ♂ and ♀). In Genetta 33% of all sniffs to the tail were directed to the base while in the civets 54% of all tail-directed sniffs were aimed at the base (♂ = 48%, ♀ = 65%). Thus in Civettictis the proximal portion of the tail and the anogenital region seem to be more important or accessible targets for sniffing. From the standpoint of hair patterning these areas are quite distinctive (Fig. 40c). The scent gland is a visually and physically prominent attribute comparable in its white-black-white pattern to the sides of the neck. The tail differs from Genetta in having most of the white hairs concentrated on the sides and under surface of the base. It is also significant that the proportionately shorter tail of the African civet provides a relatively smaller sniffing area than in the genets.

g. The Sniff-Dart Axis: Interaction through Sniffing and Head-darting: As sniffing and head-darting are prominent and causally linked elements of interaction, it is important to consider some aspects of their occurrence. The following analysis is based on the assumption that head-darting occurs predominantly as a response to a proximate animal sniffing or attempting to sniff its companion's body.

1. The Roles of Sniffers and Darters. Table 12 reveals that when a series of encounters are considered the animal with the highest sniffing score (hereafter termed the sniffer) may or may not have the highest darting score. The meaning of these summated values though is difficult to interpret because the relationship between 2 animals can change during a series of encounters. A number of patterns emerged, however, when head-darting frequencies were compared for all single encounters in which a given animal was the sniffer. Three of the 6 animals exhibited statistically significant differences (Appendix B-2).

Animal K, for example, darted significantly less than his companions when he dominated sniffing ($P < .005$). Animal C also darted significantly less during encounters with F ($P < .05$). However, there was no significant difference in her darting frequency when these encounters are combined with the other ones in which she was the predominant sniffer. Animal O, on the other hand, darted more frequently in encounters even though he was the dominant sniffer ($P = .025$). The remaining 3 animals displayed no consistent tendency to dart more or less than their companions. Thus, while there is usually a disparity in any given encounter in the relative frequencies of sniffing and darting, some sniffers predictably darted either more (O) or less (K, C) than their companions. In I, F, and M the level of darting bore no consistent relationship to who sniffed the most. Similar results were found in the 2 African civets. The ♂, who was the dominant sniffer in 8 out of 9 encounters, darted significantly less than the ♀ ($P < .01$, Appendix B-3).

In 15 out of 21 encounters in which only one genet sniffed (Appendix B-4), the sniffers darted significantly less than their companions ($P < .005$). It is notable that in only 1 out of 15 encounters did the sniffer exhibit darting. In the remaining 6 encounters, the sniffer (O) out-darted the non-sniffer 5 times, but the difference between animals was not significant. These results reveal that in the majority of encounters in which only one animal sniffed its companion the sniffer refrained from darting. Of 68 encounters in which both animals sniffed, in only 10 (14.7%) did the sniffed animal refrain from darting. When the sniffed animal does dart, the level of darting varies individually both within and between encounters. These findings tentatively suggest that the sniffer refrains from darting as long as the companion darts but does not smell back.

2. Individual Variation of Target Selection. The overall distribution of sniffs and head-darts to body targets may not be indicative of the specific distribution exhibited by a given animal. That is, the sniffing and head-darting orientation of any one animal may or may not vary with different companions. To test the hypothesis that target distribution was independent of encounters with different companions, sniffing and head-darting targets were grouped into 4 arbitrary categories: (1) head and neck, (2) trunk (including shoulders, chest, spinal crest, midback, rump, anogenital region, and belly), (3) legs (fore- and hindlegs and feet), and (4) tail (including tailbase). Frequency tabulations were ranked for these 4 body regions on each companion that was encountered by a given animal, and the results were tested with the Friedman two-way analysis of variance (Appendix B-5).

The null hypothesis for sniffing was rejected at a probability of $\leq .017$ for 4 of the 6 animals (K, C, I and O). For head-darting only animals C and I deviated from a random variance ($P \leq .054$). These results indicate that though most animals darted and sniffed more often at certain regions than others, the relative frequencies to these regions often were not consistent with different companions. Though the head and neck were the predominant head-darting targets, the absence of scores for the other regions resulted in rank ties that produced insignificant variance. Thus, while almost all animals exhibited disproportionate contact distributions to their companion's body regions only 4 of the 6 animals were consistent in the way they sniffed their companions, and only 2 of these were consistent in head-darting at their companions.

3. The Sniff:Dart Ratio and Target Selection. Tables 16 and 17 summarize the relationship of head-darting to sniffing and sniffing targets in Genetta and Civettictis. The frequencies of these 2 patterns were converted to rates to facilitate comparison. Though the rates varied between encounters, the overall sniffing rates of the civets were comparable to the highest rates shown by the genets. The overall darting rate in the ♀ civet was 2 times greater than the highest rate displayed by a genet; the ♂ displayed a darting rate comparable to the lowest rates in the genets. On the average then, the civets sniffed and darted at relatively high rates. It is also evident that the variation in sniff:dart ratios does not reflect the overall rates of sniffing and darting during an encounter or series of encounters.

It can be hypothesized that the distribution of sniffs to the body parts is partially determined by the relative proportion of sniffs that are responded to with darts (i.e. the sniff:dart ratio). As head-darts usually cause a sniffing animal to desist (at least momentarily), it appeared that a predominance of tail and hindbody sniffing might be a strategy permitting maximal olfactory sampling at minimal risk of being darted at.

To test this hypothesis, the body was divided into 3 sections that maximally reflect the longitudinal polarity of sniffing

Table 16. The Relationship of Head-darting to Sniffing Frequency and Body Target in <u>Genetta tigrina</u>.

Animal		Sniff		Head-dart		Sniff:Dart Ratio[1]	Sniffing Targets[2]						Total Duration of Encounters per Pair (hr:min:sec)
		Total	Per 10 min.	Total	Per 10 min.		Forebody N	Forebody %	Midbody N	Midbody %	Hindbody N	Hindbody %	
F	♂	401	10.4	31	0.8	1:0.15	129	32.3	149	37.3	122	30.5	6:24:06
O	♂	444	11.5	62	1.6	1:0.07	65	14.6	137	30.8	242	54.5	
C	♀	233	6.6	170	4.8	1:0.18	44	18.8	58	24.9	131	56.2	5:52:57
K	♂	161	4.6	42	1.2	1:1.10	24	15.0	50	31.3	86	53.7	
M	♀	234	7.6	16	0.5	1:0.03	54	22.7	52	21.8	132	55.5	5:08:39
K	♂	218	7.1	8	0.3	1:0.07	47	21.6	44	20.3	126	58.1	
I	♀	160	5.0	24	0.7	1:0.05	30	18.9	60	65.2	68	73.9	5:18:24
K	♂	92	2.9	8	0.3	1:0.26	21	22.8	33	35.8	38	41.3	
C	♀	58	2.6	49	2.2	1:0.07	15	26.3	12	21.1	30	52.6	3:57:25
I	♀	60	2.6	4	0.2	1:0.82	18	30.0	19	31.6	23	38.3	
C	♀	58	1.4	17	0.4	1:0.36	15	25.9	9	15.5	34	58.6	6:41:20
M	♀	64	1.5	21	0.5	1:0.26	25	39.1	6	9.4	33	51.6	
F	♀	1	0.3	57	1.7	1:0.70	6	7.6	9	11.4	64	81.8	5:29:40
C	♂	79	2.4	0	--	---	0	--	1	--	0	--	

Table 16. (continued)

Animal	Sniff		Head-dart		Sniff:Dart Ratio[1]	Sniffing Targets[2]						Total Duration of Encounters per Pair (hr:min:sec)
	Total	Per 10 min.	Total	Per 10 min.		Forebody N	Forebody %	Midbody N	Midbody %	Hindbody N	Hindbody %	
I ♀	0	--	9	0.3	---	0	--	0	--	0	--	5:54:02
O ♂	43	1.2	30	0.9	1:0.21	3	6.9	3	6.9	37	86.0	
C ♀	5	0.2	33	0.9	1:0.80	2	--	3	--	0	--	5:34:16
O ♂	38	1.1	4	0.1	1:0.86	11	28.9	2	5.3	25	65.8	
I ♀	8	0.2	4	0.9	1:0.87	6	75.0	2	15.0	0	--	6:45:39
M ♀	30	0.7	7	0.2	1:0.13	5	16.6	5	16.6	20	66.6	
I ♀	1	<0.1	12	0.3	1:2.00	1	--	0	--	1	--	5:52:44
F ♂	2	<0.1	2	<0.1	1:6.00	0	--	0	--	1	--	

[1] Ratio of the number of companion-directed sniffs to the number of head-darts received from the companion.

[2] Forebody = head and neck; midbody = forelimbs, chest, shoulder, side, back, spinal crest, and belly; hindbody = tail, rump, hindlimbs, anogenital region. Percentages calculated only when sniffing frequency $\leq$ 30.

Table 17. The Relationship of Head-darting to Sniffing Frequency and Body Target in *Civettictis civetta*.

Encounter and Animal		Sniff		Head-dart		Sniff:Dart Ratio[1]	Sniffing Targets[2]						Encounter Duration (Min:sec)
		Total	Per 10 min.	Total	Per 10 min.		Forebody N	Forebody %	Midbody N	Midbody %	Hindbody N	Hindbody %	
1	♂	105	23.8	4	0.9	1:0.35	18	26.8	18	26.8	31	46.3	44:00
	♀	69	15.6	37	8.4	1:0.05	19	32.7	15	25.8	24	41.4	
2	♂	46	13.2	10	2.4	1:0.82	0	--	10	--	18	--	34:39
	♀	20	5.7	38	10.9	1:0.50	0	--	3	--	12	--	
3	♂	22	4.0	1	0.2	1:1.72	0	--	7	--	10	--	53:54
	♀	3	0.5	38	7.0	1:0.33	0	--	0	--	1	--	
4	♂	8	1.2	3	0.4	1:4.50	0	--	2	--	4	--	59:24
	♀	4	0.7	36	6.1	1:0.75	0	--	0	--	3	--	
5	♂	23	6.6	2	0.5	1:2.39	6	--	5	--	11	--	36:30
	♀	23	6.6	55	15.8	1:0.08	11	--	1	--	4	--	
6	♂	15	4.3	2	0.6	1:1.80	2	--	1	--	9	--	33:15
	♀	3	0.9	27	8.1	1:0.66	2	--	0	--	1	--	
7	♂	45	11.1	4	0.5	1:0.55	2	4.8	11	26.8	28	68.3	38:30
	♀	23	5.8	25	6.5	1:0.17	3	--	1	--	13	--	
8	♂	16	3.2	0	--	1:6.81	0	--	1	--	14	--	48:24
	♀	1	0.1	109	22.5	---	0	--	0	--	1	--	
9	♂	2	0.5	0	--	1:8.00	1	--	0	--	0	--	40:26
	♀	18	4.2	16	3.8	---	2	--	1	--	10	--	
Total	♂	282	7.2	26	0.7	1:1.35	29	13.8	55	26.3	125	59.8	388:22
	♀	164	4.2	381	9.9	1:0.15	37	29.1	21	16.5	69	54.3	

[1] Ratio of the number of companion-directed sniffs to the number of head-darts received from the companion.

[2] Forebody = head and neck; midbody = forelimbs, chest, shoulder, side, back, spinal crest, and belly; hindbody = tail, rump, hindlimbs (anogenital region excluded).

distribution (Tables 16 and 17). The frequency distribution of sniffs to these 3 body parts was tested for low and high sniff:dart ratio encounters with the Friedman two-way analysis of variance (Appendix B-6). In genets exhibiting sniff:dart ratios $\geq$1:05, there was a highly significant variance of the sniff distribution to the 3 regions ($P < .001$). When the same genets had sniff:dart ratios $\leq$1:0.33, the variance between body regions did not differ from random. Thus, though both groups showed an overall increasing gradient of sniffs from fore- to hindbody, the pattern was consistent only in encounter series characterized by low sniff:dart ratios.

These results are at odds with the prediction that high levels of darting restricted sniffing to the hindquarters. On the contrary, high sniff:dart ratios do not predictably indicate a sniffing bias to the hindbody, and genets strongly inclined to sniff the fore- and midbody did so in spite of the frequent darts they received. It appears that though head-darting is often elicited by sniffing it does not predictably constrain the companion's sniffing to the rear-end.

In the African civets, sniffing variance between the 3 body regions was statistically significant in situations of high and low sniff:dart ratios ($P < .05$), but a distinct difference in rank order was exhibited. Though the hindbody was usually the most frequently sniffed region in both groups (Table 15), the forebody ranked second highest in high ratio encounters and lowest in low ratio encounters. Thus, though there was no difference in variance between the 2 conditions, the forebody was a high frequency target more often when sniff:dart ratios were high. In view of the limitations of the small number of animals, the data do not lend themselves to further interpretation.

3. Discussion.

a. Vocalizations among viverrids.

Table II reveals that there is relatively little variation between species in the number of calls and their distribution within basic call groups. The most widespread calls, namely hissing, whining, screaming, and growling are known to occur in several other mammalian orders. Whining, a characteristic call of infants given under a broad variety of circumstances, is probably homologous to the tremelo groan of Fossa and the bleating call in Nandinia. All are emitted repeatedly as responses to temperature changes, hunger and other sources of discomfort or pain. Nandinia differs most from the other species in retaining the call into adulthood, when it is produced in response to tactile stimulation and apparently mild pain.

Low intensity whines are occasionally produced by adult genets and African civets, but screaming is the call that is usually emitted. Unlike whining, screaming is a response to specific painful stimuli that often arise during interaction with other animals. It appears that during development whining becomes decreasingly responsive to general discomfort stimuli, and is almost always exhibited in an intense form (as screaming) to painful stimuli.

From the standpoint of avoidance context, hissing and snorting are esentially identical calls. In all species they are often associated with head-darting, but in Paguma this linkage appears to be obligatory. Humming seems to be a specialized derivative of growling. While long duration is shared by both calls, humming is frequency modulated and the species that display it do not growl. Though usually not produced under circumstances conducive to growling, when disturbed from rest the Paguma often hummed after a series of snorts. In Nandinia, animals mimic the gradual frequency oscillations of one another, but the function of the call is obscure.

Hooting and neighing are unique only to the 2 palm civets (Nandinia and Paguma) as no repetitive sound having equivalent intensity was heard in any other species. EISENBERG (pers. comm.) has heard a whinnying call in Paradoxurus that approximates my description of neighing in Paguma. All 3 of these species are solitary arboreal omnivores with a strong predisposition for fruit. It is feasible that these calls function in spacing, for their brief, loud, and repetitive sound properties make them easily localized over relatively long distances (WHITFIELD 1971).

Though these species also have perineal scent glands, animals and museum specimens I have examined indicate low secretory rates of relatively weak-smelling scents. If it is assumed that the paradoxurines evolved from semi-arboreal ancestors in which scent markings served a spacing function, it is conceivable that high intensity calls have assumed at least some presumptive scent functions. The advantage of sound communication in a "volume environment" is that it can be broadcasted over long distances in all directions. While scent is also effective over long distances, its transmission is dependent on air current, and it is doubtful that all parts of a civet's living volume are equally accessible for sampling. It is curious that none of the terrestrial foraging civets (Genetta, Civettictis, Fossa) have repetitive high intensity calls in their repertoires. These calls occur predominantly in small arboreal mammals (galagos, tree hyraxes, monkeys), and terrestrial species that are large (felids) or medium-sized and social (canids). This pattern of occurrence suggests that such a call might predispose a small ground-living species to predation.

In terrestrial species scent would seem to be a more effective means of distance communication because (1) the probability of a strange animal entering the active space of a scent-mark would be greater in a 2-dimensional than 3-dimensional environment, and (2) scent-marks do not betray an animal's immediate whereabouts.

Coughing vocalizations were exhibited only by the terrestrial-foraging species. While the physical properties of this call are probably quite similar between species, the temporal patterning is distinctive. Coughs in Genetta and Fossa are emitted singly or in volleys, the interval distribution being dispersed over a wide range of time (<1- >60 sec.). In Civettictis and probably Viverricula, individual coughs are almost always temporally clustered into bouts composed of 5-6 elements, and these volleys are usually separated from others by relatively long periods of time (> 60 sec.).

In Civettictis, Viverricula and Genetta, coughing is probably homologous. In all 3 species it clearly results from respiratory hesitation often associated with sniffing, and stance and locomotory transitions. In the adult African civets, it was infrequently exchanged between animals. However, in the mother-infant association it clearly functions as a contact call: "the call is most frequently heard from kittens and is given by an individual who finds himself alone. The litter-mate at once responds by repeating the call and moving to the caller...the response of young kittens is completely automatic and invariable, and I never heard a call that failed to evoke a response" (R. F. EWER, pers. comm.). The contingency analysis of this study revealed that the callers were approached or sniffed 12-20% of the times they coughed. As noted by EWER,... although responsiveness to the call does not disappear, it gradually becomes more and more conditional upon other factors in the situation (EWER and WEMMER in prep.).

The presumptive stimuli evoking this call are always present, but animals do not cough continuously. Certain conditions appear to lower the threshold for calling. Confinement in an unfamiliar area and separation from other animals or the keeper are common conditions in which this call is given. When an animal is sufficiently aroused, the coughing may be spontaneous and bear no clear relationship to ongoing activities. Prior to copulation, for example, ♂ genets coughed repeatedly while following the ♀.

Coughing in volleys probably arose from a tendency for the glottis to close immediately after a single cough and then snap open again. In Genetta coughs are usually linked with expiration one for one, but doublets and triplets also occur during single expirations. The explusion of volleys of coughs during expiration in Civettictis could have arisen from the doublet and triplet condition in Genetta. Temporally dispersed coughing then probably represents the primitive condition.

Coughing in Fossa resembles that of Genetta, except that it can be evoked by human imitation (WEMMER 1970). It seems probable that the call arose independently in this species. Curiously, like Civettictis, Fossa is strictly a ground-living species.

b. Non-vocal interaction in Genetta and Civettictis.

A large number of patterns are shared by both Genetta and Civettictis; a small number of patterns are different. The differences are best elucidated by a consideration of timing and spacing. In Genetta back-arching, crouching, and tail-flaring are associated with mutual or uni-directional visual fixation; they occur in the companion's proximity, but out of his reach. Back-arching and crouching are characterized by the tonic retention of a lateral or frontal orientation to the other animal. During minimal contact interaction, sniffing may be uni-directional or reciprocal; sniffing and head-darting roles are frequently distinct, and mutual head-darting is rare. Interaction is terminated by the departure of one or both animals.

In Civettictis, back-arching and tail-flaring are absent and crouching is infrequent. Visual fixation thus is not specified by tonic postural variants. Minimal contact interaction is composed of mutual sniffing, and sniffing and head-darting; unlike Genetta, reciprocal head-darting (sparring) is also common. The recipient of darting frequently assumes (1) a lateral or tangential orientation to the companion, with the face deflected away, and/or (2) a reclining position on the ground. After the delivery of more head-darts, the episode is terminated by the darting animal's departure.

Lateral or tangential body orientation to the companion is a common component of contact interaction in canids and has been referred to as the T-position (GOLANI and MENDELSSOHN 1971) and scruff-shoulder orientation (FOX 1971). In the golden jackal, the lateral animal is the contact recipient; the companion may sniff, paw at, or bite him, or may rest his head or forelegs on the lateral animal's back. The T-position terminates with circling or genital licking (GOLANI and MENDELSSOHN 1971). In the wolf, dog, and coyote, a reclining position may be assumed if the lateral animal is pushed (FOX 1971). Lateral recumbency (passive submission: SCHENKEL 1967) is also a reaction to being sniffed in the genital region. According to SCHENKEL (1967, p. 324) the most obvious characteristic of the recumbent animal is "... the readiness to actively enter into contact with the superior..." animal; the reclining animal may whine, make licking movements, push with its nose, and wag the tail. In reclining civets, only the head and neck are moved in response to the proximity and head-darts of the standing animal; motion only appears to provoke further darting. Nevertheless, while types of contact differ, *Civettictis* is basically similar to these canids in that contact is received during lateral orientation and recumbency is a response to contact.

While there are individual differences in the orientation of sniffs and darts, in both species there is a general trend for the forebody to be the darting target, and the fore- and hindbody to be sniffing targets. Though other workers have not quantitively documented observations of oriented contact, it has been suggested that certain body markings serve as contact targets (FOX 1969, KLEIMAN 1967).

The body targets of sniffing and darting are the same in these 2 species, but the hair patterning differs. There is thus an indication that white body markings may serve several different functions. Presumptive general functions can be arrived at by evaluating (1) whether the marking is always prominent or can be hidden, (2) whether the size, proportions or shape of the design is strongly influenced by body configuration, and (3) whether the marking is characteristically oriented to companions or oriented to by companions. The contrasting markings on the bodies of Genetta and Civettictis do not exhibit these characters equally. In the African civet, the white spinal stripe is only visible during crest erection and the white perineal gland is often concealed by the tail; only the gland receives oriented contact. The design of neither marking is altered significantly when viewed from different positions.

The design properties of the eye spots and tail of Genetta and the face and neck markings of Civettictis however alter considerably during positional or postural changes in relation to the viewer. Only in Civettictis though is there a correspondence between the location of contrast patterns and oriented contact. On the basis of these differing properties, contrast markings may (1) enhance visibility of the body or its movements in animals that are nearby but out of contact range, (2) specify postural configurations of the body or the part of the body carrying the mark, and (3) specify targets of companion-oriented contact.

The following outline summarizes some of the possible changes associated with the transition from a genet-like grade of behavioral organization to that exhibited by the African civet. It is based on the assumption that Genetta is a relatively primitive viverrine and that Civettictis evolved from an ancestor resembling Genetta. Items are lettered for convenience, but the separation does not imply a lack of causal relationship between items.

(a) Relative shortening of tail length and degeneration of its highly patterned design; loss of tail-flaring capacity.

(b) Loss of ability to maintain protracted arched-back stances; compensatory development of the spinal crest but retention of the tendency to maintain a lateral body orientation to other animals during maximal crest erection.

(c) Origin of lateral body orientation cum neck deflection, and its incorporation with reclining body positions as intermediary components in the sniff-dart axis; concomitant elaboration of highly patterned head and neck markings from a basic genet-like design.

(d) Enlargement of the perineal gland and elaboration of its coloration; derivation of the normal quadrupedal stance from a squatting or reversed quadrupedal upright; specialization of Flehmen.

The genet and African civet are more similar behaviorally to one another than to other species of carnivores. While lateral orientation and reclining are also components of contact interaction in canids, it is probably a simplification to view Civettictis as a more social species. There is no evidence suggesting it is anything but solitary. Perhaps the exigencies of a totally ground-living existence select for an interaction design that permits the establishing of social roles in minimal time. It is conceivable that the assumption of oriented stances in the African civet facilitate transition from sniffing and darting to maximal contact interaction.

c. Epilogue.

The second part of this study described patterns and modes of interaction between animals. As the behaviors occurred mainly in a social context and seemed to affect the relative probabilities of different behaviors in the other animal, they were assumed to be communicative (ALTMANN 1967). That a certain pattern is communicative, however, is often difficult to demonstrate, for the properties of mammalian non-vocal behavior are not easily isolated for experimental testing.

Much discussion has centered on characteristics that distinguish communication from other types of stimulus-response interaction. The latest dissertation on the topic confirms the present uncertainty of thought (BURGHARDT 1970). Some prominent concepts of animal communication have limited utility in defining certain forms of mammalian interaction. Whereas the production and reception of auditory and visual patterns are often temporally exclusive and usually physically different events, the sender-receiver dichotomy becomes hazy during interaction involving contact. When an animal, for example, smells a companion, tactile stimulation is mutual and concurrent, but only the sniffer receives olfactory information. While it does not seem appropriate to regard the sniffed animal as a sender, by its failure to avoid or prevent contact, it transmits information that limits the behavioral alternatives of the sniffer. On the other hand, an animal can receive information in the absence of the stimulating animal. When the stimulus is general and uni-directional, transmission is usually considered to be non-communicatory. If the stimulus is specialized, as for example a scent-mark, transmission is regarded as communicatory. It is clear that whether an act is defined as communicative depends upon the implicit assumption that the process has resulted from natural selection and is thus adaptive to the sender and perhaps the receiver.

Contact properties can presently be neither measured nor described as accurately as the sounds or the motions of single animals. During intense contact interaction, such as wrestling, fighting or copulation, it seems doubtful that a component analysis at the sender-receiver level would accurately approximate the relevant communicative dimensions. Perhaps additional measures, such as tactile qualities of the skin and the bodies' volume and density properties, would permit more insight into processes of contact communication.

Though this verges on the impossible, it bears importantly on 2 realms to be bridged in the study of animal communication, the subject's and the observer's Umwelt. There can be little doubt that scientific epistemology structures the understanding of some phenomena in a way that approximates reality in but a vague way. Failure to employ alternative heuristic frameworks has probably been an important factor that has limited the ethological approach to communication study. The display concept espoused by MOYNIHAN (1970) and SMITH (1969), for example, is a useful one in dealing with ritualized vocalizations and movements; its criteria are not fulfilled however by olfactory and tactile patterns because visual manifestations of delivery and reception are not the relevant properties. The ethologist then sees tactile and olfactory events "as through a glass darkly." On the other hand, the measurable parameters of several non-verbal communication modalities have been systematically described and investigated by American psychologists (DUNCAN 1969). Detailed transcription systems have been developed for the study of kinesics (body motion) (BIRDWHISTELL 1952), paralanguage (voice qualities and nonfluencies) (TRAGER 1958, 1961), and proxemics (usage of space) (HALL 1963). Compared with these sophisticated methods, only elementary gains have been made in the study of vertebrate non-vocal communication patterns.

In the course of this study, I have become increasingly aware of the limitations of the present state of ethological methodology. For the purpose of communication study and perhaps for the purpose of comparative ethology, there is a need for systematic guidelines of behavioral description. The development of a methodology with fine and coarse grade levels of resolution might be a feasible means of achieving descriptive confidence limits at the descriptive and analytical levels.

The descriptions and analysis I have presented are rough approximations of some of the major features of interaction in captive genets and civets. How these animals interact in the wild is unknown. I believe that many, perhaps most of the patterns exhibited in my animals have a very similar expression in the wild, but probably occur at far less frequent intervals and for shorter periods of time. While it is of great interest to know how time and space are used by these species in the natural condition, to confirm in the wild findings on only the mechanics of interaction would probably meet with quixotic success.

APPENDIX A

ENCOUNTER SCHEDULES FOR GENETTA TIGRINA AND CIVETTICTIS CIVETTA

Genetta tigrina: Male-male Encounters.

Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
1	6-IX-1969	F	3:30	1900	52:53
2	8-IX-1969	O	3:50	1940	45:47
3	10-IX-1969	F	3:50	1915	31:24
4	12-IX-1969	O	4:10	1910	34:20
5	14-IX-1969	F	3:45	1645	34:09
6	16-IX-1969	O	3:25	1630	33:35
7	18-IX-1969	F	4:00	2010	40:24
8	20-IX-1969	O	4:15	1935	46:10
9	22-IX-1969	F	4:10	1945	31:39
10	24-IX-1969	O	4:20	1930	33:45
Female-female Encounters (C and I).					
1	20-VI-1969	I	4:15	2030	30:58
2	9-VII-1969	I	--	1900	33:44
3	17-VII-1969	I	3:50	2010	32:56
4	25-VII-1969	C	3:45	1930	32:22
5	31-VII-1969	C	2:45	1900	32:55
6	7-VIII-1969	I	3:40	2040	33:11
7	15-VIII-1969	I	2:05	2000	31:19

Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
Female-female Encounters: C and M (Unfamiliar)					
1	18-VIII-1969	C	4:30	2130	34:57
2	20-VIII-1969	M	3:15	1945	40:50
3	22-VIII-1969	C	1:15	1630	36:31
4	24-VIII-1969	M	2:30	1845	33:34
5	26-VIII-1969	C	4:47	1855	34:45
6	28-VIII-1969	M	2:45	1930	49:22
7	30-VIII-1969	C	3:12	1930	46:15
8	1-IX-1969	M	4:05	2000	35:55
9	3-IX-1969	C	3:50	1910	39:01
10	5-IX-1969	M	4:50	2020	50:10
Female-female Encounters: I and M (Unfamiliar)					
1	25-IX-1969	M	3:20	1950	35:25
2	27-IX-1969	I	4:25	2050	37:17
3	29-IX-1969	M	3:00	1905	37:27
4	1-X-1969	I	3:00	1900	41:01
5	3-X-1969	M	3:35	1915	45:19
6	5-X-1969	I	2:40	1930	39:42
7	7-X-1969	M	3:00	1615	45:23
8	9-X-1969	I	3:20	1940	48:38
9	11-X-1969	M	3:30	1630	36:34
10	13-X-1969	I	3:30	1930	38:53

Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
Male-female Encounters: K and M					
1	9-VI-1969	M	4:00	2100	29:54
2	16-VI-1969	M	3:10	2010	30:06
3	23-VI-1969	K	3:30	2030	31:22
4	30-VI-1969	M	3:50	1620	36:16
5	7-VII-1969	K	3:45	1915	32:11
6	14-VII-1969	M	3:00	1930	33:06
7	21-VII-1969	M	2:25	1715	22:32
8	28-VII-1969	K	6:50	1630	27:04
9	4-VIII-1969	M	2:15	1915	32:49
10	11-VIII-1969	K	3:15	1930	33:19
Male-female Encounters: K and C					
1	14-X-1969	K	3:00	1635	35:14
2	16-X-1969	C	3:40	1940	35:44
3	18-X-1969	K	3:40	2030	34:04
4	20-X-1969	C	4:05	2050	36:21
5	22-X-1969	K	3:05	1940	36:11
6	24-X-1969	C	3:25	2040	35:31
7	26-X-1969	K	3:30	2000	39:47
8	28-X-1969	C	4:00	2000	34:24
9	30-X-1969	K	3:20	1940	33:44
10	1-XI-1969	C	4:05	2010	31:57

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Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
Male-female Encounters: F and I					
1	2-XI-1969	F	3:45	1925	39:10
2	4-XI-1969	I	2:50	1620	33:32
3	6-XI-1969	F	6:20	1950	36:36
4	8-XI-1969	I	3:00	1615	31:16
5	10-XI-1969	F	3:15	1645	33:06
6	12-XI-1969	I	3:22	1652	39:48
7	14-XI-1969	F	3:50	1940	34:14
8	16-XI-1969	I	3:25	1655	33:14
9	18-XI-1969	F	5:05	2030	38:38
10	20-XI-1969	I	4:30	2100	33:10
Male-female Encounters: O and C					
1	21-XI-1969	O	3:00	1850	39:32
2	23-XI-1969	C	2:55	1625	36:39
3	25-XI-1969	O	2:55	1840	34:55
4	27-XI-1969	C	4:10	1740	31:39
5	29-XI-1969	O	3:48	1658	30:23
6	1-XII-1969	C	3:00	1920	33:56
7	3-XII-1969	O	3:55	2015	28:11
8	5-XII-1969	C	4:00	1930	32:18
9	7-XII-1969	O	3:00	1630	35:24
10	9-XII-1969	C	4:20	2020	31:19

Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
Male-female Encounters: F and M					
1	11-XII-1969	F	3:00	1600	11:40
Male-female Encounters: O and I					
1	30-XII-1969	O	3:30	1930	32:14
2	1-I-1970	I	3:20	1905	34:44
3	3-I-1970	O	3:35	1935	52:50
4	5-I-1970	I	4:05	2040	32:54
5	7-I-1970	O	3:50	1950	35:08
6	9-I-1970	I	4:50	2050	33:16
7	11-I-1970	O	2:40	1940	33:01
8	13-I-1970	I	3:40	1940	34:16
9	15-I-1970	O	3:00	1900	32:43
10	17-I-1970	I	3:10	1610	32:56
Male-female Encounters: F and C					
1	18-I-1970	F	3:30	1915	32:11
2	20-I-1970	C	2:20	1845	32:58
3	22-I-1970	F	3:05	1930	35:40
4	24-I-1970	C	3:20	1650	34:42
5	26-I-1970	F	3:15	1845	29:45
6	28-I-1970	C	4:10	2010	32:27
7	30-I-1970	F	3:00	1845	28:20
8	1-II-1970	C	4:25	2020	33:35
9	3-II-1970	F	4:15	2015	36:03
10	5-II-1970	C	4:05	2000	33:59

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Encounter Number	Date	First Animal Introduced	Duration in Cage Prior to Encounter (Hrs.:Min.)	Second Animal Introduced	Encounter Duration (Min:Sec)
Male-female Encounters: K and I					
1	6-II-1970	K	3:00	1945	32:57
2	8-II-1970	I	3:30	2000	27:21
3	10-II-1970	K	4:15	2015	30:32
4	12-II-1970	I	3:20	1640	29:42
5	16-II-1970	K	4:00	2000	35:20
6	18-II-1970	I	3:30	2000	33:30
7	20-II-1970	K	4:00	2000	33:27
8	22-II-1970	I	3:45	1845	36:27
9	26-II-1970	K	3:30	1630	29:56
10	2-III-1970	I	3:00	1900	29:12

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Civetticictis _civetta_: Male-female Encounters.

Encounter Number	Date	Encounter Onset Time	Encounter Duration (Min:Sec)
1	2-XI-1970	1500	44:00
2	3-XI-1970	1530	34:39
3	4-XI-1970	1445	53:54
4	5-XI-1970	1500	59:24
5	9-XI-1970	1530	36:30
6	10-XI-1970	1515	33:15
7	12-XI-1970	1500	38:30
8	13-XI-1970	1500	48:24
9	16-XI-1970	1530	40:25

APPENDIX

STATISTICAL PROCEDURES

Wilcoxon matched-pairs signed ranks test; Number = the number of series of encounters in which at least one animal jaw-gaped and both animals tail-flared (see Table 13); Variable = tail-flaring frequency; Significance level (two-tailed) = .05.

Tail-flaring Frequency						
Jaw-gaper		Companion		d	Rank	Statistics
(K)	7	(C)	13	-6	-3	
(M)	5	(K)	19	-14	-6	
(I)	20	(M)	27	-7	-4	
(C)	22	(M)	23	-1	-1	
(I)	2	(O)	11	-9	-5	N = 7
(F)	1	(C)	8	-7	-4	T = 2
(I)	3	(F)	1	+2	+2	P = .05

APPENDIX

STATISTICAL PROCEDURES

Wilcoxon matched-pairs signed-ranks test; N = the number of single encounters in which (1) the animal in question sniffed more frequently than its companion, and (2) at least one animal head-darted, Variable = head-dart frequency; significance level = .05.

Head-dart Frequency						
Sniffer		Sniffed		d	Rank	Statistics
(K)	0	(I)	3	-3	-3	
	8		37	-29	-9	
	0		9	-9	-7	
	0		4	-4	-5.5	
	7		32	-25	-8	
	3		6	-3	-3	
	0	(M)	4	-4	-5.5	N = 9
	0		1	-1	-1	T = 0
	2		5	-3	-3	P = <.005
(C)	33	(K)	9	+24	+18	
	15		5	+10	+14	
	20		5	+15	+17	
	13		4	+9	+12.5	
	3	(I)	0	+3	+5	
	9		1	+8	+10.5	
	0	(M)	8	-8	-10.5	
	0		2	-2	-4	
	8		4	+4	+6	
	1		0	+1	+2	
	5	(O)	4	+1	+2	
	0	(F)	7	-7	-9	
	0		6	-6	-8	
	0		9	-9	-12.5	
	0		11	-11	-15	
	0		1	-1	-2	N = 18
	0		14	-14	-16	T = 54
	0		5	-5	-7	P = >.05 (n.s.)
(C)	0	(F)	7	-7	-4 04	
	0		6	-6	-3	
	0		9	-9	-5	
	0		11	-11	-6	
	0		1	-1	-1	N = 7
	0		14	-14	-7	T = 0
	0		5	-5	-2	P = .05

Head-dart Frequency				
Sniffer	Sniffed	d	Rank	Statistics
(I) 18	(K) 0	+18	+8.0	
0	2	-2	-3.5	
2	0	+2	+3.5	
0	4	-4	-7.0	
1	2	-1	-1.5	
1	(F) 0	+1	+1.5	
0	(M) 3	-3	-5.5	N = 9
3	(C) 0	+3	+5.5	T = 17.5
0	37	-37	+9.0	P = >.05 (n.s.)
(M) 3	(I) 0	+3	+9.0	
0	1	-1	-3.5	
0	1	-1	-3.5	
7	(C) 0	+7	+11.0	
0	1	-1	-3.5	
0	2	-2	-7.5	
0	1	-1	-3.5	
0	4	-4	-10.0	
2	(K) 1	+1	+3.5	N = 11
0	1	-1	-3.5	T = 23.5
1	3	-2	-7.5	P = >.05 (n.s.)
(O) 0	(F) 1	-1	-2.0	
5	6	-1	-2.0	
10	8	+2	+6.0	
6	8	+2	+6.0	
6	(I) 2	+4	+10.5	
2	0	+2	+6.0	
9	2	+7	+14.0	
5	1	+4	+10.5	
0	1	-1	-2.0	
6	1	+5	+13.0	
0	(C) 2	-2	-6.0	
0	9	-9	+15.0	
0	2	-2	-6.0	N = 15
0	4	-4	+10.5	T = 24*
0	4	-4	+10.5	P = .025
(F) 1	(O) 0	+1	+2	
0	1	-1	-2	
1	17	-16	-6	
0	1	-1	-2	N = 6
5	14	-9	-5	T = 2
2	8	-6	-4	P = >.05 (n.s.)

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* The negative sign of the T value indicates statistical significance for the opposite hypothesis.

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APPENDIX

STATISTICAL PROCEDURES

Wilcoxon matched-pairs signed ranks test; N = number of encounters;

Variable = head-dart frequency; Significance level (one tailed) = .025.

Head-dart Frequency				
Sniffer	Sniffed	d	Rank	Statistics
4	37	-33	-5.5	
10	38	-28	-4.0	
1	38	-37	-7.0	
3	36	-33	-5.5	
2	27	-25	-3.0	
4	25	-21	-2.0	$N = 8$
0	109	-109	-8.0	$T = 1$
16	0	+16	+1.0	$P = < .01 > .005$

APPENDIX

STATISTICAL PROCEDURES

Wilcoxon matched-pairs signed ranks test; N = the number of single encounters in which an animal did not sniff its companion, but at lease one animal head-darted; Variable = head-dart frequency.

Significance level = .05.

Enc.	Head-dart Frequency								
No.	Non-sniffer		Sniffer		R''	d	R'	Rank	Statistics
1	(I)	1	(F)	0		+1	+2.0	+3.5	
8	(I)	1	(M)	0		+1	+2.0	+3.5	
10		1		0		+1	+2.0	+3.5	
4	(C)	2	(M)	0		+2	+7.0	+8.5	
8		1		0		+1	+2.0	+3.5	
1	(C)	2	(O)	0		+2	+7.0	+8.5	
5		9		0		+9	+13.5	+19.5	
6		2		0		+2	+7.0	+8.5	
7	(O)	4	(C)	5		-1	-2.0	-3.5	
8	(C)	4	(O)	0		+4	+9.0	+12.0	
1	(F)	7	(C)	0		+7	+12.0	+17.5	
2		6		0		+6	+11.0	+16.0	
3		9		0		+9	+13.5	+19.5	
6		11		0		+11	+15.0	+21.0	
10		5		0		+5	+10.0	+14.5	
3	(I)	2	(O)	6	5	-4	-5	-12.0	
4		0		2	2	-2	-2	-8.5	
5		2		9	6	-7	-6	-17.5	
6		1		5	3	-4	-3	-12.0	N = 21
8		1		0	1	+1	+1	+3.5	T = 68.0
10		1		6	4	-5	-4	-14.5	P = [illegible] >.05

N = 15 (Rank')
T = 2
P < .005

N = 6 (Rank'')
T = 1
P > .05

APPENDIX B5

STATISTICAL PROCEDURES

Friedman two-way analysis of variance; Conditions = 4 general body targets (I-IV)*; Number = animals encountered; Variable = nasal contact frequency; Significance level = .05.

(N)	Conditions (k)								
Animals	I		II		III		IV		
Encountered	N	Rank	N	Rank	N	Rank	N	Rank	Statistics
Individual K									
C	24	2.0	57	3.0	9	1.0	70	4.0	
I	21	2.0	40	4.0	4	1.0	26	3.0	
M	47	2.0	79	3.0	9	1.0	82	4.0	$X_r^2 = 8.2$
		6.0		10.0		3.0		11.0	P = .017
Individual C									
K	44	2.0	52	3.0	27	1.0	97	4.0	
M	14	3.0	12	2.0	4	1.0	28	4.0	
F	6	2.0	18	3.0	3	1.0	52	4.0	
O	2	3.0	3	4.0	0	1.5	0	1.5	
I	15	3.0	24	4.0	6	1.0	12	2.0	$X_r^2 = 6.6$
		13.0		16.0		5.5		15.0	P = $<$.01
Individual I									
M	6	4.0	2	3.0	0	1.5	0	1.5	
F	0	2.0	0	2.0	0	2.0	1	4.0	
C	18	3.0	29	4.0	5	1.0	8	2.0	
K	30	2.0	59	4.0	24	1.0	45	3.0	$X_r^2 = 11.7$
		13.0		13.0		5.5		10.5	P = $<$.001
Individual M									
I	5	2.0	7	3.0	1	1.0	17	4.0	
C	25	3.0	10	2.0	2	1.0	27	4.0	
K	54	2.0	74	3.0	17	1.0	93	4.0	
F	1	4.0	0	2.0	0	2.0	0	2.0	$X_r^2 = 6.3$
		11.0		10.0		5.0		14.0	P = .094
Individual O									
F	65	1.0	125	3.0	69	2.0	185	4.0	
I	3	2.0	5	3.0	2	1.0	33	4.0	
C	11	3.0	1	1.0	3	2.0	23	4.0	$X_r^2 = 8.4$
		7.0		7.0		5.0		12.0	P = $<$.017
Individual F									
I	0	2.0	0	2.0	0	2.0	1	4.0	
O	129	3.0	151	4.0	48	2.0	72	1.0	
C	0	2.0	1	4.0	0	2.0	0	2.0	
M	1	4.0	0	2.0	0	2.0	0	2.0	$X_r^2 = 1.5$
		11.0		12.0		8.0		9.0	P = .754

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* I = head and neck, II = trunk, III = legs, IV = tail.

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APPENDIX

STATISTICAL PROCEDURES

Friedman two-way analysis of variance; conditions = 4 general body targets (I-IV)*; number = animals encountered; variable = head-darting frequency; significance level = .05.

Animals Encountered	Conditions: I N	I Rank	II N	II Rank	III N	III Rank	IV N	IV Rank	Statistics
Individual K									
C	34	4.0	1	1.0	2	2.5	2	2.5	
I	2	4.0	0	2.0	0	2.0	0	2.0	
M	6	4.0	0	1.0	1	2.5	1	2.5	$X_r^2 = 6.6$
		12.0		4.0		7.0		7.0	P = [illegible]
Individual C									
K	135	4.0	12	3.0	9	2.0	3	1.0	
M	16	4.0	0	2.0	0	2.0	0	2.0	
F	28	4.0	0	2.0	0	2.0	0	2.0	
I	4	4.0	2	3.0	0	1.0	1	2.0	$X_r^2 = 8.1$
		16.0		10.0		7.0		7.0	P = .033
Individual I									
M	3	4.0	0	2.0	0	2.0	0	2.0	
O	12	4.0	0	2.0	0	2.0	0	2.0	
C	20	4.0	0	2.0	0	2.0	0	2.0	
F	7	4.0	0	2.0	0	2.0	0	2.0	$X_r^2 = 7.2$
		16.0		8.0		8.0		8.0	P = .054
Individual M									
I	7	4.0	0	2.0	0	2.0	0	2.0	
C	20	4.0	0	1.5	0	1.5	1	3.0	
K	6	4.0	0	1.0	2	2.5	2	2.5	$X_r^2 = 6.1$
		12.0		4.5		6.0		7.5	P = <.148
Individual O									
F	31	4.0	5	2.0	8	3.0	1	1.0	
C	4	4.0	0	2.0	0	2.0	0	2.0	
I	12	4.0	0	2.0	0	2.0	0	2.0	$X_r^2 = 4.2$
		12.0		6.0		7.0		5.0	P = .148
Individual F									
I	2	4.0	0	2.0	0	2.0	0	2.0	
O	23	4.0	1	2.0	1	2.0	1	2.0	
C	36	4.0	0	2.0	0	2.0	0	2.0	$X_r^2 = 5.4$
		12.0		6.0		6.0		6.0	P = .175

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* I = head and neck, II = trunk, III = legs, IV = tail.

APPENDIX

STATISTICAL PROCEDURES

Friedman two-way analysis of variance; conditions = 3 general body targets (I-III);* number = encounter series in which the sniff:dart ratio was $\gtrsim$ 1:0.5 (first test) or $\lesssim$ 1:0.36 (second test); variable = nasal contact frequency; significance level = .05.

Animal and Companion	Conditions						
	I		II		III		
	N	Rank	N	Rank	N	Rank	Statistics
K (I)	21	1.0	33	2.0	38	3.0	
I (K)	30	1.0	60	2.0	68	3.0	
C (K)	44	1.0	58	2.0	131	3.0	
K (M)	47	2.0	44	1.0	126	3.0	
M (K)	54	2.0	52	1.0	132	3.0	
M (I)	5	1.5	5	1.5	20	3.0	
C (M)	15	2.0	9	1.0	34	3.0	
M (C)	25	2.0	6	1.0	33	3.0	
C (I)	15	2.0	12	1.0	30	3.0	
O (I)	3	1.5	3	1.5	37	3.0	
O (F)	65	1.0	137	2.0	242	3.0	X_r^2 = 19.1
F (O)	129	2.0	149	3.0	122	1.0	P = <.001
		19.0		21.0		34.0	
K (C)	24	1.0	50	2.0	86	3.0	
I (M)	6	3.0	2	2.0	0	1.0	
I (C)	18	1.0	19	2.0	23	3.0	
O (C)	11	2.0	2	1.0	25	3.0	
C (O)	2	2.0	3	3.0	0	1.0	
C (F)	6	1.0	9	2.0	64	3.0	
F (I)	0	1.5	0	1.5	1	3.0	X_r^2 = 2.3
I (F)	1	2.5	0	1.0	1	2.5	P = <.30 (n.s.)
		14.0		14.5		19.5	

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* I = forebody, II = midbody, III = hindbody.

APPENDIX

STATISTICAL PROCEDURES

Friedman two-way analysis of variance; Conditions = 3 general body targets (I-III);* Number = encounters in which the sniff:dart ≥ 1:0.5 (first test) or ≤ 1:0.33 (second test); Variable = nasal contact frequency; Significance level = .05.

Encounter and Animal	Conditions						
	I		II		III		
	N	Rank	N	Rank	N	Rank	Statistics
2 ♂	0	1.0	10	2.0	18	3.0	
2 ♀	0	1.0	3	2.0	12	3.0	
3 ♂	0	1.0	7	2.0	10	3.0	
4 ♂	0	1.0	2	2.0	4	3.0	
4 ♀	0	1.5	0	1.5	3	3.0	
5 ♂	6	2.0	5	1.0	11	3.0	
6 ♂	2	2.0	1	1.0	9	3.0	
6 ♀	2	3.0	0	1.0	1	2.0	
7 ♂	2	1.0	11	2.0	28	3.0	df = 2
8 ♂	0	1.0	1	2.0	14	3.0	$X_r^2 = 9.8$
9 ♂	1	3.0	0	1.5	0	1.5	P = $<$0.01
		17.5		18.0		30.5	
1 ♂	18	1.5	18	1.5	31	3.0	
1 ♀	19	2.0	15	1.0	24	3.0	
3 ♀	0	1.5	0	1.5	1	3.0	df = 2
5 ♀	11	3.0	1	1.0	4	2.0	$X_r^2 = 6.4$
7 ♀	3	2.0	1	1.0	13	3.0	P = $<$ .05
		10.0		6.0		14.0	

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* I = forebody, II = midbody, III = hindbody.

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