Comparative Ethology of the Large-spotted Genet (*Genetta tigrina*) and Some Related Viverrids

CHRISTEN M. WEMMER

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ABSTRACT

Wemmer, Christen M. Comparative Ethology of the Large-spotted Genet (*Genetta tigrina*) and Some Related Viverrids. *Smithsonian Contributions to Zoology,* number 239, 93 pages, 37 figures, 18 tables, 1977.—The study describes and analyzes the behavior of the large-spotted genet (*Genetta tigrina*) in captivity, and treats selected aspects of behavior in eight viverrid genera occupying five different subfamilies. The natural history of the genus *Genetta* is reviewed, and the relationships of the living members of various subfamilies are discussed. The behavior of solitary animals is treated by considering locomotion, stances, and object- and self-oriented contact patterns. Scent-marking with glandular products, urine, and feces is considered with reference to the communicative properties of the marking behavior and the substance. Sonographic and contextual analyses are used to classify vocalizations and serve to establish homologies between the calls of several species. Further analyses of social behavior in *Genetta* and *Civettictis* are based on encounters within all possible pairs of animals. A small number of behavior patterns predominates during most interactions between animals of both species. The primary differences in the communication systems of these two species are probably related to semi-arboreal as opposed to terrestrial habits.

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Contents

Comparative Ethology of the Large-spotted Genet (*Genetta tigrina*) and Some Related Viverrids

Christen M. Wemmer

Introduction

Background

The genus *Genetta* occupies the niche of the small, semiarboreal, solitary, nocturnal, insectivore-carnivore. The dozen or so species comprising the genus are structurally coherent, exploit nearly all natural and cultivated habitats over most of Africa and southwest Europe, 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, 1961). The view that the viverrines are the most structurally conservative viverrids, however, rests 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, 1961; and 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, 1961; and Romer, 1945). Whether the lineage of the more terrestrial civets (*Viverricula, Viverra, Civettictis*) or the semiarboreal civets (*Poiana, Genetta, Prionodon*) represents the least altered derivative of the common ancestor is debatable, for the fossil record is inadequate. What little is known about *Poiana richardsoni,* though, suggests that a semiarboreal 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 having disparate distributions to be stabilized forest forms that 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 that presumably emerged early in its lineage.

Contrary to the prevailing view of the genet, it is herein acknowledged as a 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 present study attempts (1) to establish qualitative and quantita-

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tive behavioral characteristics, and to outline the principle features of the communication system in captive genets, and (2) to compare certain behaviors of selected viverrids and interpret the results in light of known taxonomic affinities.

INTRA-VIVERRID AFFINITIES

Because modern taxonomy strives to arrive at evolutionary classification by delimiting taxa on the basis of common ancestry and subsequent divergence (Mayr, 1968), behavioral evolution must ultimately derive from morphologically based appraisals of systematic position. Though behavioral criteria are often useful in elucidating relationship (Lorenz, 1953; Lawrence and Novick, 1963; and McKinney, 1965, 1966), 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. Many genera are rare or confined to remote tropical regions, resulting in a scarcity of study animals as well as few preserved specimens. In addition, a number of genera and perhaps one subfamily exhibit character traits that defy a simple scheme of filial relationship. While the pretense of a solution might be made by referring only to the most recent synopses of taxa (Anderson and Jones, 1967; Wenzel, 1972), it would ignore the problematic status of several genera dealt with herein.

Though a large number of viverrid species was available to me for comparative study, it became increasingly apparent, as it had to others (Dücker, 1971; Ewer, pers. comm.), that the mongooses (Herpestinae) exhibited a more uniform and distinctive level of behavioral organization than other viverrids. Similar observations were made by Pocock (1916b) and Gregory and Hellman (1939) who had advised elevation of the mongooses to familial status on the basis of their uniformity in foot, dental, and glandular characteristics. This suggestion was subsequently endorsed by Wurster and Benirschke (1968:374), who found that eight species and seven genera of mongooses examined karyotypically were "all nearly identical to one another and without exception, they bear no satellited marker chromosome." In addition, Ewer (1973), noting that all four known herpestine genera had horizontal oval pupils, stated 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 (Table 1; cf. Walls *in* Ewer, 1973). Lastly Radinsky (1971) has shown that in 25 of the 36 living genera representing all subfamilies, Crytoprocta, 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 in distinguishing the mongooses (Herpestinae) from the bulk of the viverrids. Both cranially and in gross body form the subfamily shows a strong affinity with the herpestines, but unlike the latter they possess the carnivore satellite chromosome (Table 1). Carlsson (1910) showed that *Galidia elegans* shared 14 anatomical features with the other Malagasy civets (including *Cryptoprocta* and *Eupleres*), 10 with the mongooses, and 7 with the viverrines, but he concluded that relegation of the Galidiinae to either the viverrids or herpestids would obscure its position as a stem form that differentiated prior to the evolution of either the herpestine or viverrine grade of organization. Gregory and Hellman's decision to place the galidiines within the Viverridae was consistent with their implicit belief that the 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. Although Pocock (1916a) gave the fossa familial status, Gregory and Hellman placed it as a subfamily within the Felidae, believing 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, the presence of an anal pouch (and the absence of the perineal gland) prompted Mivart to ally this species with the mongooses (in Gregory and Hellman, 1939). Karyotypically, however, the fossa has much in common with the paradoxurines, hemigalines, and galidiines (Wurster and Benirschke, 1968). Thus, without interpreting the fossa's affinity, it appears to be an early viverrid

TABLE 1.—Comparisons of major characteristics among viverrid subfamilies and genera (– = absence within taxon, + = presence within taxon but not necessarily universal, ± = present in some members of taxon, when no character alternatives 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...............	+	-	-	-	-	-	-	+	-

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 its skull. On the basis of its more trenchant carnassials and cartilaginous auditory bulla Gregory and Hellman surmised, however, 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 the presence of a preputial scent gland prompted Pocock (1915b) to separate *Nandinia* as a family. Ironically, the species strongly resembles the viverrines in its possession of a subtelocentric 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 the viverrines in general, *Prionodon* lacks the metatarsal pads, the perineal gland, and the second upper molar. These differences were interpreted by Pocock (1915a) as specializations justifying a distinct subfamilial status. Similarly, Gregory and Hellman relegated the linsang to a viverrine tribe (Prionodontini).

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

Behavioral Classification and Description

Ethological studies have traditionally relied upon both functional and motivational criteria in categorizing a species' behavioral repertoire. Many behavior patterns, however, can be assigned 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 overreductionistic, 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 accurate understanding of these factors requires both experimental validation and a knowledge of the species in its natural realm. Because these labors exceed the requirements of faithful description, it seems more objective to classify behavior on observable and measurable characteristics of form, rather than on deduction about motivational state, for instance. 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 fuctionally meaningful acts unabstracted by the observer's conceptual processes. But in mammals, at least, it is questionable whether the discrete phasic properties of action continua accurately represent all the meaningful dimensions of animal conduct. Symposia titles such as "The Search for Natural Units of Behavior" [1] 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 (1965, 1966) studies on duck behavior. In particular, there have been few critical attempts to establish either indices of variability or typical intensity (Morris, 1957) of mammalian displays (Le Boeuf and Peterson, 1969, is one exception).

The Eshkol-Wachmann Movement Notation Method (Golani, 1969), which permits fine-grain temporal and spatial resolution of behavior, has remained an unexploited descriptive tool. With rigorously objective description, the method provides a valuable alternative to the interpretive methods that have prevailed up to now, though from the standpoint of comparative ethology it

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[1] A lecture presented by S. A. Altmann at a symposium titled "Analytic Problems in the Study of Animal Behavior," 67th Annual Meeting of the American Association for the Advancement of Science (1970).

requires considerable 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 integral to the analysis and description of body motion as sonograms are to 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. The system replaces functional and motivational pigeonholing. For example, the patterns usually ascribed to the maintenance (or grooming) behavior category are herein subdivided into classes of self- and object-oriented contact patterns. The latter category also encompasses behaviors that 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 does not claim to be consistent in its criteria. 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.

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* and *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 *G. pardina* occurs in forest-savanna ecotone, woodland, and Guinea savanna. Drier nonforest areas are occupied by *G. genetta, tigrina* (sensu latu), *villiersi,* and *abyssinica* (Bigalke, 1968; Coetzee, in press). Although Dorst and Dandelot (1970) state that *G. villiersi* inhabits forests, a large number of this species in the National Museum of Natural History was collected from Sudan and Guinea savannas in Ivory Coast and Upper Volta. At least in Botswana, *G. genetta* penetrates considerably drier areas than *tigrina,* though both species are often found together (R. H. N. Smithers, pers. comm.). Displaying a tolerance for habitats ranging from low forest to woodland and savanna, *G. tigrina* has been collected from elevations as high as 2560 m (8500 ft) on the slopes of Mt. Kenya (Hollister, 1918). It often appears to be a "culture-follower," inhabiting the vicinity of villages and cultivated land (Rahm, 1966).

There appears to be a distinct sexual dimorphism as to size in some populations of *G. tigrina* (i.e., *stuhlmanni,* pers. observ.), 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,* sensu lato) varies from an average of 87.5 mm in females to 90 mm in males, while in high rainfall areas skulls of both sexes average 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; Maliniak, pers. comm.). The natural frequency of the melanistic morph in the wild is unknown. At the National Zoo a wild-type female 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 female's antagonism towards its male cage mate suggests that the sexes remain separate during the rearing of young. Verheyen's (1951) statement that the male participates in providing food for the young is doubtful.

The exact nature of the social system, however, is unknown. Presumably a land tenure system exists, but information is sparse regarding activity in and defense of the home area. In the course of capture and release work with genets inclined toward poultry thievery, Carpenter (1970) recaptured four of six female *G. rubiginosa* (= *G. t. rubiginosa* sensu lato) at their original capture points within days after release from as far away as 20 miles. Six of 11 males were taken again at poultry runs, but none was recaptured at the original trapping site. He attributes the fact that most poultry thieves are males to their greater mobility, and suggests that females, unlike males, 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; and Carpenter, 1970). The tentative and somewhat contradictory nature of all these findings clearly indicates that more work must be done to elucidate this aspect of the genet's natural history.

Breeding in *G. genetta* and *G. tigrina* (sensu lato) occurs during the wet seasons in both Kenya (Taylor, 1969) and Botswana (Smithers, pers. comm.). Taylor (1969) collected lactating and pregnant females 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 females from Botswana were also taken during the warmer wet period from October to February (Smithers, pers. comm.). Whether wild females 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; and Verheyen, 1951).

The types of resting, parturition, and rearing sites are probably influenced by habitat. Holes in trees, in fallen logs, and burrows in kopjes and cliff areas seem to be usual locations (Shortridge, 1934). Rowe-Rowe (1970) located three 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. In a sample of 78 *G. genetta* from Botswana Smithers (pers. comm.) found that the three 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, followed by Coleoptera and Orthoptera. Cobb (1970) reported that on the basis of stomach contents, fecal samples, and observation, the genets of Turkana, northern Kenya fed 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 humans for food and fur. According to Dekeyser (1956), *G. villiersi* is killed by the Bassari of Itiolo, Senegal, for its tail, used in ceremonial rituals. *Genetta*'s climbing ability probably provides an important niche parameter, not only in facilitating escape into arboreal refuge, but also in making accessible sources of food and cover that are denied to strictly terrestrial animals.

MATERIALS AND METHODS

Table 2 presents personal history information concerning the 11 genets on which the results of this study are based. Eight of these animals were born in the Small Mammal House at the National Zoological Park, Washington, D.C. For convenience they are referred to in the text by the following abbreviations: K (Kitzi), C (Clawdina), I (Ivy), Mo (Monika), M (Marvin), O (Oscar), E (Elsie), Fr (Froda), and F (Felix). The origin of the parental pair is unknown, though comparison of skins and skulls of the previous offspring of this pair with specimens at the Smithsonian Institution reveals similarity to *Genetta tigrina stuhlmanni*, a sub-

TABLE 2.—Caging history (cage locations, cagemate(s), periods of confinement, cage dimensions in meters) of study animals (*Genetta tigrina*)

Subject	Sex	Date of birth	University of Maryland		National Zoo	
Parent (P)	♂	Before 1966			♀ P	Duration of study
Parent (P)	♀	Before 1966			♂ P	Duration of study
Kitzi (K)	♂	22 Apr 67	C,I	Nov 1967--Jun 1970 1.37 x 2.43 x 2.43	C	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03
Clawdina (C)	♀	22 Jul 67	K,I	Nov 1967--Jun 1970 1.37 x 2.43 x 2.43	K	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03
Ivy (I)	♀	22 Jul 67	C,K	Nov 1967--Jun 1970 1.37 x 2.43 x 2.43	F	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03
Monika (Mo)	♀	01 Feb 68	M	Aug 1968--Dec 1968 1.37 x 2.43 x 2.43		Sep 1970--Jun 1971 .91 x .91 x 1.21
			--	Dec 1968--Jun 1970 1.37 x 2.43 x 2.43		
Marvin (M)[1]	♂	01 May 68	Mo	Aug 1968--Dec 1968 1.37 x 2.43 x 2.43		
Oscar (O)	♂	24 Apr 69	--	Oct 1969--Jun 1970 1.37 x 2.43 x 2.43	E	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03
Elsie (E)	♀	14 May 70			O	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03
Froda (Fr)	♀	05 Aug 70			--	Sep 1970--Jun 1971 .71 x 1.21 x 1.21
Felix (F)[2]	♂	? Jan 70	--	Jul 1969--Jun 1970 1.21 x 1.21 x 2.43	I	Sep 1970--Jun 1971 1.90 x 1.90 x 2.03

[1] Died during anesthesia in January, 1969.

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

species 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 day of birth or the day after and were confined to a box containing a heating pad and a blanket until they were able to move about by themselves. The first three hand reared genets had unrestricted freedom in our house; subsequent animals were confined to one room for most of the day. Their diet consisted of warm Esbilac (Borden 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 produced repeated vomiting that was remedied by substituting cow's milk mixed with egg yolk. Weaning was initiated by feeding morsels of raw meat from the nursing bottle nipple. Infants were triggered to urinate and defecate by massaging the perineum with a moist paper towel.

A couple of months after weaning, the hand reared genets were transferred to a laboratory at the University of Maryland. As the windows were open most of the year, to some extent the animals experienced local temperatures and humidity, except during thunder showers, cold spells, and winter

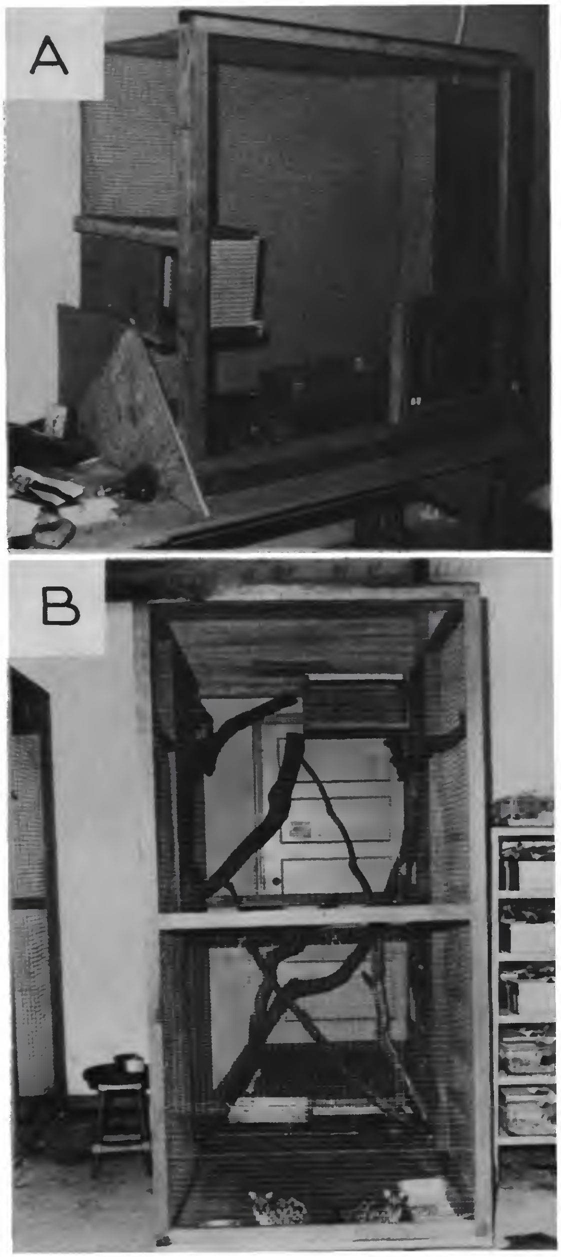

FIGURE 1.—Genet cages used at the University of Maryland: A, a cage for single animals (0.71 × 1.21 × 1.21 m); B, a large cage for two or three animals (1.37 × 2.43 × 2.43 m).

when the windows were closed and the room maintained at about 13°–19° C (55°–60° F). During the summer when temperatures reached 27° C (80° F) an electric fan circulated the air.

Cages of various sizes 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 corncob litter (Sanicel) that served as elimination sites for urination and defecation. Diet consisted of chunk horsemeat with 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 the animals in my care were moved to the Division of Scientific Research at the National Zoological Park (Table 2) and were installed in their permanent cages there by September of that year. Maintenance was thereafter under the supervision of Mr. Gene Maliniak, head keeper for the research collection.

Individuals of the following viverrid species were also studied: a pair of *Civettictis civetta* (African civet), two males and a female *Nandinia binotata* (African palm civet), a pair of *Paradoxurus hermaphroditus* (Asian palm civet), a male *Paguma larvata* (Formosan masked civet), a pair of *Arctictis binturong* (binturong), a male and two female *Hemigalus hartwicki* (banded palm civet), two pairs of *Fossa fossa* (fanaloka), three male *Galidia elegans* (Malagasy ring-tailed mongoose), and a male *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 male *Nandinia,* procured in 1967 from Kinshasa at about the age of six weeks, was kept at home and later at the University of Maryland until 1970. An adult female *Nandinia* was also held at the University from 1968 to 1970, as was the male *Paguma.* In addition, a male *Fossa* born in 1969 was hand reared at home from the day of birth, and then held at the University until 1970. The male *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 female was received. (These animals were descendents of stock from Sierra Leone

(Mallinson, 1969).) In addition to the standard meat diet, the *Civettictis, Nandina,* 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 tape recorders, on moving charts, and on still and cine film. Equipment 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 cine 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). Figures and descriptions are based in part upon selections from a total of 443.9 m (1400 ft) of 16 mm and 243.9 m (800 ft) of 8 mm film. Sound spectrograms of tape recordings were made using a Kay Electronic Sonograph (Model 6061 A) (85–8000 cps spectrum analyzer) and a Kay Electronic Missile Data-Reduction Spectrograph. Further details of method are described under specific chapter headings.

ACKNOWLEDGMENTS

Many people have contributed to different phases of this study and to all of them I am grateful. I especially thank James Murtaugh, Robert Cox, Leon Davies, Robert Horwich, Murray Itzkowitz, Richard Jachowski, George McKay, and Nicholas Smythe for their contributions in materials, efforts, thought, and companionship. I am grateful to Larry Collins for his fellowship in work and for his efforts in obtaining the facilities for genets at the National Zoological Park; to Wyotta Holden for her invaluable secretarial expertise and good natured tolerance; to Mary McComas and Marleigh Hartman for typing the final revision; to Gene Maliniak for his care of the animals; and to R. H. N. Smithers for the unpublished data he kindly placed at my disposal. I thank Douglass Morse and Wolfgang Schleidt for generously extending facilities, discussion, and enthusiasm during the course of the study. My dissertation advisor, John Eisenberg, must be credited with making the study possible and for creating the stimulating and unique research atmosphere at the National Zoo. I extend my sincere appreciation to the University of Maryland for graduate research financial assistance, without which the work could not have been done; and to the Smithsonian Institution for electing me a research associate while this report was being prepared. Finally, I thank my wife for her dedication and help in hand rearing eight genets and for her goodwill to the animals that lived with us.

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 limited to a specific context, 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 "solitary" behaviors and those whose occurrence is more exclusively linked to an association with other animals is one of degree rather than kind.

PRIMARY SENSES

EYES.—*Genetta tigrina* has moderately large semifrontal eyes with vertically elliptical pupils. The shape of the pupil varies from a narrow linelike 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) it is a dark grayish brown that matches the pelage. During development the color of the eye fades to a medium brown, but with a slightly more reddish hue than the fur. Though the eyeballs can move within the socket, their mobility is limited, and animals rely heavily on head movement even to maintain visual fixation of objects moving over small distances. Although the eyelids usually blink synchronously, it is not uncommon to see a resting animal blink only one. Dücker (1965) concluded that *G. tigrina* was color blind when study animals were unable to distinguish between colored cards and gray ones matched for brightness.

EARS.—The ear pinna of *Genetta,* like that of other viverrids, is of the basic aeluroid type described by Pocock (1916b) and Mohr (1952). But it differs from other genera, with the exception of *Hemigalus,* by having a finer layer of hair internally and externally, and in being slightly larger though lighter in build. The mobility of the pinna and the relationship between ear motion and the reception of different sounds merits special study. 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. The orientation of the pinna confers only slight changes in the size and shape of the orbit when the ear is erect. The size of the orbit, however, is greatly reduced when the pinna is folded backwards, a position achieved when the posterior edge 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 twitch once or several times in rapid succession in response to loud sounds or to tactile stimuli of the pinna or surrounding hair. The second type of movement consists of alternating, asynchronous, horizontal deflections of the pinnae accompanied by visual orientation toward a sound and/or movement (Preyer's reflex: Nuboer, 1959).

In the absence of a visual target, the head often scans from side to side in the direction of the sound, gradually narrowing its arc. Alternating ear movements of diminishing amplitude accompany the head scanning, and when the head is motionless, the ears are often jerked alternately and sporadically, but with minimal amplitude. This movement appears to be an important means of localizing unknown sources of sound, but the exact mechanism remains to be elucidated. Certainly this behavior is more pronounced in the genet than in the other species.

NOSE.—The nose is important for both olfactory and tactile perception. The thin mucous film of the rhinarium (Figure 15F) probably facilitates olfaction by providing a continuous solvent interphase from the external to internal nares. Also wind direction may possibly be detected by differential evaporation and/or cooling of the rhinarial surfaces. Scent perception requires air passage across the nasal epithelium, and apparently this is almost always accomplished by accelerated, low amplitude respiration. Though smelling (or sniffing) is often a distinctive activity, it is sometimes difficult to separate from respiration. In newborn genets, for instance, the respiratory rhythm is often sporadic; periods of rapid and shallow breathing alternate with slow, deep breathing. In a six-day-old animal (K), asleep after feeding, the number of respiratory cycles varied from 27 to 41 per minute ($\bar{x}$ = 34.6, N = 8).[2] Audible sniffing was first noticed at the age of two weeks (K, O, and E; N = 3). In its mildest form it involved rapid but slight expansion and contraction of the belly and rib cage and slight changes in nostril shape. Intense sniffing is audible and an extension and retraction of the mystacial vibrissae in apparent synchrony with inspiration and expiration can be seen. Sniffing is frequently accompanied by a slight head-bobbing. While smelling, the animal's body is stationary and the head elevated but without an orientation to a specific scent source (testing the air). On the other hand, close range smelling of a specific object or area often involves contact and usually occurs as the animal walks.

LOCOMOTION AND ITS ONTOGENY

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 thoracolumbar 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 aids in adjusting 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. Table 3 shows, for example, that the body proportions of the arboreal *Nandinia* and *Poiana* are more closely approximated by those of *G. genetta* and *G. villiersi,* both of which usually inhabit savanna. Assuming the measurement 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 habitat. Additional biogeographic

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[2] Based on visual detection of rib cage movement; one to three minutes interrupted each successive observation minute.

TABLE 3.—Some mean body measurements, proportions, sources and origins of several species of *Genetta* and allied genera (top group of species from savannah, middle group from woodland and forest, bottom group from forest; all measurements for specimens in National Museum of Natural History, Smithsonian Institution, taken from specimen labels; measurements given in millimeters)

Species	Source	Origin	Number	Measurement of body parts			Percent of head and body length	
				Head and body	Tail	Hind foot	Tail	Hind foot
G. villiersi ♂	USNM	Senegal,	16	427.6	413.8	79.7	96.1	18.6
♀		Upper Volta	19	409.2	400.3	77.8	97.8	19.0
♂♀			35	417.6	406.5	78.7	97.3	18.8
G. genetta ♂	USNM	Nigeria,	10	474.7	471.2	88.0	99.2	18.5
♀	and	Kenya,	13	474.1	459.3	86.3	96.2	18.3
♂♀	Hollister,	Senegal,	23	474.3	463.5	87.1	97.7	18.3
	1918	Upper Volta						
G. tigrina ♂	USNM	Kenya,	24	463.5	418.4	81.4	90.2	17.5
♀	and	Uganda	11	446.2	401.6	78.5	90.0	17.5
♂♀	Hollister,		35	458.3	413.1	80.5	90.1	17.5
	1918							
G. pardina ♂	USNM	Ghana,	4	510.0	418.7	91.5	82.9	17.8
♀		Ivory Coast	6	507.3	416.8	91.8	82.1	18.9
♂♀			10	508.7	417.6	91.6	82.1	18.0
♂	Allen,	Congo	9	455.0	470.0*	86.0	103.5	18.9
♀	1924		4	457.0	406.0	85.0	88.9	18.6
G. servalina ♂	Allen,	Congo	8	489.0	475.0	92.5	97.1	18.9
♀	1924		10	485.0	446.0	88.7	91.9	18.3
G. victoriae ♂	Allen,	Congo	13	573.0	444.0	101.0	77.4	17.6
♀	1924		5	573.0	448.0	100.0	78.1	17.4
Nandinia ♂	USNM	Ivory Coast,	11	467.3	498.9	88.7	106.7	18.9
binotata ♀		Togo	7	464.5	529.2	88.8	113.9	19.1
♂♀			18	466.2	510.7	88.7	109.5	19.2
♂	Allen,	Congo	7	510.0	570.0	92.0	111.7	18.3
♀	1924		11	480.0	544.0	88.0	113.3	18.3
Poiana								
richardsoni ♂	Allen,	Congo	1	332.0	380.0	64.0	114.4	19.2
	1924							

* This figure appears to be an error: if the value was a misprint of 407.0, the corrected proportion of tail to head and body, 89.4%, would be in accordance with the other values. Furthermore, the male servalina specimen pictured in Allen (1924: Plate XIV, Figure 1) appears to have a tail shorter than its head and body.

factors may be operative; indeed, longer tails may be thermally adaptive in warmer, low rainfall areas (Allen's rule: Mayr, 1963). Of the four woodland and forest species of *Genetta* listed in Table 3, all but *servalina* have relatively short tails and *G. victoriae*, the largest genet, has the smallest feet.

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 they are also capable of relatively unrestricted 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 have relatively less surface area than *Nandinia*'s, but more than *Civettictis* (Figure 2). Climbing ability is proportional to the extent of foot pad development. Figure 2 depicts a series of feet with decreasing arboreal specialization.

With regard to the ontogeny of locomotion, voluntary movement following birth is minimal, though infants are usually capable of crawling by the age of one or two days. The distinctive pattern of movement at this 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 brush along the substrate. The legs, unable to support the body, are extended to the side with the soles of the feet down; forward progress is achieved by pulling movements of the forelimbs. Until four or five days of age this locomotion produces a curving or circular path of movement. As animals begin to support their forebodies when walking, the path straightens, and head-sweeping becomes both less frequent and stereotyped. This movement of the head and forebody, appropriately termed "Kreisbogenschlagen" by Frank (*in* Dücker, 1965), apparently aids in tactile localization of the nipple, the mother, and siblings.

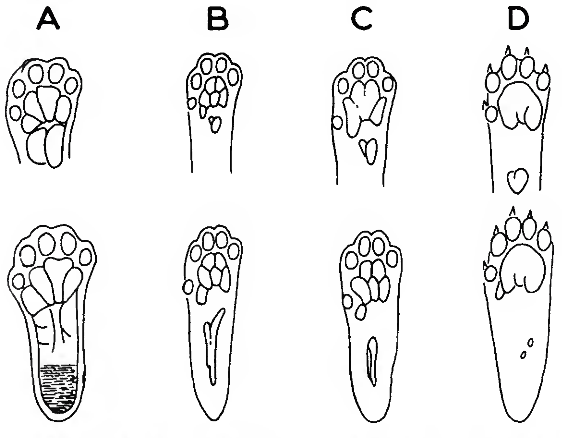

FIGURE 2.—Pad structure of the manus (upper row) and pes in four viverrids: A, the African palm civet (*Nandinia binotata*); B, the large-spotted genet (*Genetta tigrina*); C, the giant forest genet (*Genetta victoriae*); and D, the African civet (*Civettictis civetta*). (Not to scale.)

At about the age of one week, young genets are capable of supporting themselves and walking for brief periods on the fore- and hindlegs, 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 for the first 8–14 days and easily snag on irregular surfaces. Progression across a smooth woolen blanket, for example, is greatly encumbered, but on sloping and vertical surfaces the claws clearly assist clinging (Figure 15A).

Even before infant genets are able to walk they manifest a pronounced facility for maintaining partially suspended and precarious positions. When suspended by the head or neck, the tail and hindquarters execute a twirling motion common to young of many species of mammals (Horwich, 1972). If suspended by the tail, the forelimbs extend, 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 subsequently performed regularly until the animals had developed the strength and coordination at about 3–4 months of age to right themselves by flexing their torsos and climbing up their tails.

Once walking becomes steady other locomotor patterns appear to occur in clusters: it seems that the capacity to perform various gaits develops over a brief period and that the occasion of the first performance is simply subject to circumstances. Trotting, running, galloping, and jumping were observed for the first time in all animals between the ages of 20–30 days, the unsupported bipedal posture between 30–40 days, and vertical looping (see "Climbing" below) up and down steeply inclined surfaces from 32–40 days. As Dücker (1965) noted, the first climbing experiences are characterized by an unwillingness to descend without assistance. The types of locomotion in *G. tigrina* can be divided into walking, trotting, running, galloping, climbing, jumping, and postures associated primarily with all of the preceding. 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.

Walking (Figure 3A).—Although walking velocity varies greatly, the footfall sequence during a walking stride remains consistent: hindfoot, then forefoot of one side, followed by the same order on the opposite side. The durations (based on 8 mm film, 18 fps) of three consecutive walking strides in an animal (O) moving moderately fast were 0.45, 0.45, and 0.54 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 and walked away, four strides measured 0.77, 0.83, 0.66, and 0.72 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).

Trotting.—One brief film sequence of this gait reveals a resemblance to that described for the white-tailed mongoose (Taylor, 1970); the footfall sequence is left hind, right forefoot followed by right hind, left fore; however, the hindfoot-forefoot sequence is not inflexible according to Muybridge (1957). In my 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 in O was 0.23 sec.

Running.—Running and rapid trotting are identical, as both involve diagonal limb extension with two support-free transit phases. Though no film adequate for an analysis of running was made, 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.

Galloping (Figure 3B).—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 sequence, 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.

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 flat or contoured surfaces inclined at greater than 45° with the horizontal.

A walking gait can be efficiently used on any vertical surface that permits 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 antero-posterior 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. The limits of the genet's climbing skill are tested when ascending a smooth and narrow vertical surface, such as the edge of a house door. In this situation the majority of the body weight is sup-

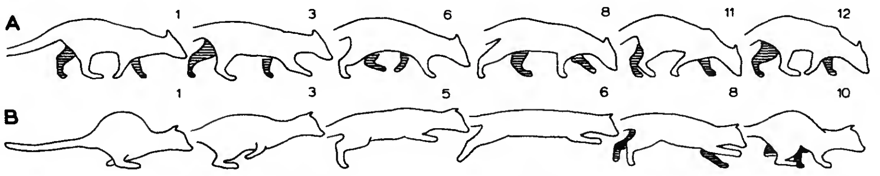

Figure 3.—Two gaits of the genet: a, walking in a year-old animal (animal O; 24 fps—the head is depressed in frames 8–12 as the animal smelled the substrate); b, galloping in the same animal at the age of 10 weeks (64 fps).

ported by the forelimbs; these are adducted with the forefeet opposed and exerting a compressing force. The hind feet 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 progressively higher grasps. Vertical looping under these circumstances 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. Because climbing in an inverted horizontal position requires three feet in contact at all times, only the walking gait can be used.

JUMPING.—This movement consists of 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 expressed by alternating up and down motions of the forebody and adjustment of foot position. The length of the metatarsus touches the ground and the hindlegs are strongly flexed (Figure 4A). The propulsion phase begins with a push by the forelegs that apparently guides the torso into a position where the hindlegs can be straightened with maximum effectiveness (Figure 4B). The vibrissae are extended foreward, and, as the hindlegs propel the body up and forward, the forelimbs swing into an extended position (Figure 4C). During suspension-free transit, the third phase, the hindlegs partially flex beneath the body. On landing the forefeet strike first, but unlike galloping they usually hit simultaneously (Figure 4D). Landing impact forces the forebody down so that the vibrissae often contact the substrate. Contact of the hindlegs is preceded by a strong flexion of the upper forelimb segments, a forward shift of the torso, and a flexing of the spine (Figure 4E). 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 walking motion propel the hindquarters up. In short jumps, none of the limbs may land simultaneously (Taylor, 1970). Occasionally and 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 backwards.

Hall-Craggs (1965) states that *Galago senegalensis* maintains a gaze fixed on the landing target at least until leaving the ground. During the photographing of Figure 4, the electronic flash was once positioned in front of the jump path and discharged several times when the genet was in midair. The animal often over- and undershot its landings, suggesting visual feedback is important during the jump.

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 5B–E).

Based on still photographs and film, Figure 5 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 5B). 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 5E). Though a few short steps may be taken in the extreme postures (Figure 5A,F) slow sustained locomotion does not appear to be possible unless the stances are modified to approximate the next most similar postures.

In addition to the postures associated with gaits that often occur in a social context, a crouched elongated posture is assumed during an irregular walking approach toward novel objects. Once an object is in range, the animal shifts the trunk forward between the limb girdles and leans toward it. During the approach and leaning phases, the

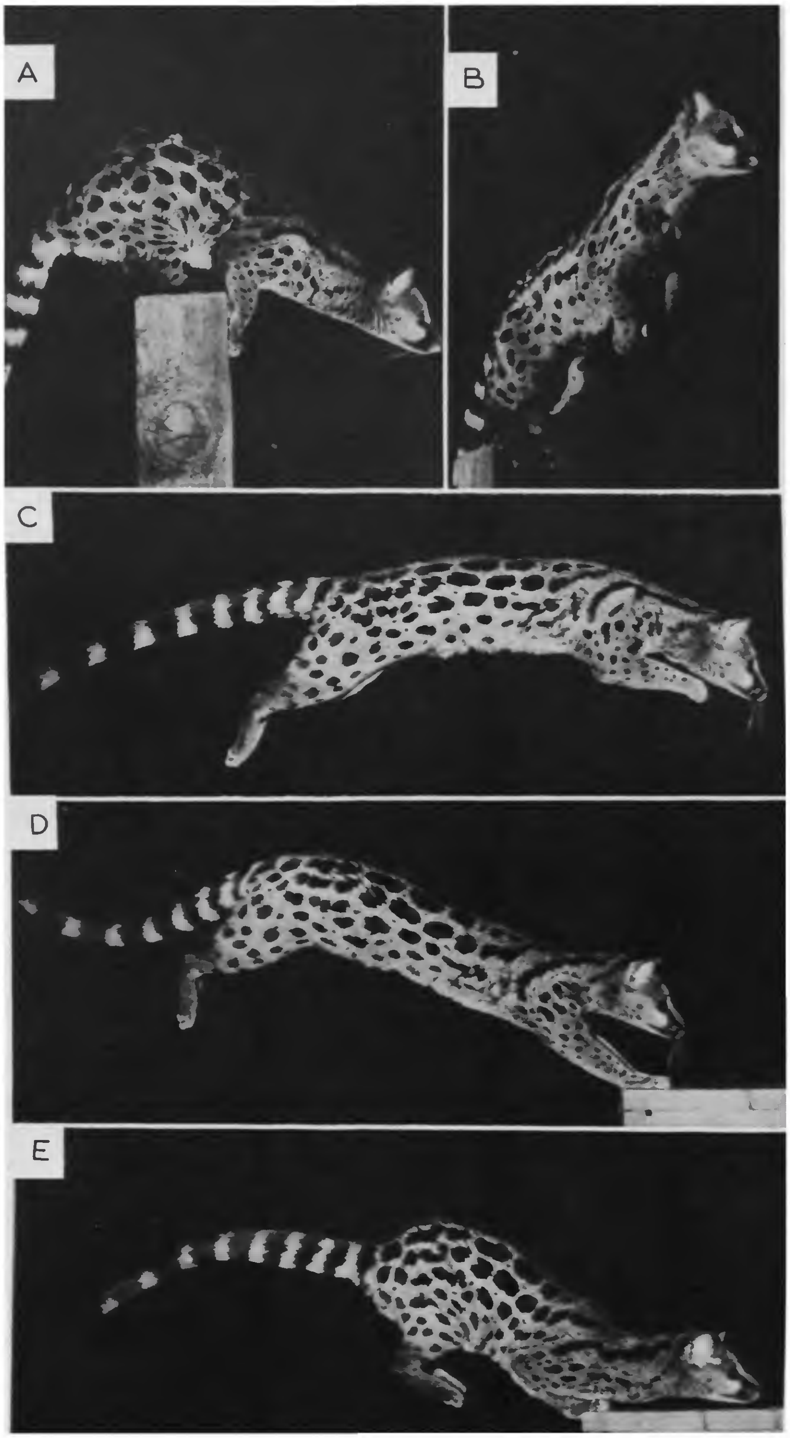

FIGURE 4.—Phases during jumping in the genet: A, quadrupedal stationary phase (take-off position); B, propulsion; C, suspension-free transit; D, landing (simultaneous touchdown of the feet); and E, landing (forward swing of the torso and flexing of the spine).

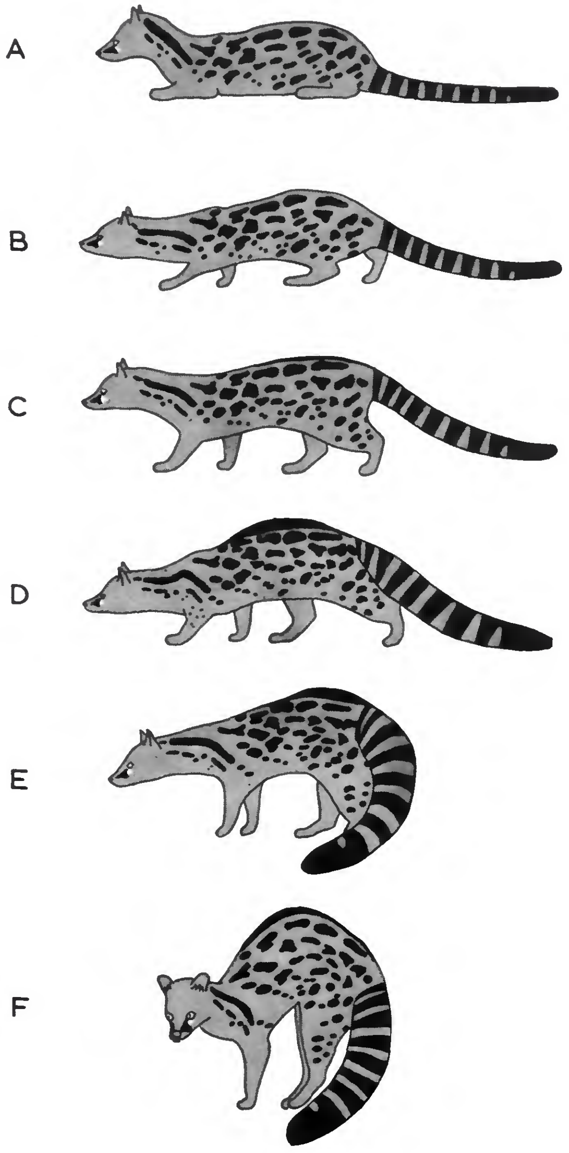

FIGURE 5.—Postural variation associated with stationary body positions and the walking gait in the genet: A, retracted-limb ventral reclining position; B, crouched fore- and hindquarters, minimal spinal curvature; C, normal walking and standing; D, semicrouched forequarters and semiraised hindquarters, moderate spinal curvature; E, semiraised 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 from photos and movie film).

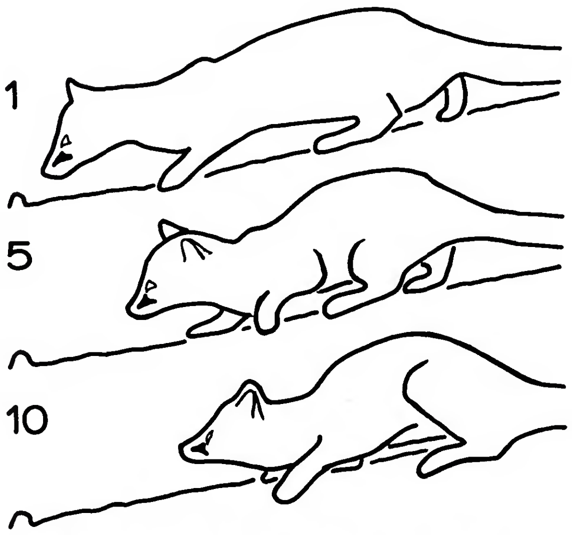

FIGURE 6.—A startle or sudden change in body position in the genet (animal E; 24 fps); within less than a half second E made half a reversed walking stride and became motionless in a crouched quadrupedal stance.

direction of movement often vacillates, but usually no more than several steps are taken in the reversed direction.

Startling produces a sudden change in body position followed by flight or immobility. This is often succeeded by a crouched stance in which the legs are spread and the ventrum may touch the ground (Figure 6).

Shaking and Twitching Movements

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 ganzen 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 approximates 30 or more degrees. Shaking of the torso seems to be facilitated by a simultaneous circular motion of the vertebral axis that is sufficiently forceful to cause the hindlegs to take one or two steps in place. An analysis of slow motion film would greatly help our understanding of these involved movements.

Shaking of the head and body appears to be a response 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 fur 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 observed, for example, after an animal struck a hard object with its open mouth, received a bite on the face, or had mystacial vibrissa pulled out by another animal. Moreover, it is elicited by repeated mild tactile stimulation to the ear (see "Ontogeny of Shaking, Stretching, and Self-Directed Behaviors in *Genetta*" below) and once as a bolus of regurgitated food passed from the esophagus into the mouth.

Limb Twitching.—Both the fore- and hindfeet are twitched and shaken. The movement, often occurring in bi- and tripedal stances or during walking, involves a slight flexion of the limb followed by a rapid snapping extension and retraction (Figure 7). 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.

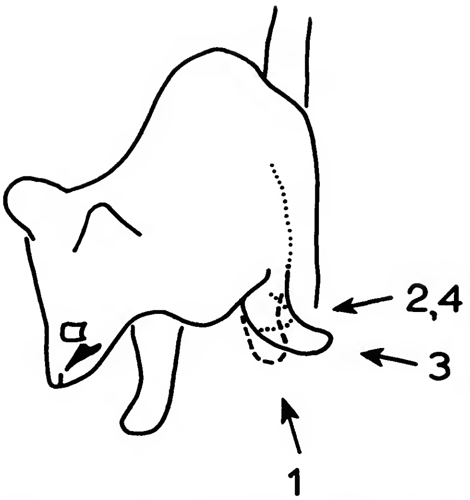

FIGURE 7.—Twitching of the forelimb in the genet (animal E; 24 fps): in frames 1 and 2 the wrist is flexed; in frame 3 it is rapidly extended and in frame 4 it snaps back into a flexed position. The twitching of this leg occurred as it moved a step forward.

Animals are often seen to twitch their hindlimbs when their feet become wet from the puddle created during urination. At other times, when the body is completely wet, each foot is often raised and shaken. Animal K shook and twitched its forefoot repeatedly after being bitten between the toes by a rat it was attempting to catch. In addition, the forefeet and, to a lesser extent, the hindfeet sometimes twitch spontaneously while an animal is asleep or resting. Forelimb twitching has also been seen in a variety of social situations that can be subjectively interpreted as containing elements of surprise, apprehension, or conflict.

STATIONARY BODY POSITIONS

Stationary body positions may occur as relatively short-termed interruptions of locomotion, or more frequently as protracted periods of rest. Although "posture" is the term generally used for motionless body attitudes, it will be used herein to refer to configurations of the spine and limbs, and positions of the soft anatomy and hair at any time irrespective of locomotion. This is consistent with its general meaning of "relative arrangement of the different parts," and "state and condition at a given time."[3] In the following discussion the term "stance" will be used for the basic types of foot position assumed by immobile standing animals. The term "reclining position" is self-explanatory. The descriptions under these categories are not equally complete because 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

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[3] *Webster's Seventh New Collegiate Dictionary*, 1963.

of spinal curvatures is possible during quadrupedal and tripedal stances. The list of reclining positions includes those most commonly seen and does not consider postures that result from spatially confining circumstances.

QUADRUPEDAL STANCES.—The animal stands with the four legs providing body support. In an upright quadrupedal stance the forelegs rest against an elevated surface, the trunk of the body is inclined upwards, and the weight is mainly sustained by the hind feet.

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.

BIPEDAL STANCES (Männchenmachen).—Three variations of bipedal body support have been observed. Support may be provided by the toes and interdigital pads (high-sit: Ewer, 1963), by the entire metatarsus (semibipedal: 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.

SITTING.—This posture is characterized by three zones of contact with the substrate: 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 (Figure 8C). Occasionally one foreleg may be elevated.

VENTRAL RETRACTED-LIMB RECLINING POSITION (aufrechten liegen mit Vorderpfoten nach innen: Leyhausen, 1956).—In addition to the three zones of contact that characterize sitting, 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).

SEMILATERAL, SEMIEXTENDED RECLINING POSITION.—This position differs from the retracted-limb reclining position in that the hindlegs are usually extended and the lateral surface of one leg contacts the ground broadly (Figure 8E).

EXTENDED BODY RECLINING POSITION (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.

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 hind legs and is covered by the tail which is wrapped about the body contour.

ASSUMPTION OF RECLINING POSITIONS.—Unlike ungulates viverrids have low centers of gravity and versatile limb mechanics that impose few restrictions on the method of reclining or standing (Zannier-Tanner, 1965). Retracted-limb 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 rearend and then sits on the side of the hip.

STRETCHING MOVEMENTS

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 three phases: (1) a usually unequal anterior extension of the forelegs, extension of the neck, and a slight concave arching of the back; (2) an extension of the hindlegs, depression of the hindquarters, and an accompanying shift forward 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. Partial versions of this stretching movement omit either the first or the latter two phases. When initiated from a sitting position, the stretch may involve only the first phase but without the spinal concavity, or may continue in a standing position to completion (Figure 9).

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 sometimes unsheathed during this movement.

ARCHED-BACK STRETCH (Figure 8G; Streckbuckel:

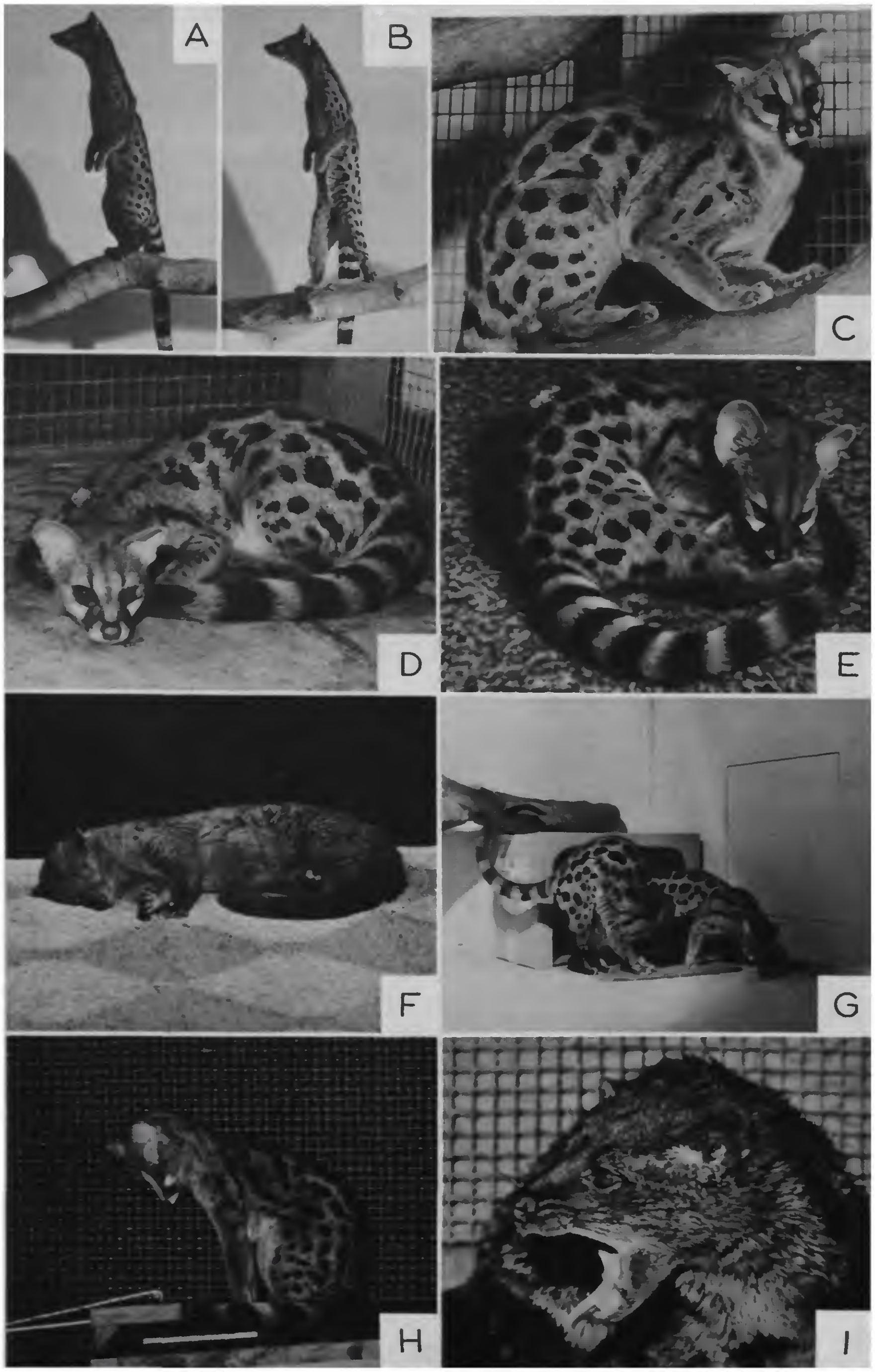

FIGURE 8.—Stationary body positions and stretching movements in the genet and the African palm civet (*Nandinia*): A, bipedal stance with the metatarsus touching the substrate; B, with only the toes touching the substrate; C, sitting position; D, ventral retracted-limb reclining position; E, semilateral semiextended reclining position; F, extended lateral reclining position; G, arched-back stretching; H, sitting stretch; I, yawning.

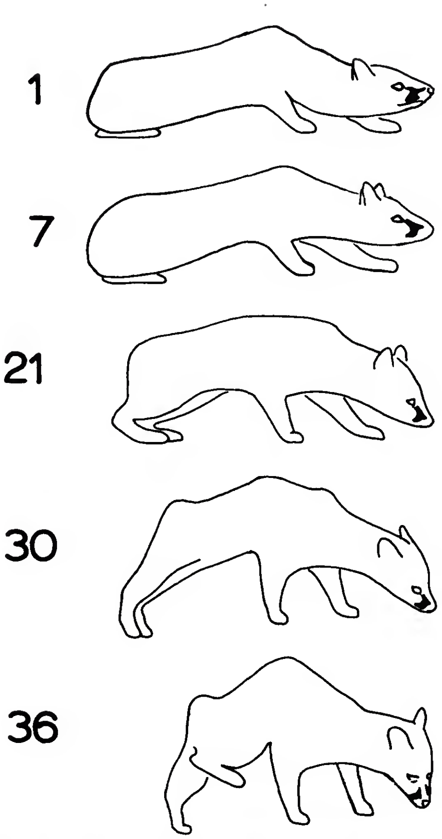

Figure 9.—A walk stretch in the genet initiated from a sitting position on a log (animal C; 18 fps): frames 1–7, stretching of the forequarters (notice unequal extension of the forelimbs); frames 21–30, stretching of the hindquarters (typically the hindlegs are unequally extended); frame 36, a hindleg is moved forward (the tail is obscured by the animal's body).

Leyhausen, 1956).—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" below) is also a modified type of arched-back stretch.

Sitting Stretch (Figure 8h).—The forelimbs are extended and the scapulae elevated while the neck is ventrally flexed and the head pointed down and the chin tucked in.

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.

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).

Object-oriented Contact Patterns

Metatarsus Scuffing (Figure 10).—In a posture similar to sitting (with the metatarsus but not the tailbase contacting the substrate), the hindfeet alternately stroke backwards with the pads scuffing the surface. The claws are not extended, and the feet may or may not be lifted when brought forward

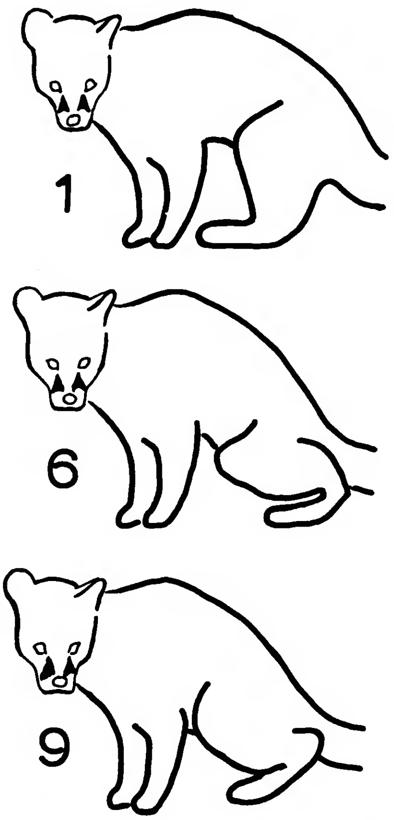

Figure 10.—Metatarsus scuffing in the genet (animal K; 24 fps): frames 1–6, the visible leg is thrust posteriorly and the metatarsus dragged on the substrate; frame 9, the leg returns to its initial position.

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 elevated on 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.

Substrate-clawing (Krallenscharfen: 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 be tensed 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 substrate-clawing 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 sheath, 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.

Arched-Back Rubbing (Figure 11).—Though this behavior resembles in posture the arched-back stretch, it differs in that the animal leans against a vertical or diagonal surface while slowly walking forward. 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, neck, and occasionally the side of the head.

Head and Neck Rubbing (Figure 15b).—The variety of stationary body positions assumed during head and neck rubbing depend upon the location of the object being rubbed. If the animal effects this on a horizontal or diagonal surface, a sitting or flexed-limb reclining position is adopted; 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 strokelike head extension in which the lips on one side of the rostrum maintain contact with the substrate.

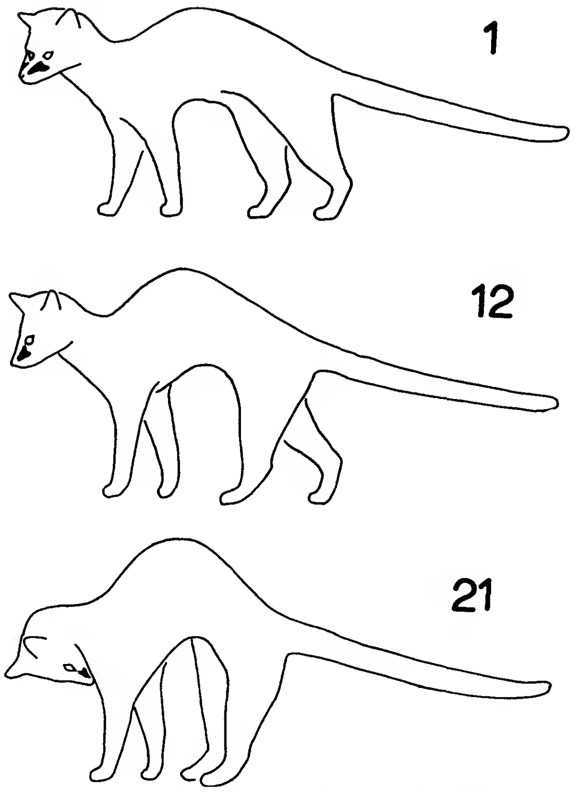

Figure 11.—Arched-back rubbing in the genet (animal K; 18 fps): frames 1–21, changes in the extent and center of spinal curvature; frame 21, the animal is beginning to lick its breast.

Certain aromatic substances are especially effective in eliciting this behavior. Animal O would consistently rub his head and neck against my hair when it was scented with hair oil. On these occasions the animal maintained a supported quadrupedal stance on my shoulders, clasped my head with its forepaws, and alternated the rubbing with Flehmen and licking my hair. (See "Sniffing" under "Companion-oriented Contact Patterns" below.)

Reclining, Rubbing, and Rolling.—Though

genets occasionally lie down and rub and roll with sinuous movements of the spine similar to a dog, the behavior is performed most frequently if the animal's fur is 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.

Perineal-Gland Marking.—All of the postures employed during the apposition of the perineal scent gland to the substrate 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. In marking elevated vertical objects or the undersides of elevated horizontal and diagonal surfaces a reversed upright quadrupedal position is used. 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 "handstand" position; and, with one exception, only females have been seen to mark in a squat position. The presence of elevated scent marks in cages occupied only by females, however, suggests the handstand 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 restrained by hand or held by the tail and, at least in females, eversion accompanied by a lordotic posture can be evoked by rubbing the area between the labia of the relaxed gland.

The gland is a longitudinally folded muscular pad having the appearance of two densely-furred labia situated between the anus and vulva or the scrotum and penile aperture. With muscular contraction of the gland the labia part and the inner surface everts to form a firm, raised, oval-shaped pad covered with a fine layer of white hair (Figure 12). 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 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" (1915c:190). Some species apparently exhibit sexual differences in the number of secretory crypts (Pocock, 1915c).

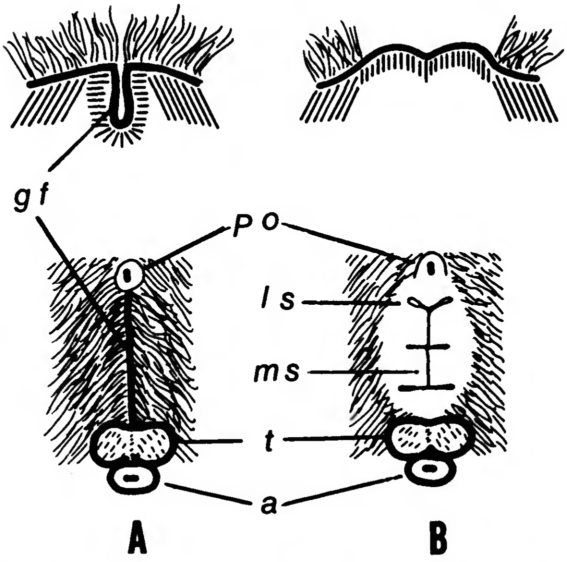

FIGURE 12.—The perineal scent-gland of the genet: A, closed condition; B, everted condition, top row showing profiles of the closed and everted gland (po = penile opening, gf = glandular fold, t = testes, a = anus, ms = median sulcus, ls = lateral sulcus).

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 incidental motion of the folded labia and capillary action distribute the contents of the crypts within the folded pad. With repeated deposition on wood or metal the clear exudate becomes a dark brown coagulum. Kingston (1965) also reported this color change for the perineal secretion of the African civet (*Civettictis civetta*). Repeatedly deposited scent can penetrate wood to a depth of several centimeters (Figure 15c) and retains its redolence for at least four years. The odor is a mildly sweet musk that according to D. Müller-Schwarze (pers. comm.) resembles civetone from which impurities such as skatole have been removed.

On three occasions when females displayed signs of sexual receptivity, both 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 female (C) exhibited an erratic pattern of intense marking (Figure 13). Curiously, 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-marking did not occur in the immediate context of scent-sniffing. This suggests that in this situation the odor of scent perceived at close range is not important in releasing or orienting the marking act. A heightened rate of secretion 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 organs. Estrous females also dribbled urine on scent marks independent of rubbing the perineal gland.

Anal Drag.—The animal assumes a sitting posture with partially spread hindlegs and walks forward with small steps dragging its anus on the ground. Though dragging of the perineum in a similar manner has not been observed, genets seem to be physically capable of modifying the emphasis of the movement so that this is possible.

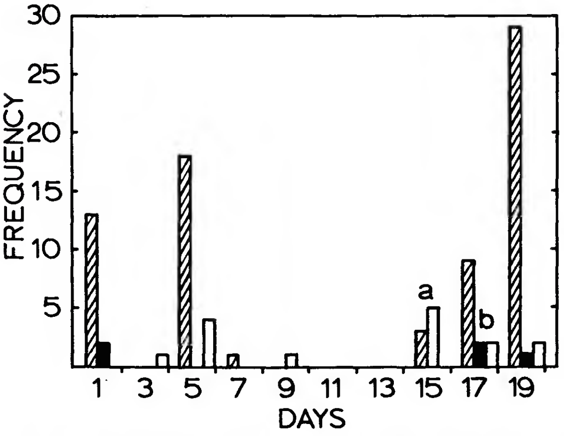

Figure 13.—Frequency of perineal scent marking and scent sniffing in a female genet (animal C) on days before, during, and after sexual receptivity (shaded bar = scent marking; white bar = scent-mark sniffing independent of scent marking; black bar = scent-mark sniffing following scent marking; a = female observed in copulo, presumably indicating day of peak estrus; b = female observed mounting her cagemate).

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 semisupinated forepaw. The object may be drawn 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. For instance, I have seen an animal push a large cardboard box away from a wall. For this the limb 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 semisupinated. For clasping an object the attitude of the hindlegs is the same used for climbing down a narrow vertical log; the pads are completely or semisupinated with the object held between or pressed against the belly.

Nose.—Often the rhinarium lightly touches the surface an animal is smelling, and leaves behind a trace of watery mucous. The ventro-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 a zone that is quite sensitive to tactile stimuli. This area is used to lightly touch objects being smelled, or to playfully push a small object along the floor. On a few occasions an animal was seen forcefully pushing its rhinarium against a novel object; such behavior is far more prevalent in *Civettictis* than in *Genetta.*

Object-oriented Contact Patterns in Other Genera

Perineal-Gland Marking.—The scent-marking 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, partially fused anteriorly, and divergent posteriorly. The gland's pouchlike 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 female's pouch, where they remained for at least several hours before being deposited with a scent mark.

A normal quadrupedal stance is employed by male and female *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 backwards; the tail is elevated and/or deflected laterally, and the gland is pressed against the surface for two seconds or less, usually without accompanying pelvic motion. The female, however, was once seen executing a weak lateral oscillation against a 1 cm mesh wire, and sometimes dipping the rear end slightly as she ended glandular contact. The gland usually closes as soon as contact terminates. Though *Civettictis* have not been seen marking low-lying objects in a squatting stance, scent marks on a cement floor (Figure 15H) may have been deposited in this way. They may also have been made passively as the animal was sitting.

Nandinia and *Paradoxurus* have been observed dragging and wiping (without locomotion) their scent glands on inclined and horizontal logs. While these methods of marking differ from one another in duration, both show only minor differences in posture from dragging and wiping the anus. Unlike *Genetta* and *Civettictis*, the glands in these genera are thin walled, hairless, and devoid of secretory accumulation. *Nandinia*'s pregenitally situated gland can be freely opened into a flat, elongate oval area even 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 male became excited a sweet odor was detected, but it is unknown whether or not 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.

The male and female *Hemigalus* and the three female *Galidia* were observed occasionally wiping the hindquarters both spontaneously and after urination, but whether these movements resulted in the deposition of specialized dermal gland exudates is unclear. Gregory and Hellman (1939) briefly mention the existence of small perineal glands within the Hemigalinae, but more precise information on their occurrence and structure apparently remains to be discovered. Likewise, little is known concerning the perineal glands of the Galidiinae.

NECK-SLIDING (Figure 14).—*Civettictis, Nandinia,* and *Paguma* exhibit this behavior with only minor differences. It is always preceded by sniffing 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 target until the shoulder approaches or touches it. Foreleg support of the body is sometimes relinquished and the animal slides onto the shoulder. The neck and forebody is then raised, the head repositioned over the target (which may again be sniffed briefly), and the motion is repeated though frequently on the opposite side of the neck.

The main differences between the neck-sliding 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 rump of *Civettictis* is held almost as high as in normal standing. In consequence of its higher center of gravity, *Civettictis* sometimes tends to lose its balance once it slides onto its shoulder. Rather than falling over, however, the animal usually quickly regains a quadrupedal stance. Sliding onto the shoulder is infrequent 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 anteriorly 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 the posterior cheek region and the sides of neck are primarily marked in *Nandinia* and *Paguma.*

Neck-sliding seems to be both released by and oriented to certain odors, but the source need not be tactily or visually discernible. The high degree

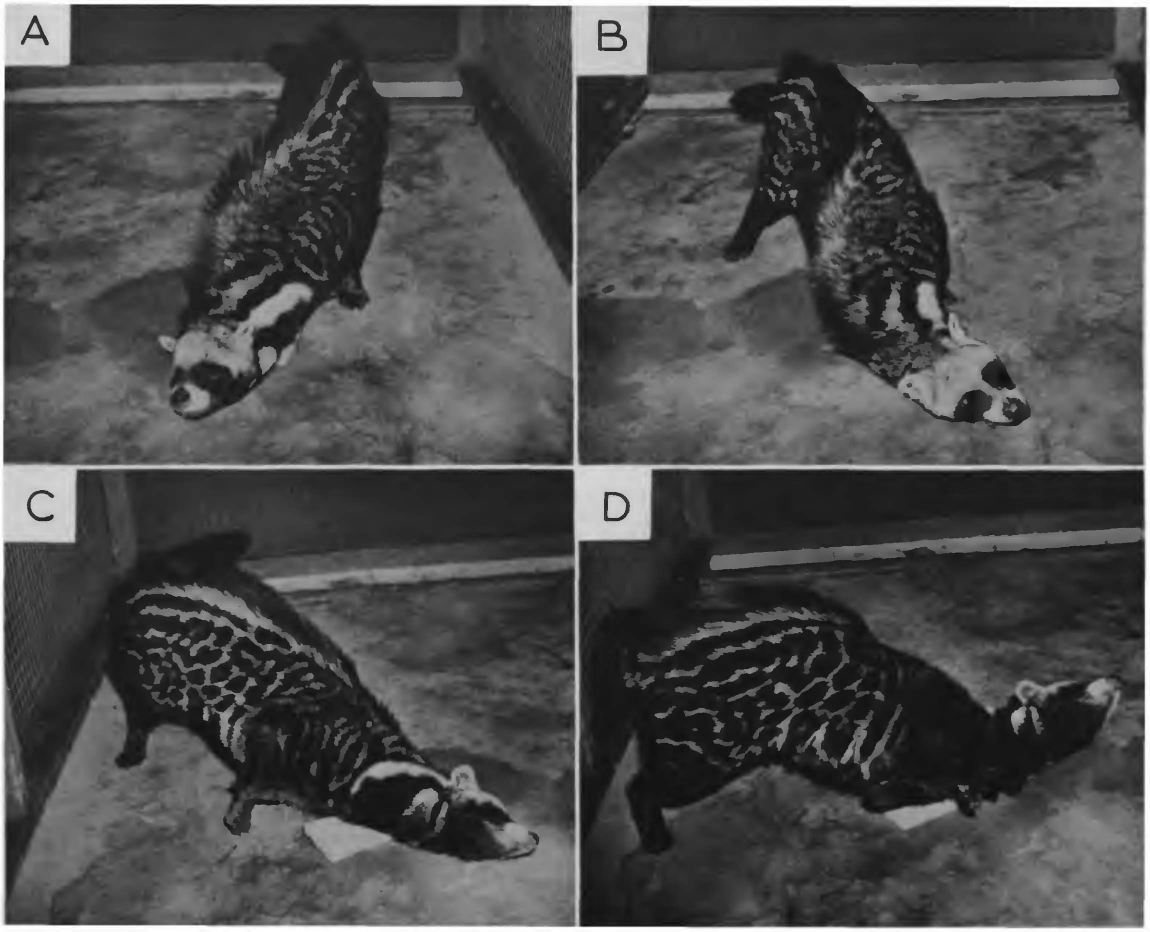

FIGURE 14.—Neck-sliding in the African civet (*Civettictis*): A, B, frontal views of alternate sides of neck-sliding over a sponge soaked in a lemon-scented detergent; C, sliding onto one shoulder (3 feet and the neck-shoulder are supporting the body); D, sliding without foreleg support.

of target specificity results from the initial sniffing orientation, and also, but not necessarily, from contact with the object. Both *Nandinia* and *Paguma* executed neck-sliding upon dead rats and mice and in their own and other animals' (civet, genet) urine and feces. Dücker's (1971) male and female *Nandinia* would slide the chin, neck, and sides of the head, as well as the breast for up to 15 minutes on a board that had been used for cutting liver. This behavior was also elicited by solutions of heliotrope (Baldriantinktur) and cologne.

On several occasions after the male *Paguma* killed large (400 g) rats it directed its neck-sliding to the prey's lower abdomen and genitalia which forced a flow of urine from the carcass. In these instances the animal's activity was clearly released by and oriented to the smell of the anogenital region; the crushed heads of the prey were left alone, though they certainly provided a distinct alternative scent. Dead smelt, mice and rats, live mouse pups, genet urine, and a lemon-scented dish detergent were all highly effective elicitors of this behavior in *Civettictis;* occasionally a piece of horsemeat worked. All species sometimes lick the neck-sliding target, and if the target is food it is usually ingested afterwards.

The effect of the neck motion on the scent source varies. Soft substances 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 especially if their axis is parallel 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. After an animal neck-slides on animal carcasses, they are usually eaten.

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) on vertical surfaces. The sides of objects, such as vertical tree trunks, are grasped with the forefeet while the hind feet rest on the floor on either side of the trunk, alternately extending and flexing to produce an up and down rubbing motion. The inguinal region received the majority of the rubbing in the male animal observed, while Vosseler (1929) saw two males and a female 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 removable fatty secretion on the male'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.

In the male *Cryptoprocta* I observed, ventrum-rubbing 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 on alternate sides of the head were rubbed back and forth. At times head-rubbing was interspersed with chewing on the trunk and branches. Under some circumstances, as when a new branch was placed in the cage, chewing became intense (J. F. Eisenberg, pers. comm.). Also, urine was 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 the position used during ventrum rubbing in that the hindfeet were placed several decimeters away from the trunk, and the back was bowed.

SIDE-RUBBING.—The female *Nandinia* was often seen rubbing one side of its back up and down by leaning against a screen wall in the cage and extending and flexing the legs, particularly the hindlegs. Besides massaging the skin, the movement also removed loose hair that accumulated at each rubbing site.

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 deposits that result from object-oriented patterns.

The residue of the perineal gland (presumably civetone) is subjectively the most potent source of chemical information, for its redolence persists and it 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 affected by cage structure and the scarcity 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 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 15D), or were limited to a height of 4.5 cm on the baseboards 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. The

TABLE 4.—Distribution of scent marks within genet and civet cages at the National Zoological Park (measurements in cm)

Scent-mark object	Cage occupants	Number of scent-marks per cage	Vertical distance from substrate				Length of scent-marks	
			Smallest		Greatest			
			Mean	Range	Mean	Range	Mean	Range
Genetta								
Vertical and diagonal surfaces	I, F	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	17.5	(8.0-24.5)	29.6	(19.0-44.0)	11.3	(3.5-22.5)
Undersides of logs	I, F	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	(19.0-55.5)	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)

longest marks occurred on horizontal baseboards ($\bar{x}$ = 23.8 cm), medium length marks on undersides of diagonal logs ($\bar{x}$ = 14.3 cm) and on 45° plywood edges ($\bar{x}$ = 11.8 cm), and the shortest marks were on vertical posts ($\bar{x}$ = 9.9 cm). By using the quadrupedal squat position an animal could potentially mark the upper surfaces of all the elevated branches in the cage. This, however, is not done because 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. Likewise, 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 typical standing position of the civet; and (3) *Genetta* can assume a bipedal stance and thereby more than double its detection height 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 scent of genets and African civets carries similar territorial messages, the overlapping heights of scent marks 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 genera 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 female *Arctogalidia* excepted), the vagina and penis lie directly beneath the floor of the perineal fold, and as marking undoubtedly compresses these structures, the stimulus 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 a response more to fluid accumulation within the fold and perhaps to 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. Because rubbing removes loose hair and massages the skin and also often produces an apparent complacency, both grooming and comfort functions may be assumed. 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 and Ellis, 1959), and (2) the observation that the circumstances associated with the three rubbing movements differ. Sniffing is associated with the performance of all the patterns listed in Table 5, but experimental evidence is required to ascertain whether it has a causative or directive function or is merely incidental. Probably relevant to the role of sniffing is the action of the scent-marking movement and the chemical natures of body and object borne substances. An exchange of odorous substances

TABLE 5.—Some characteristics of scent deposits resulting from object-oriented contact behaviors and from elimination in *Genetta tigrina* (first column: + = detectable by human nose, − = undetectable; volatile longevity ranked in increasing order of probable magnitude)

Behavior	Olfactory trace	Visible deposit	Volatile longevity	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	Arched-back rubbing
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

undoubtedly occurs during any contact between body and object. The action may be reciprocal or may have a primarily anointing or marking effect depending upon the chemical character of the substances involved and the olfactory sensitivity of the message recipient.

Head and neck rubbing, for example, accompanies three distinct activities. It occurs between bouts of self-directed licking, as a response to water on the fur, and to 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 its stance is modified to facilitate contact with the area. Thus, in the first two situations there is probably reciprocal exchange while in the last situation an anointing function accrues to the rubbing.

Also, arched-back rubbing and metatarsus scuffing sometimes resemble head and neck rubbing because a reciprocal exchange of odorous substances occurs and a diffuse and faintly scented field remains. The causation of these two 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 that chemical evanescence conveys recency of physical presence and hence proximity of the marker. 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, of course, that optimal rubbing targets may be in sufficiently short supply that the use of them may be communal. The collective contribution would magnify the strength of the odor and visitation to rubbing loci would become traditional, thus alleviating total dependence upon olfactory localization.

SELF-ORIENTED CONTACT PATTERNS

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 bobs down and up with the respective extrusion and retraction phases of the tongue. In nose licking (Nasenlecken: Leyhausen, 1956), the tongue slides out, up, and over the rhinarium and is retracted over the same path. In licking the rostrum (lips or "chops"; Lippenlecken: Leyhausen, 1956), the tongue extrudes 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 15F). 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 (Durchkämmern: 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 that 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 either 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 toenails, but may also dislodge particles from between the teeth.

HEAD AND NECK.—Rubbing movements of the head and neck are directed to the forefeet and the

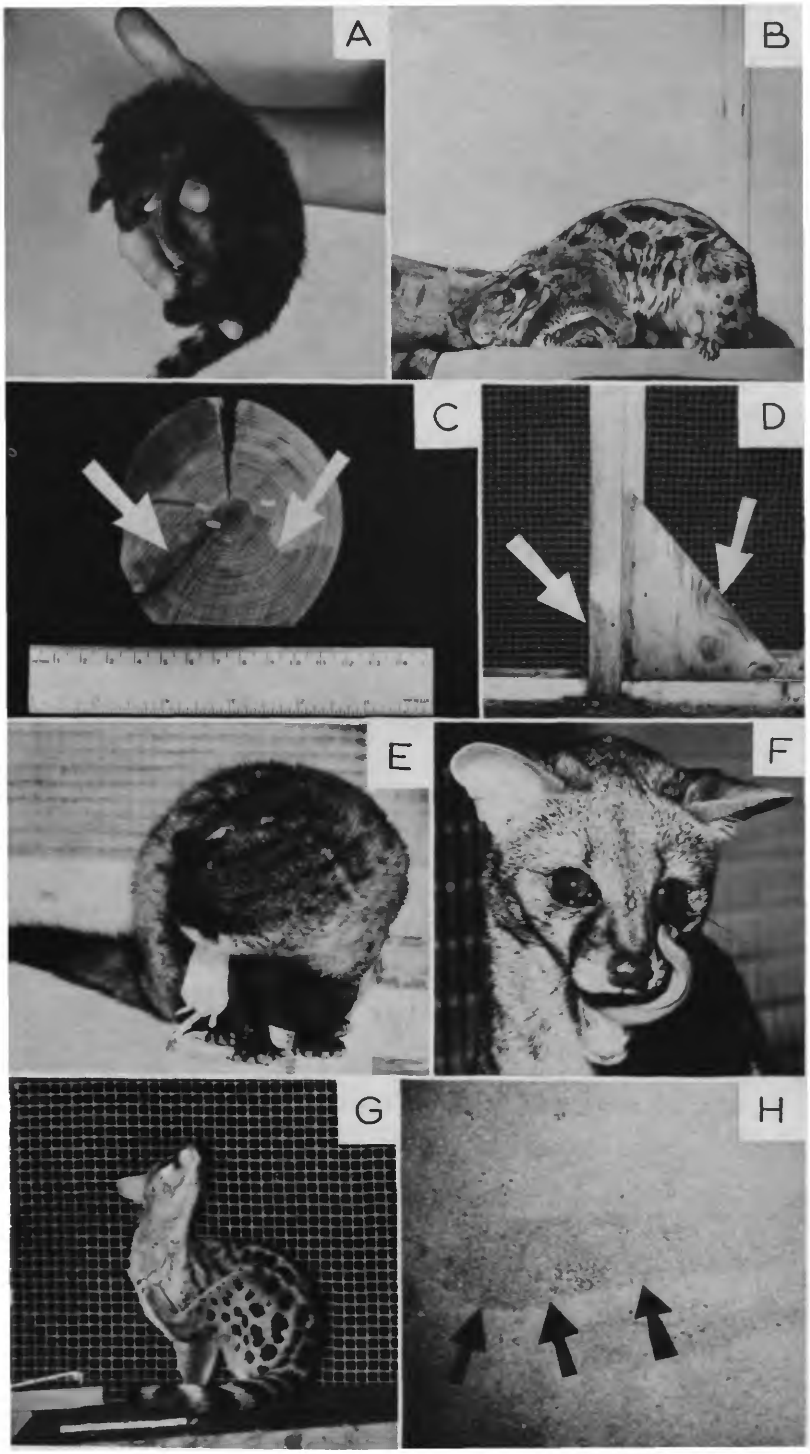
A
B
C
D
E
F
G
H

Figure 15.—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 (one week old); B, head and neck rubbing in a genet; C, penetration of the genet's perineal gland scent-mark 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 female *Paradoxurus hermaphroditus*; F, lip-licking in a genet; G, neck scratching in a genet (note how posture facilitates contact); H, a perineal gland scent-mark made by the male *Civettictis* (arrows point to 1 of 2 streaks made by the glandular lips).

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tail in the same manner described for inanimate objects. Such activity may be interspersed with other self-directed licking and nibbling movements and often follows bouts of tail-licking.

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 such behaviors.

Hindlimbs.—Though the hindlegs can clasp the tail and can be pressed against the belly if the animal is suspended by the tail (see "Locomotion and Its Ontogeny"), most self-directed movement of the hindlegs involves 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 positions (Figure 15c). All body areas can be scratched with the exception of the forepaws, anterior parts of the forelegs, rump, lower back, belly, hindlegs, and tail.

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 may hold the tail in place by standing on it. 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 16), and, compared with other self-directed patterns, usually follows a relatively fixed sequence. The movement consists of synchronous elliptical motions of the forepaws that 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 the next ascending stroke (Figure 17). During the descending stroke and possibly during ascent, the head is contacted by the medial surfaces of the manus, wrist,

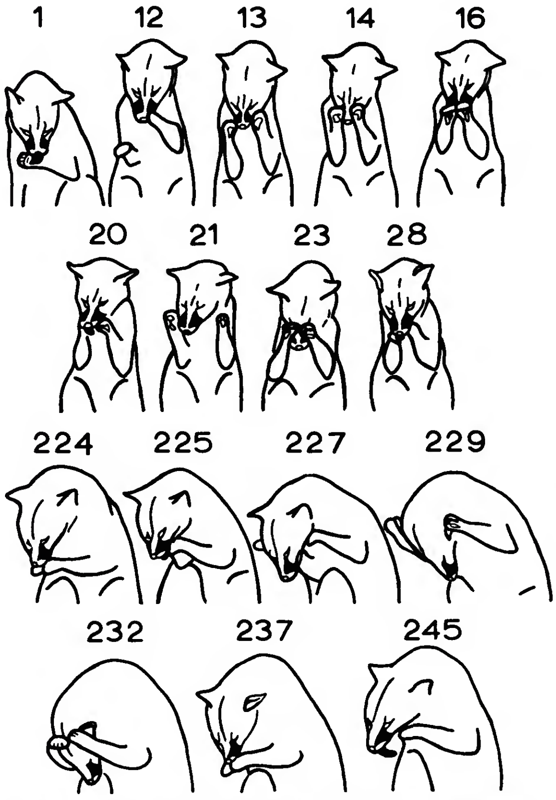

Figure 16.—Bilateral head-wiping in the genet (animal C; 18 fps): frame 1, licking of a forepaw; frame 12, initiation of the bout; frames 13–28, wiping of the rostrum and eyes; frames 224–245, wiping of the ears and crown (note the pronated forepaws and the role of head and neck movement during wiping).

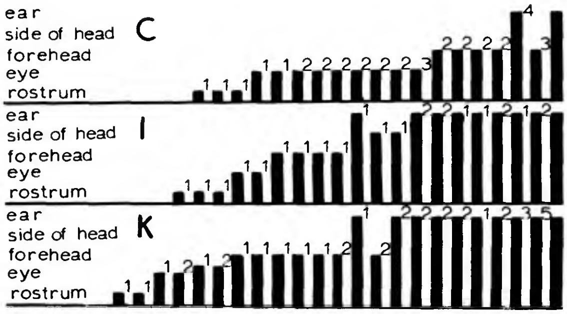

Figure 17.—Sequence of wiping targets and forepaw licking during bilateral face-wiping in three genets (animals C, I, and K; each bar represents one cycle of forelimb motion; bar height corresponds to highest body part wiped; number of licks directed to forepaws between wipes indicated between bars; data determined from 8 mm film).

and forearm. Dücker (1957) 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 30° out of phase during a downstroke.

Self-oriented Contact Patterns in Other Genera

Flank-wiping[4] (Figure 15e).—This behavior was frequently seen in the female *Paradoxurus* shortly after she began to masticate dead mice and small 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 during the early phases of feeding on each carcass. The behavior was usually no longer exhibited after about three mice had been swallowed. By this time there was often a small moist patch of fur on each 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*, did not prompt flank-wiping when placed on a paper towel.

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

Preliminary Remarks.—Shortly after birth head-shaking and gaping movements that resembled yawning could be evoked by 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 in quadrupedal body positions. The walk-stretch, first seen at 37 days of age, can probably be performed even earlier.

By two or three days the jaws can execute sustained bites with considerable pressure, and repeated biting movements resembling nibbling are directed at fingers, blankets, and other soft materials. Incipient nibbling of the body, first seen on days four and eight (O and K respectively), 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 four to eight days, and as early as the eighth day self-directed licking was seen (O and K).

Animals were first seen scratching themselves in a sitting position at the ages of 9 and 13 days (O and Mo). Dücker (1957) 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 re-

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[4] I am indebted to Gene Maliniak for bringing this behavior to my attention.

> acted 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 the animals I reared could be induced with repetitive stimulation to scratch either their head or neck by the age of four 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 stimulated area. 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 (in I, K, E, and O respectively). The capacity to wipe the side of the face with one forepaw, however, is usually manifested by the fourth day provided there is a sufficient outside stimulus. Dücker's (1957) animals were first seen employing 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 pelage. Subjectively, it appears that tactile stimuli induce 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.

Materials and Methods.—Animals I and C were tested a total of 39 and 35 days during a 50-day period beginning at the age of five days. All tests were carried out 10 to 60 minutes following the evening feeding as the animals slept in their nest box. An effort was made to be consistent in the method of "tickling" the ear during the course of testing; however, the possibility of human error obviously cannot be dismissed. Bouts lasted no longer than 10 seconds and were usually terminated sooner when the animal began to respond. An interval of two minutes separated each bout, and each test comprised from 32 to 41 successive bouts, with the following exceptions. Animal C was stimulated 11, 20, 26, 24, and 6 times respectively on age 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 two 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 became quiescent within five minutes; if an animal remained active longer, testing was resumed a half hour later. As young animals usually sleep after being fed, it was hoped that the stimulative effect of hunger could be controlled by testing shortly after feeding. Toward the end of the experiment, however, the study animals frequently played together for up to 40 minutes before going to sleep. Thus, differing hunger states may have affected the level of irritability between the beginning and end of the experimental period.

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.

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 8.0%, and other motions of the head accounted for 15.8%. Thus, of all responses, movements of the head and ear predominated (90.2%). Head-shaking and ear-twitching did not occur with equal frequency throughout the course of testing (Figure 18G,H). Head-shaking, often varying over a wide frequency range on different days, became a less numerous response by the end of the fourth week. The decline was not as 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 between day 15 and 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 18A shows that the level of the mean number of responses per bout, though oscillating, remained constant throughout the 50-day period. Frequency of occurrence for all behaviors varied widely on different days, probably as a function of a number of uncontrolled internal and external variables. Response diversity also varied between days (Figure 18B). The high values of the first four days are probably exaggerated because of the small numbers of stimulation bouts, but the elevated figures of the succeeding four days suggest that responses to localized tactile stimulation may well be more varied during early infancy than at later stages.

None of the remaining evoked behaviors contributed more than 1% to the total number of responses. They can be classified into those that 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 four 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 18F). Scratching of the neck (Figure 18E) 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 18D), the side of the head was occasionally scratched throughout the course of testing (Figure 18C).

Ear-twitching and head-shaking commonly occurred as part of larger sequences (Figure 19). Table 6 shows that ear-twitching was more frequent overall than head-shaking, more often a single act, and more common as a serial precedent. In Figure 19 the following points are apparent. First, of those series that began with ear-twitching (A) over half (58.8%) of animal C's and over a quarter (28.5%) of I's responses contained head-shaking (B) as the second serial element. Secondly, seven dyads alone accounted for the majority (87.2% in I; 80.5% in C) of all serial combinations that began with ear-

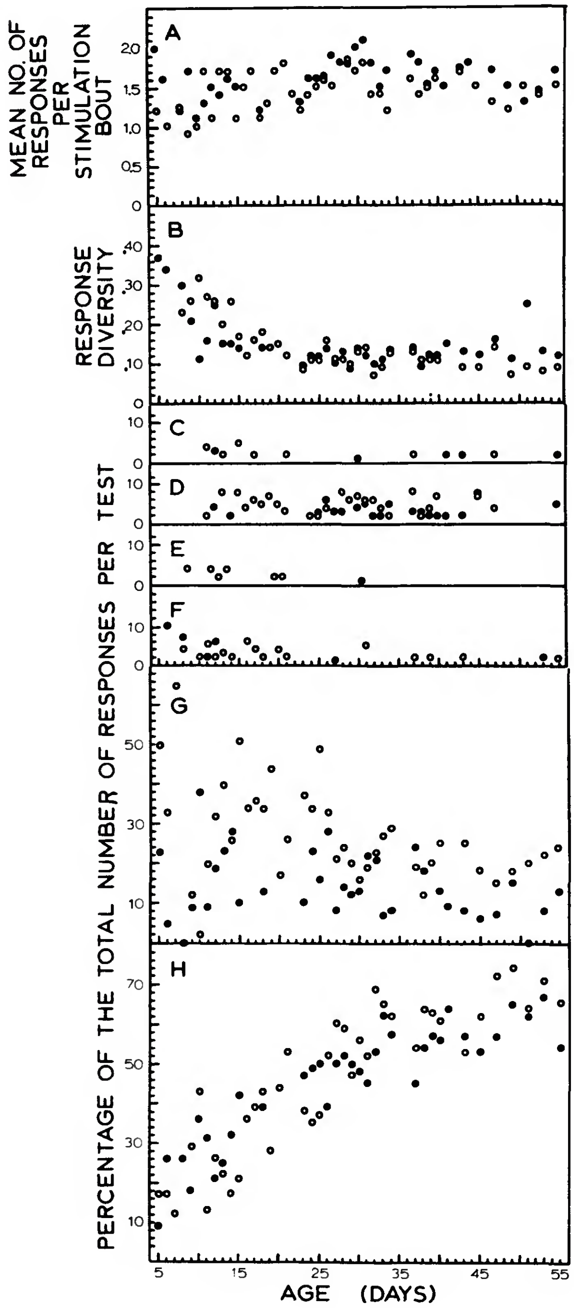

FIGURE 18.—Responses to localized tactile stimulation in two infant genets (I and C) over a 50-day period (ages 5–55 days; hollow circles = I, solid circles = C): A, mean number of responses per stimulation bout (total number of responses divided by the number of stimulation bouts completed on that day); B, response diversity (number of response types divided by the total number of responses per test; because the first two values for I are .82, they are omitted to conserve space); C–H, percentage of the total number of responses per test for the following: C, scratch side of head; D, scratch ear; E, scratch neck; F, extend hindleg; G, shake head; and H, twitch ear.

TABLE 6.—Numbers and frequency (percentage in parentheses) of two responses following bouts of localized tactile stimulation in genets I and C between 5 and 55 days of age

Circumstance	Animal I Ear twitch	Animal I Head shake	Animal C Ear twitch	Animal C Head shake
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

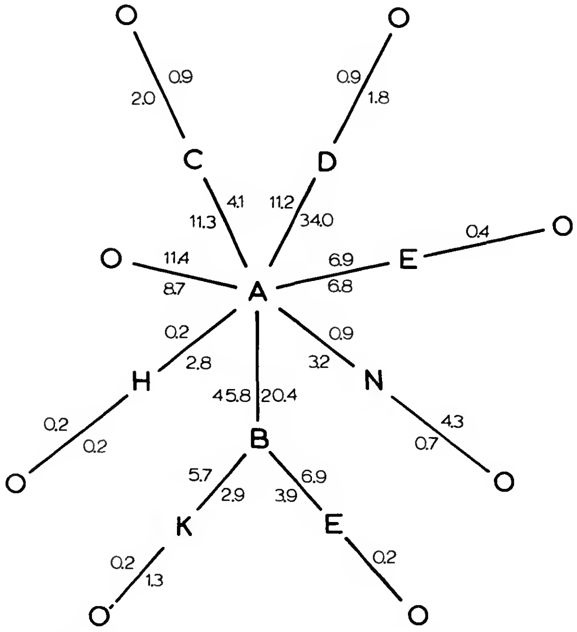

FIGURE 19.—Percentage occurrence in genets I and C of all behavioral dyads, triads, and tetrads that began with ear-twitching as responses to localized tactile stimulation of the ear (values for I lie below the lines and to the right of the line between A and B; the total of all the figures for each animal equals 100%; values between A and the inner ring of letters represent the percentage occurrences of dyads, between the inner and the second ring of letters, triads, and beyond the second 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, N = extend hindleg, O = all other behaviors).

twitching (A). Thirdly, though moving the head (D) was the most common succedent to ear-twitching in animal I, on only a few occasions did this pair of patterns give rise to triads. In both animals, on the other hand, the sequence of ear-twitching and head-shaking (AB) predominantly gave rise to triads terminating with a change of head position (E) and ear-scratching (K). Data not included in Figure 19 shows that when head-shaking was a dyadic antecedent for animal I (N = 52), the most common second elements were also change of head position, 26.9%, and ear-scratching, 21.1%. Extending the 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. First, 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 easier to execute than less common self-directed patterns such as scratching. Second, 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, ear-scratch, or change of head position). Third, 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 headshake). 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 (1957) young animals and in all of those I hand reared. It more likely results, however, from conditions of the afferent or efferent nervous pathways rather than from mechanical restrictions of body form.

ELIMINATION

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 urine is expelled, the force and volume seems to vary rhythmically, suggesting that flow is controlled by a muscular contraction rhythm in the urethra. In estrous females, on the other hand, small amounts of urine are often dribbled upon objects. In both sexes 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 litter box and other low 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 F 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.

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 this presumably coincident with closing the anal sphincter. In infants, both urination and defecation can occur spontaneously or can be evoked in reclining body postures.

ELIMINATION IN OTHER GENERA.—A squatting quadrupedal stance is assumed (with minor variation) during elimination by *Civettictis, Nandinia, Paguma, Paradoxurus, Hemigalus,* and *Fossa*. *Nandinia* was frequently seen urinating 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 (1964:198) 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 ground . . . as well as in collections on open ground areas." Because "the toddycat keeps going while relieving itself . . . ," the scats have a characteristic "strung-out" (rather than heaped) appearance (1964:198). 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 male frequently urinated and defecated in his water bowl. In South Cameroun and Senegal, *Civettictis* often defecates 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 male *Paguma* and male *Civettictis* was sometimes closely associated with hindleg movements. The *Paguma,* for example, would dribble a small amount of urine on the floor or its nestbox and then scuff its metatarsus in it. On three occasions during social interaction between the male and female *Civettictis* the male was seen urinating while walking and scratch-kicking. The urine was spurted to the rear at about 30°–40° to the horizontal as each hindfoot was alternately scratched backward with a kicking motion. The movement resembles the ground-scratching of dogs except that in the civet it occurs during urination as the animal walks, and the kicking stroke is shorter and briefer.

COMMUNICATIVE FUNCTIONS OF ELIMINATION IN *Genetta*

Table 5 shows that compared with the various types of scent deposits resulting from object-oriented contact patterns, urine and feces have a strong and enduring scent value. It is obvious that as odorous chemical mixtures both substances have an intrinsic value as media for information about individual identity, and sexual status and condition (Hediger, 1944). Defecation in the genet is locus specific and probably communal. Presumably it allows solitary animals in the wild to detect the existence (through 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 often 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 probably fades rapidly.

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*[5] 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 contributes significantly to the olfactory quality of urine. This notable feature does suggest, however, that whatever the odorous components in the urine, they may likewise be distinct and species typical.

Some Intergeneric Comparisons and Derivational Schemes

There can be little doubt that body form is a dominant variable limiting behavioral expression. Intertaxa 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 that fall into this category are sniffing, licking, and nibbling movements, scratching with the hindfoot, head and body shaking, generalized pilo-erection, squatting eliminative stance, tripedal stance, and the walking gait. Licking movements (nose, lips, and body), 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 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* hindlegs 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 headfirst 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, comparing the distribution of several behavior patterns between members of four subfamilies. I have included the first two behavioral items in Table 7 (bipedal stance and headfirst vertical descent) to give an indirect comparative measure of arboreal specialization. The assumption is that civets, unable to descend trunks headfirst 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, based in part on Table 7, similarities and differences should be viewed both in terms of locomotory adaptation and systematic status.

Both the long- and walk-stretch are probably the most common and frequently performed stretching patterns in carnivores as well as many other mammals. In their complete form, both of these patterns consist of two 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 not uniformly extended as the forequarters are

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

Table 7.—Comparisons of behavior among selected viverrid genera (+ = present, − = absent, +? or −? = probably present or absent but substantiation needed, blank = uncertain, a = personal observation, b = Vosseler 1929, c = Dücker 1957, d = Huf 1965, e = Dücker 1971, f = Albignac 1970a, g = Albignac 1970b)

Behavior	Viverrinae				Paradoxurinae				Hemigalinae	Cryptoproctinae
	Genetta	Prionodon	Civettictis	Viverricula	Arctictis	Nandinia	Paradoxurus	Paguma	Fossa	Cryptoprocta
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

depressed and the hindlegs 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 variation in forelimb positions are manifested without the hindquarter stretch (stiff-legged walk). The same holds true 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 the 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 that combined in time to produce the walk- and long-stretch. Alternatively it is possible that the widespread walk-stretch pattern was the prototype that, 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 semiprotracted 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 female make strained but synchronous forepaw contact to the nose as she reclined in a lateral extended position. The ability to touch the head simultaneously with both 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 Bürger'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 genera I have observed[6] exhibited these 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 predict accurately which species possess bilateral face wiping within their repertoires, and consequently it has little utility as a taxonomic character.

Judging 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 body form sufficiently generalized that the limbs have considerable freedom of movement in several planes. This grooming ability is displayed by nonbrachiating arboreal and semiarboreal species, and those terrestrial species having plantigrade feet. The existence of the pattern in carnivores is highly unusual and suggestive of a more widespread occurrence among the extinct viverrines that presumably gave rise to modern forms. This is confirmed by the occurrence of unilateral face-wiping in many felids (Leyhausen, 1956) 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.

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[6] 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.*

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, but because the movement lacks an association with paw licking and is directed to the entire body, it probably derives from a behavior pattern other than the one in question.

In the felids and viverrids where 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 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 directed to alternate sides of the head and neck. Though it is tempting to interpret neck and shoulder sliding as a simplified and exaggerated version of *Genetta*'s rubbing movement, two observations suggest a more logical alternative: (1) when thoroughly wet, domestic dogs, mustelids (*M. frenata, M. erminea:* pers. observation), and viverrids (*Genetta, Nandinia, Fossa*) 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 substrate contact coincides largely with the extension rather than retraction phase of the neck motion, occur in several species either as a response to a strong odor field (canids, *Eira barbara,* the three viverrids listed above), and/or in species that have a dermal scent-producing gland in 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, female domestic cats slowly glide the neck to the shoulder on the substrate while standing (Leyhausen, 1960). This behavior is apparently spontaneous.

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 (1957) neck rubbing (Kinn- und Halsscheuern) in *Viverricula* is followed by vigorous bouts of body rolling and rubbing. The factors that 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 this activity.

Considering other patterns of object-oriented contact, Table 7 attests to the intra- and interspecific variation in the methods by which the selected viverrids appress the pregenital 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 so the emphasis of contact. The physical similarity of these three 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 respectively the probable primitive cleaning movement and the scent deposition movement assumed to be its derivative.)

The hypothesized significance of autonomic elimination for the evolution of many types of anogenital 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 resulting in anogenital contamination and consequently followed by anal dragging and self-directed licking and nibbling. Contained within the autonomic elimination reflex and the circumstances of its occurrence are behavioral "building blocks" or preadaptations for specialized forms of scent-marking. The building blocks include two distinct modes of scent deposition (urine and feces), and a potential social referent and/or message receiver (the animal evoking the autonomic response). To elucidate, both autonomic defecation and evacuation of the anal gland share common features of agonistic contexts and protrusion and 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 that potentiated the development of glandular fields in the anal, perineal, and pregenital regions.

The remaining three viverrid marking patterns (Table 7; Figure 20) 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 two upright quadrupedal patterns (reversed and normal) to the perineal drag can be appreciated by visualizing the necessary adjustments in posture that would accompany rotation of the marking log seen in Figure 20 to a horizontal plane. 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 position, for example, characterize two situations that could conceivably have served as transitional activities as defined by 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 (Figure 20). The loss of this hypothetical stepping-down component, which would convert the pattern to its definitive form, could

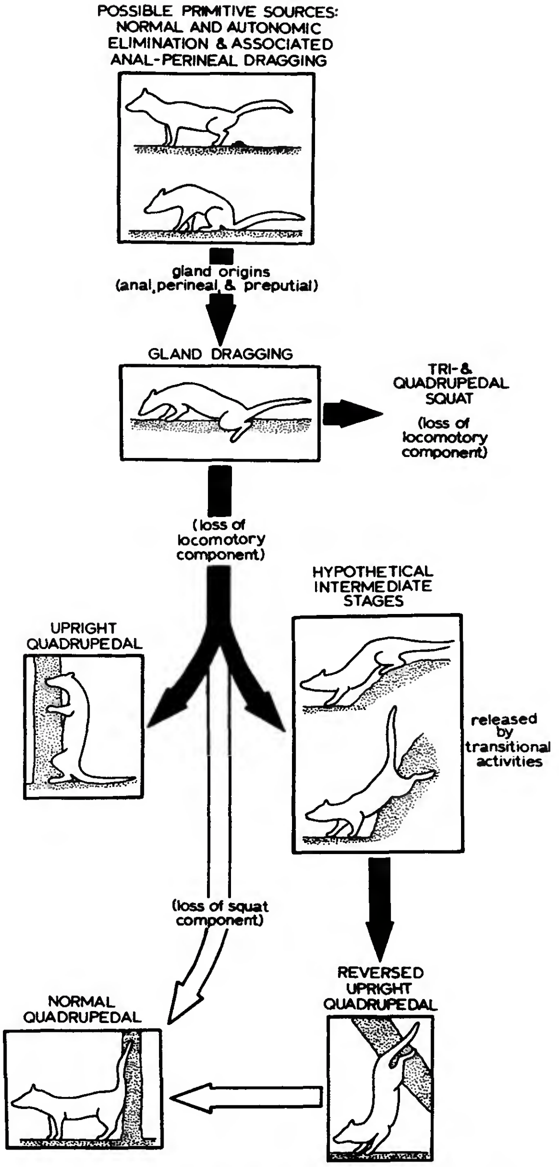


FIGURE 20.—A derivational scheme of some stances employed by viverrid carnivores during scent-marking (arrows point to specific stances exhibited by extant species and a hypothetical intermediate stage; black arrow = logical evolutionary pathways of stances in which glandular contact with the substrate is mediated by variations on the squatting theme; white arrow = two possible (but rather tentative) routes for the development of the normal quadrupedal marking stance from a squatting stance).

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 (e.g., *Genetta tigrina, Suricata suricatta, Herpestes edwardsi:* Ewer, 1968). *Cricetomys gambianus* (Ewer, 1967) and female *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 rather than climbing up backwards.

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 hindlegs and lifting of the tail, the quadrupedal marking pattern exhibits no other postural adjustments. De novo origin of this pattern is tenable only if it is assumed that perineal glands evolved independently in the semiarboreal 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.

Behavior of Associated Animals

Patterns of behavior performed by solitary animals 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 wisdom of classifying some of these behavior patterns as either solitary or social is debatable. Generalized pilo-erection, for example, is mediated through any or all of the sensory systems; the characteristics of the stimuli are not specifically limited to social contexts. Under the conditions of this study, though, certain patterns of pilo-erection were seen primarily in social contexts, hence their inclusion in this section.

The descriptions in the first part of this study defined types of body motion as they were identified and recorded during social encounters and subsequently analyzed. With the exception of vocalization that is distinguished by broadcast transmission, the behaviors in this section are classified on the basis of orientation and the spatial characteristics of their occurrence. It is assumed that these patterns have a communication function. Both 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 that may be combined within and between categories and modified by independent variables such as velocity of movement and posture. The second part of this section analyzes the organization of signals in time and the dynamics of social interaction in *Genetta* and *Civettictis.*

COMPANION-ORIENTED LOCOMOTION

An animal's locomotion is often affected by the presence of another animal. The criteria used to distinguish different types of companion-oriented locomotion are listed below.

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 specifically oriented to the other animal. As any movement of one or two animals will involve spatial changes that may have no immediate social significance, the term approach is used herein only 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 (Figure 23A).

DEPARTURE.—The term is used to describe the net movement of one or both animals away from the immediate vicinity of the companion. In most cases a departure is 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.

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

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. This definition of mutual orientation to the companion's body excludes following in which the path may also be circular.

Encircling.—Occasionally as one animal remains stationary or moves slowly, its companion walks or trots about it in a tight circle.

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 also be executed by an animal traversing a tree limb, in order to negotiate the obstacle presented by a resting companion's body.

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" under "Locomotion and Its Ontogeny"). While approaching, following, and departure may involve any gait, circling and encircling are performed only 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 5b–f are exhibited by approaching animals, while departing animals rarely exhibit postural variants involving crouched forequarters (Figure 5b,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 contiuum of noncontact-oriented behavior.

Table 8.—Associations of postural variants (companion-oriented stances of tripedal and quadrupedal types, characterized by protracted visual fixation) and torso orientation to companion in *Genetta tigrina* (+ + = most frequent association, + = less frequent association, — = uncommon association)

Postural variant	Frontal	Tangential	Lateral
Full Crouch.........	++	—	—
Normal..............	++	++	+
Crouched fore- and semi-raised hindquarters..........	++	+	—
Semi-raised fore- and hindquarters..	—	+	++
Maximum raised fore- and hindquarters..........	—	+	++

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 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 (Figure 23a). 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.

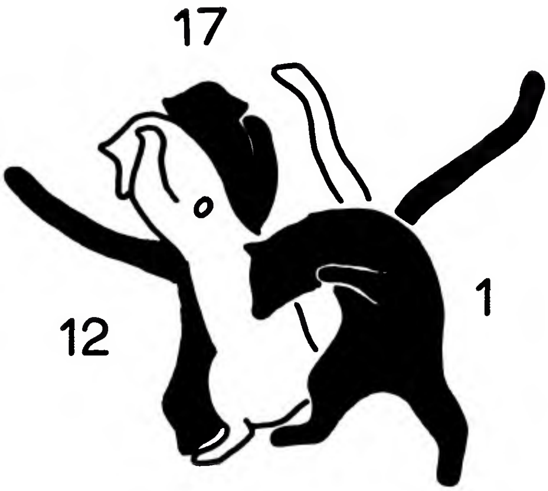


FIGURE 21.—Bipedal pivot of the African palm civet (*Nandinia*) based on tracings of 16 mm film (24 fps), in which the animal took several bipedal steps.

The bipedal stance and the elongate quadrupedal crouch are usually maintained for relatively brief periods, the latter being associated with approaching a companion and establishing nasal contact.

SIMILAR STANCES IN OTHER GENERA.—*Civettictis, Paradoxurus, Paguma, Nandinia,* and *Fossa* are capable of assuming a crouched posture while stationary or walking. Though not all these genera display equal facility in maintaining this position, crouching is fairly widespread among civets. With the exception of *Paguma,* the posture involving semicrouched forequarters and semiraised hindquarters (Figure 5D) is also seen in these genera as a companion-oriented stance. This body position can be converted to a low-intensity arched-back posture by straightening the forelegs and slightly arching the back. This has been seen in *Paradoxurus, Nandinia,* and *Fossa.*

In the male *Nandinia,* this half crouched, half raised body carriage was associated with slow and deliberate walking on branches, accompanied by visual fixation of the observer or another animal. The male would reverse the direction of his movement by rising "stiff bodied" into a bipedal position and pivoting on his 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 male toward a strange female (Figure 21). The animal quickly approached the female, rose into a high bipedal position, and pivoted to one side while holding the forelegs up and tightly flexed to the sides of the body. It can be seen in Figure 21 that the animal actually took several steps while standing upright.

Intense arched-back postures have been seen only in *Fossa.* I am reasonably certain that it does not occur in *Civettictis* and *Nandinia,* but neither *Paradoxurus* nor *Paguma* was seen under conditions conducive to this behavior (e.g., fighting). Intense arching 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 because 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 maintained in the same plane (Figure 22A) or deflected downwards to as much as 60° (Figure 22B). The head is usually rotated slightly upwards in the partner's direction (Figure 22A,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 (Figure 22B), it is more common for the trunk axis to be tangential or lateral to the companion's head and neck (Figure 22A,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 (Figure 22C), or in reclining positions (Figure 22A,D).

NONCONTACT BODY MOVEMENTS

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 when an animal is approached or followed. Such erratic motions result from a 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.

ALTERNATING EAR MOTIONS.—As described under

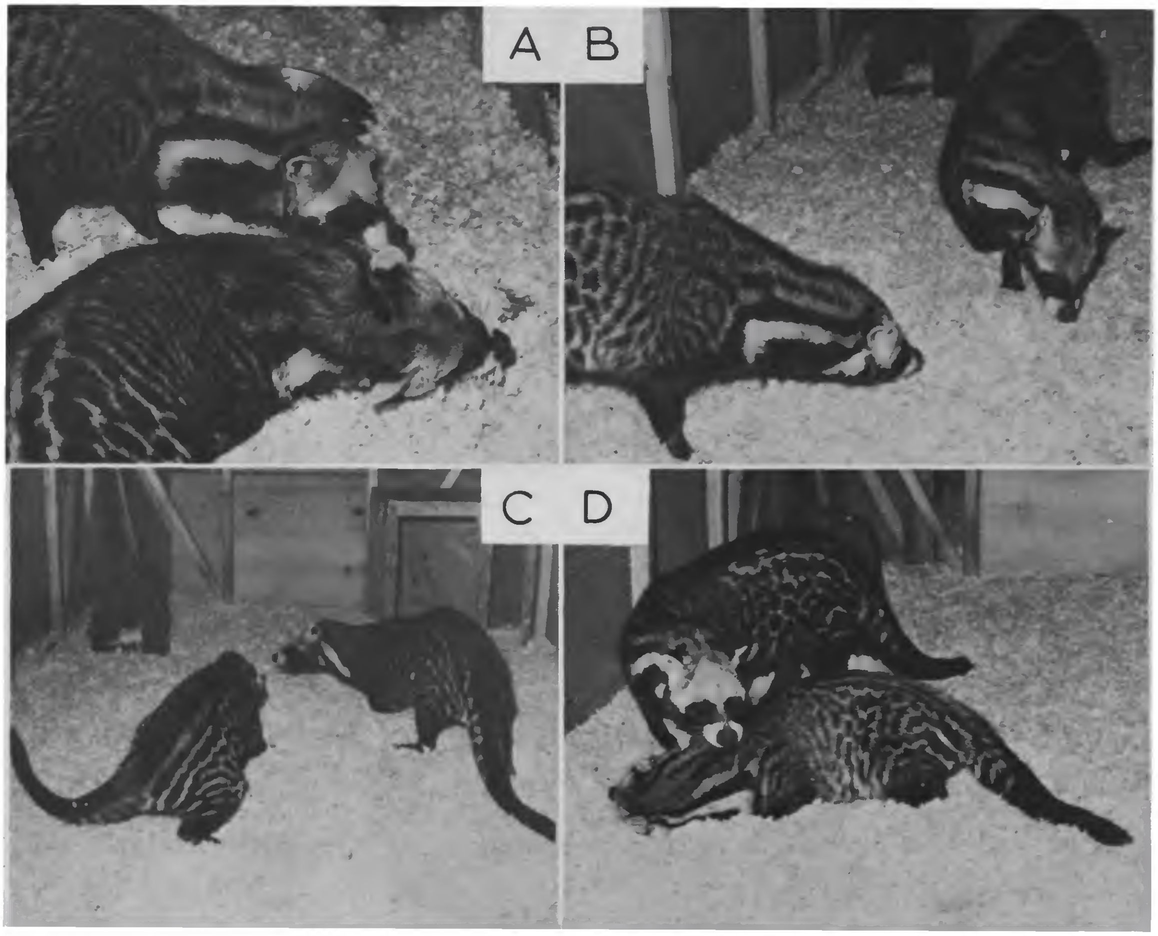


FIGURE 22.—Lateral and tangential orientations of the head, neck, and body in the African civet (*Civettictis*): A, head and neck deflection in a reclining animal; B, lateral head and neck orientation by an approaching animal (male); C, assumption of a reclining position by an animal receiving head-darts; D, head deflection by a recumbent animal towards the superior companion.

the primary senses, this behavior may be directed toward another animal or to an area of interest. It is difficult to discern whether the movement itself or the independent perception of sound triggers the same response in companion animals.

TURNING TOWARD.—Any motion of the body or its parts resulting in a frontal orientation of the face toward the companion is defined as turning towards. Facial exposure can be achieved by either turning the neck or 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.

TURNING AWAY.—Any movement that terminates facial exposure to a companion is defined as turning away.

TAIL WIGGLING.—An erratic and rapid bending and extension of the tail along its length produces a spasmodic jerking motion that 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.*

ANAL GLAND SCENT EMISSION.—The emission of anal gland scent is associated with fighting, intense attempts to avoid or escape from another animal or 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 two dozen small drops that traveled about 2 decimeters before striking a surface. The force of the emission is weak, and the associated circumstances are such that scent is usually deposited close to the interacting animals. The scent almost always contaminates the fur of the tail and that surrounding the anus; 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 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 that is detectable at close range; washing with detergent and water will not completely remove it from clothing.

PILO-ERECTION PATTERNS.—The longer hair on the head, trunk, upper legs, and tail is erected in a variety of circumstances that 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 contact, 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.

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 (Figure 26). Erection and depression can be either 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.

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 (Figure 23B); moreover, it appears that the spinal crest itself can be

TABLE 9.—Average hair lengths (in mm; range in parentheses) of spinal crest and tail in a sample of 18 *Genetta tigrina* skins in NMNH (sides = 3 cm from dorsal midline; tail base = third white tail ring to rump; tail tip = distance from end equal to tail base distance from rump)

		Spinal Crest						Tail			
		Shoulder		Midback		Rump		Base		Tip	
♀♀	dorsum	17.7	(16-20)	21.7	(20-24)	25.8	(22-30)	24.8	(21-27)	20.4	(16-23)
	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)
	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)
	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	

raised to a greater extent than surrounding hair. Maximal and prolonged erection of the crest, however, seems to be linked with a uniform level of erection in the torso hair. When the body hair is depressed, there is no indication of a crest.

Tail Hair: The degree of 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 (Figure 23C). Lengthwise piloerection gradients are usually unidirectional with either the terminal black segment or the first 2–4 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, stepwise. That is, rapid flux in erection or compression is followed by a period of very slow change in either direction.

NONCONTACT MOVEMENTS IN OTHER GENERA.—With the exception of alternating ear motions and tail wiggling, *Civettictis* exhibits all the noncontact 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 stepwise 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.

COMPANION-ORIENTED CONTACT PATTERNS

Head

SNIFFING (NASAL CONTACT).—Sniffing of another animal does not necessarily involve contact, but if not repelled an animal will almost always bring its nose into contact with 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 (Figure 23D). 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 (Figure 23D). When the perineal gland, vagina, 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 Jacobsen's organ. The mouth is usually slightly opened, the eyes squinted, vibrissae retracted, and the orbits of the ears directed laterally in a semierect position.

LICKING AND NIBBLING.—As described for the solitary animal, these patterns may also be directed to a companion. Both types of mouth contact are usually associated with a relaxed facial expression. The eyes may be squinted or closed and the ears oriented laterally in a semierect position.

BITING.—Duration of contact, force of compression, and head movements during contact are three biting parameters that probably form a graded continuum. Mouthing occurs when an animal's jaws engage with another animal's body but there is little or no compression (Figure 23E); biting occurs 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 they are not folded above the notch (Figure 23E).

HEAD-DARTING (Figure 24).—This is a highly variable movement consisting of several components and 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 25 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

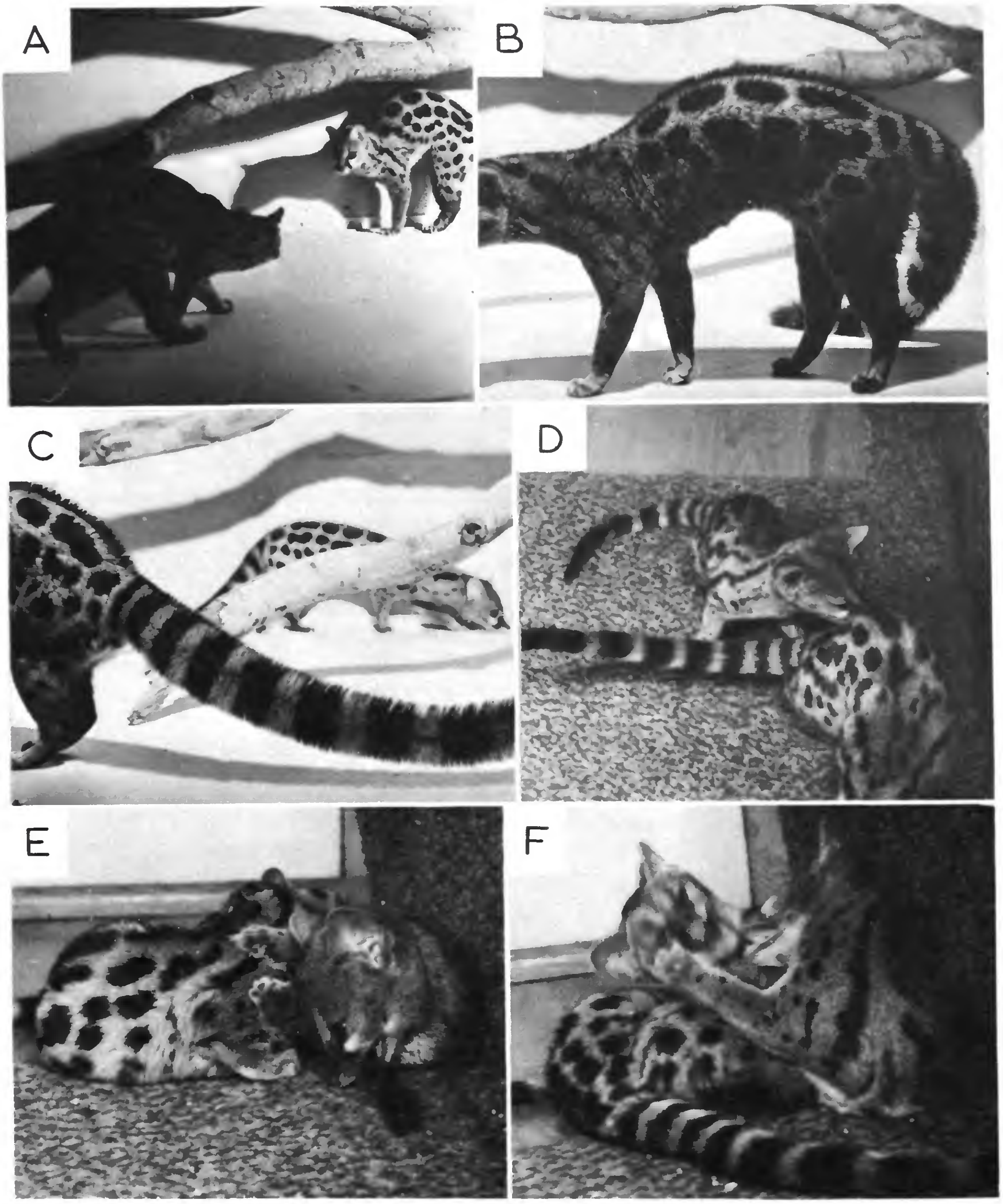


FIGURE 23.—Patterns of companion-oriented locomotion, movement, and contact in the genet: A, crouching animal approaching a companion exhibiting an arched-back stance; B, low intensity arched-back stance exhibiting general pilo-erection and the spinal crest; C, maximal pilo-erection of the tail; D, juvenile genet sniffing the spinal crest hair of another animal (note facial expression); E, juvenile animal mouthing its companion's tail; F, pawing by an animal engaged in wrestling.

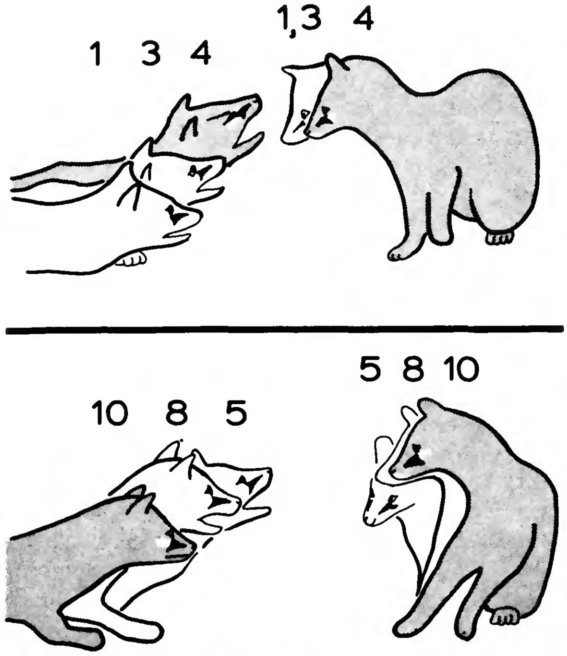


Figure 24.—Extension and retraction phases of head-darting in the genet (animals E and Fr; based on 16 mm film, 24 fps; shaded images represent last frame in series; in this sequence recipient began to respond in less than ¼ second).

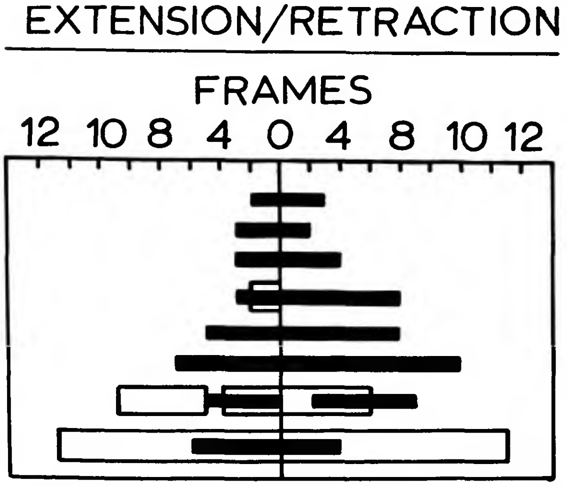


Figure 25.—Duration of extension and retraction phases in eight samples of genet head-darting recorded on 16 mm film (24 fps) of E head-darting at Fr (none involved contact with Fr and the occurrence of hissing is not indicated; black bars = extension and retraction of the head, clear bars = opening of the mouth).

not involve contact with a companion. When it 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 (Figure 24). A backward 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.

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 head-dart at a companion. The mouth may be opened briefly and repeatedly while the animal is staring and as it inhales between growls.

Erratic Head Movements (see "Noncontact Body Movements").—When executed in the close proximity of another animal virtually any part of the head or neck may touch the companion's body.

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 (Figure 23F; cf. "Object-Oriented Contact Patterns"). Stepping and standing on another animal is distinguished from pawing because the force of the contact is presumably greater and the animal establishing contact is usually in a superior or elevated position. Clasping of another animal's body occurs in the same manner described for an inanimate object. As a partner's body is clasped the hindlegs may also be pumped rapidly back and forth with the major thrust occurring during the backstroke. 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.

Kicking, the hindleg analog of pawing, 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.

Trunk

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 its 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 an animal may creep forward over the other's body with small steps.

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 contact may also occur in jumping over another animal.

Brushing Against.—An animal may briefly brush any part of its body against that of another animal in passing.

Somersaulting Against.—Occasionally as two animals engage in long bouts of contact behavior, one may place the side of the head on the ground and perform a lopsided somersault by rolling over onto the neck, shoulder, and then the side.

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 complementary. This category is used 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.

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.

Grappling.—Standing bipedally upright, the animals paw at and clasp one another about the head, neck, shoulders, or chest while head-sparring or head-darting and biting each other's head, neck, forelimbs, and shoulders.

Wrestling.—Animals engaged in this activity maintain a broad 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, pump, bite, or head-spar. When in body contact, one animal's belly contacts the other's side, back, or belly.

Fighting.—Combat between two animals resembles wrestling but it almost always involves a cross body or head-to-head orientation and is usually accompanied by screaming, urination, and anal scent emission of one animal. Wrestling may grade into fighting, but if fighting movements are more rapid, body contact is usually briefer, and usually the initiator repeats the attack. Animals matched in size, 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 does not occur. When a considerable size disparity exists between combatants, the larger one subdues the smaller by clasping and may bite it severely.

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

Companion-oriented Contact Patterns in 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 are unable to effectively restrain one another by clasping during wrestling or fighting. In addition, the following contact patterns merit special attention.

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 female'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 accompanying facial expression is not assumed during sniffing or licking, it is assumed during the nonsniffing phase. Occasionally the eyes are closed and the tip of the tongue extends 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 nonsniffing phase is terminated by licking the nose and lips and sometimes a brief head shake. This may be followed by another activity or resumption of sniffing.

Perineal Gland Scent-marking.—On one occasion the male *Civettictis* was seen to evert the perineal gland, back up, and lightly press it against the female's neck as she was sniffing the wall of the cage.

Head- and Neck-wiping.—While walking past the female the male *Civettictis,* on a number of occasions, extended his head or neck toward her and, with a brief extension movement, wiped some part of her body.

Vocalization

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

Coughing (Muckern: Herter, 1952).—The cough, a brief sound pulse having a broad energy distribution and a narrow intensity latitude (Figure 27A), 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 continues throughout life. Production of the sound is preceded by a bumplike expansion of the throat. Expiration of air through the glottis and out the nostrils is accompanied by the disappearance of the bump and a single jerking compression of the rib cage. Spectrograms were occasionally obtained from animals O, K, and C showing a weakly harmonic pulse and a wide noise band that seem to fit the apparent glottal and nasal events, (Figure 27A).

Hissing (Fauchen, Explosive Hiss, Spucken).—This vocalization, phonetically rendered as a noisy "hcchhh," is another brief duration 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°–40° 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 opened at or near the end of the exten-

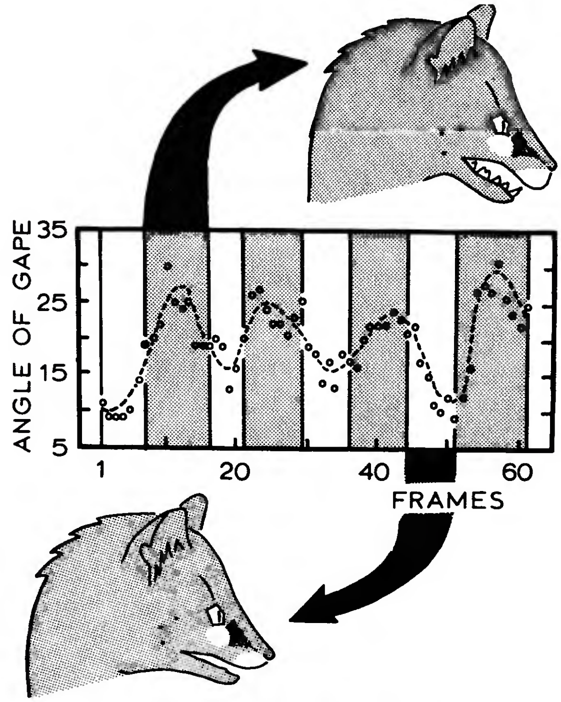
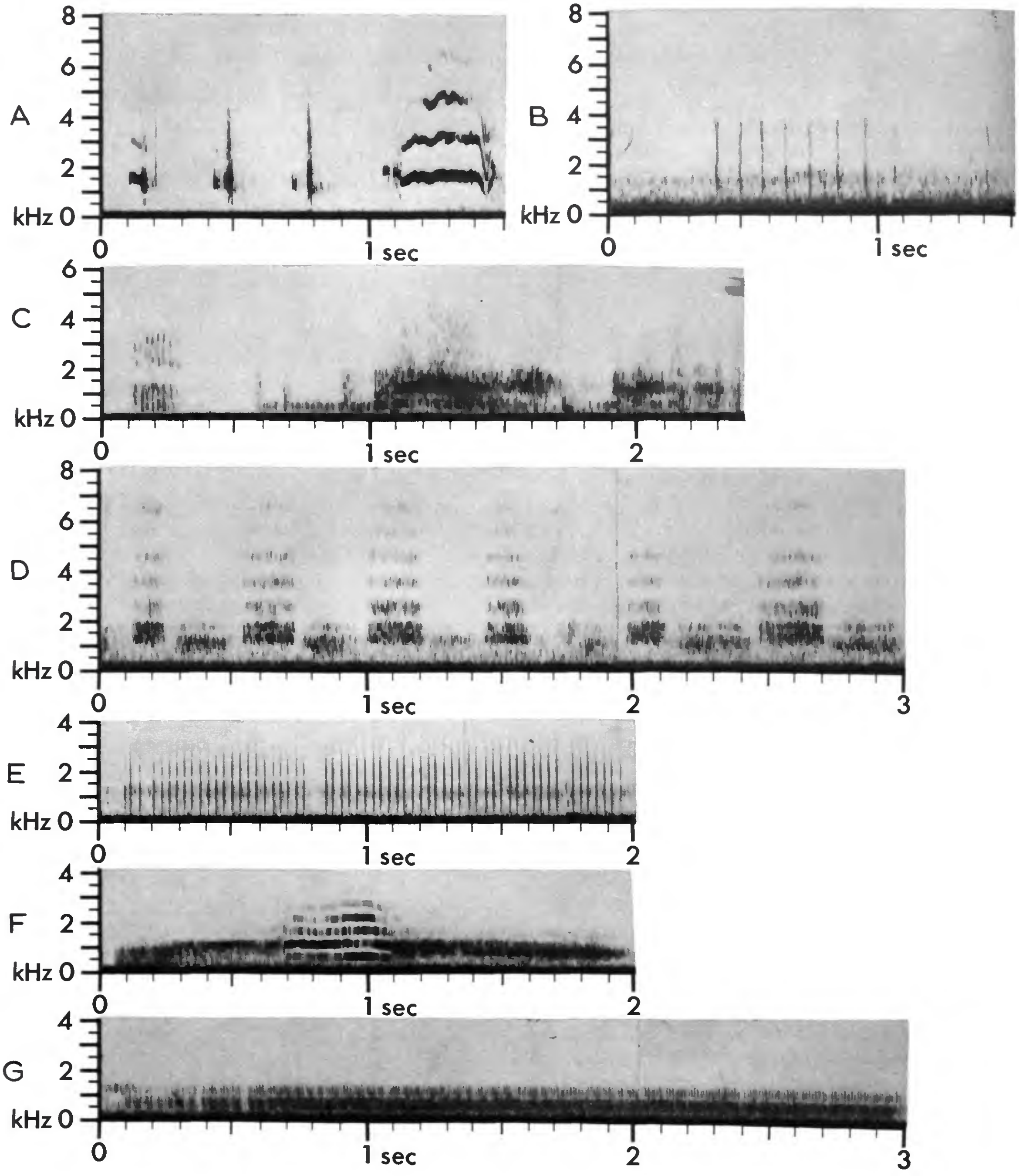


Figure 26.—Facial expression during the panting-hiss in the genet (animal E; 24 fps; shaded and clear columns = expiration and inspiration respectively, estimated from rib cage movements; circles = measurements of the jaw-gape angle in degrees estimated from the film; the curve was fitted by eye).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sion phase. Eye closure may or may not coincide with the production of this sound but often occurs if the mouth contacts the recipient.

PANTING HISS.—This call shares many of the physical characteristics of the explosive hiss, but its temporal organization is a function of accelerated respiration (Figure 26). The expiration phase of this sound produces a broad frequency range with bands of energy concentration resembling dissipated harmonics, while inspiration produces low frequencies with lower intensity (Figure 27D). The facial expression of this call is characterized by retracted lips and a jaw-gape that 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 (Figure 26); 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 age of two days (Fr), five days (M and E), 13 days (O, I, and C), and 16 days (K). Both forms of hissing may occur with growling and screaming.

WHINING (Nestgezwitscher: Goethe, 1952; Quicken: Dücker, 1957).—This vocalization varies widely within and between individuals in harmonics, intensity, and duration (Figures 28A–C). The leading and/or trailing segment of a whine may be frequency modulated. Harmonic form often varies between bouts, and is probably a function of the animal's activity 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.

SCREAMING (Schreien).—The scream is essentially a very high intensity whine but having a greater number of overtones (Figure 28C). The distribution of the overtones suggests that two 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, consequently, a narrower range of energy distribution (Figure 28E, left). The sound was infrequently heard, but it could sometimes be evoked by rough handling in animals that had not yet been weaned. 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 that accompanies this call. Very high intensity screams display degeneration of harmonic structure and broad noise distribution (Figure 28E, right). In such cases screams appear to grade into noisy explosive hisses.

PURRING (Schnurren).—Purring is composed of continuous and rapid volleys of low intensity clicks produced during both inspiration and expiration (Figure 27E). Usually clusters of sound pulses with similar interval length are separated from other such clusters by longer intervals; these breaks in the sound undoubtedly correspond to the change from inspiration to expiration. 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; this probably explains why it was not detected in my first animals. Some genets continued to purr until they were six months old, but these were raised singly and were exceptionally tame. As noted by Dücker (1957), purring probably does not occur in adults.

GROWLING (Knurren).—Growling is a noisy, usually continuous, moderate intensity vocalization with a repetitive pulse. As in purring, the rhythm of growling conforms to the period of the respiratory

FIGURE 27.—Vocalizations of the genet, African civet (*Civettictis*), and the lesser oriental civet (*Viverricula*): A, sequence of three coughs and a whine in *Genetta* (O); B, series of eight coughs in *Viverricula* at the age of 18 days; C, sequence of calls in the female *Civettictis:* snort (0.2 sec), growl (0.6–1.0 sec), and two 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 (six 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 returning to a growl 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).

TABLE 10.—Characteristics of genet vocalizations (frequency in kHz, duration in seconds, duration range in parentheses)

Type and number of vocalizations	Frequency Range		Fundamental frequency	Duration	
	Total	Dominant		Smallest discrete elements	Call
Cough (O) 28 (K) 12	0.85-8.0	0.85- 7.0	--	< 0.07	< 0.07
Explosive hiss (O) 7	0.85->8.0	0.85->8.0	--	--	$\bar{x}$=0.13 (0.07-0.27)
Panting hiss (M) 12	0.85-7.5	0.85-4.0	~1.0-2.0	$\bar{x}$=0.18 (0.11-0.27)	variable >1.0
Whine (O) 94	1.4->8.0	1.4- ~6.0	~1.4	--	$\bar{x}$=0.76 (0.11-3.59)
Scream (O) 9	0.5- ~7.0	0.5- ~4.0	~0.7	--	$\bar{x}$=0.86 (0.42-1.5)
Purr (K) 6 (F) 6	0.85->8.0	0.85- ~3.0	--	<0.007	variable >1.0
Growl (M) 6 (O) 8	0.85- ~1.5	0.85- ~1.5	--	<0.007	variable >1.0

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 two 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 (Figure 27F). Though first heard at the age of 80 days (O), it can probably be evoked earlier.

VOCALIZATION IN OTHER GENERA

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

COUGHING.—Unlike the coughing of *Genetta*, the call in *Viverricula malaccensis*[7] has a clicking quality and is produced in bouts composed of several cough elements (Figure 27B). Of seven recorded coughing bouts, two were composed of six and two of seven elements, and three bouts contained eight elements. The intervals separating the cough elements varied from 0.03–10.46 sec. The majority of intervals (79%) fell within the range of 0.06–10.12 sec. The coughing vocalization in *Civettictis civetta*, like that of *Genetta*, is the most common adult call. It is emitted with the mouth closed and is always a rapid series of sound bursts composed of from 2 to 14 elements (Figure 29). The sound is phonetically similar to, but deeper than coughing in *Genetta*. Coughing in the fanaloka, *Fossa fossa*, has a distinctive quality rendered phonetically as "chuck." The intervals between coughs are variable; while the sound is most commonly repeated in a rapid series as with *Civettictis*, is is also emitted singly at longer sporadic intervals.

HISSING (SNORTING).—Hissing or snorting was heard in all the observed genera with the exception of *Viverricula*. Dücker (1957), however, recorded "spitting" (Spucken) in this species (Table 11). 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

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[7] A recording of coughing and whining in an 18-day-old male born at the Chicago Zoological Park, Brookfield, Illinois, was kindly made available to me by Dr. Robert Horwich.

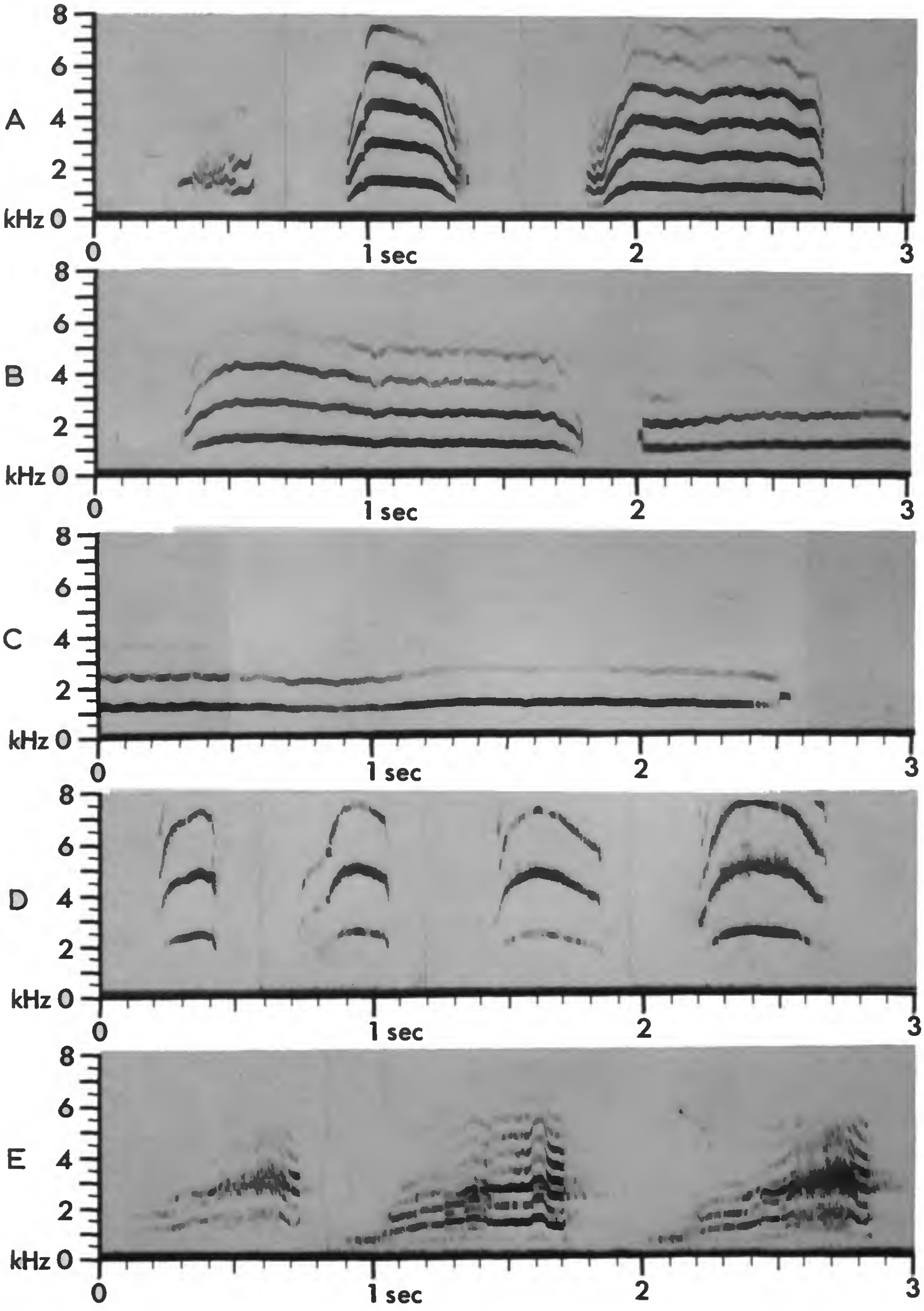


FIGURE 28.—Vocalizations of the genet and the lesser oriental civet (*Viverricula*): A–C, six variations in the whining call of genet K (not a series); D, four examples of whining in *Viverricula* (not a series); E, three examples of screaming in the genet O (not a series).

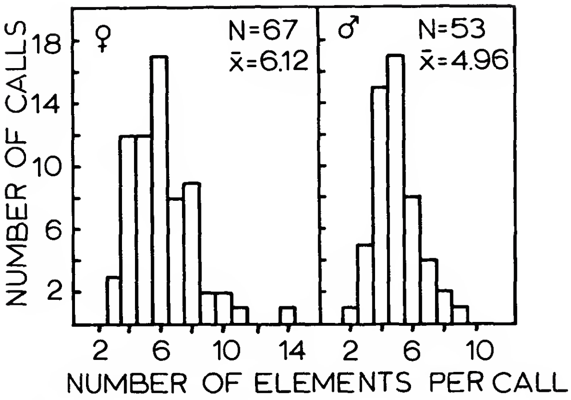


FIGURE 29.—Variation in the number of elements composing coughing series in the male and female African civet (*Civettictis*).

is possible that hissing may replace snorting in the early life of *Civettictis* (Figure 27C; Table 11). Though snorting or hissing may be associated with head-darting in all the observed species, limited observations on the male *Paguma* revealed that snorting was always associated with a modified method of head-darting. The snort was produced as the animal extended and raised its neck while swinging the head upwards. At times the animal would quickly rise up off its forefeet while snorting.

WHINING (GROANING, BLEATING) AND SCREAMING.—Four *Viverricula* whining calls from a recording of 21 are reproduced in Figure 28D. In form these calls resemble those of *Genetta* except that the harmonics are more widely spaced and there is relatively little variation in call duration. The one kHz

TABLE 11.—Distribution of vocalizations in social situations for selected viverrid genera (+ = present, − = absent, +? or −? = probably present or absent but substantiation needed, blank = uncertain; calls divided into 6 major families on basis of overall physical similarity)

Vocalization	Viverrinae			Paradoxurinae			Hemigalinae
	Genetta	Viverricula	Civettictis	Nandinia	Paradoxurus	Paguma (isolated)	Fossa
Cough...........	+	+	+	-	-	-	+
Hiss............	+	+*	+?	+	+	-	+
Snort...........	-	-	+	-		+	-
Whine...........	+	+	+?	-	+?		-
Tremelo groan...	-		-	-	-	-	+
Bleat...........	-		-	+	-	-	-
Scream..........	+	+?	+	-?	+?		+
Purr............	+			+			-
Growl...........	+	+*	+	-	-	-	+
Hum.............	-		-	+	+?	+	-
Hoot............	-		-	+?		-	-
Neigh...........	-		-	-	+?	+	-
Summary.........	6	5	6	5	5	3	5

* Described in literature

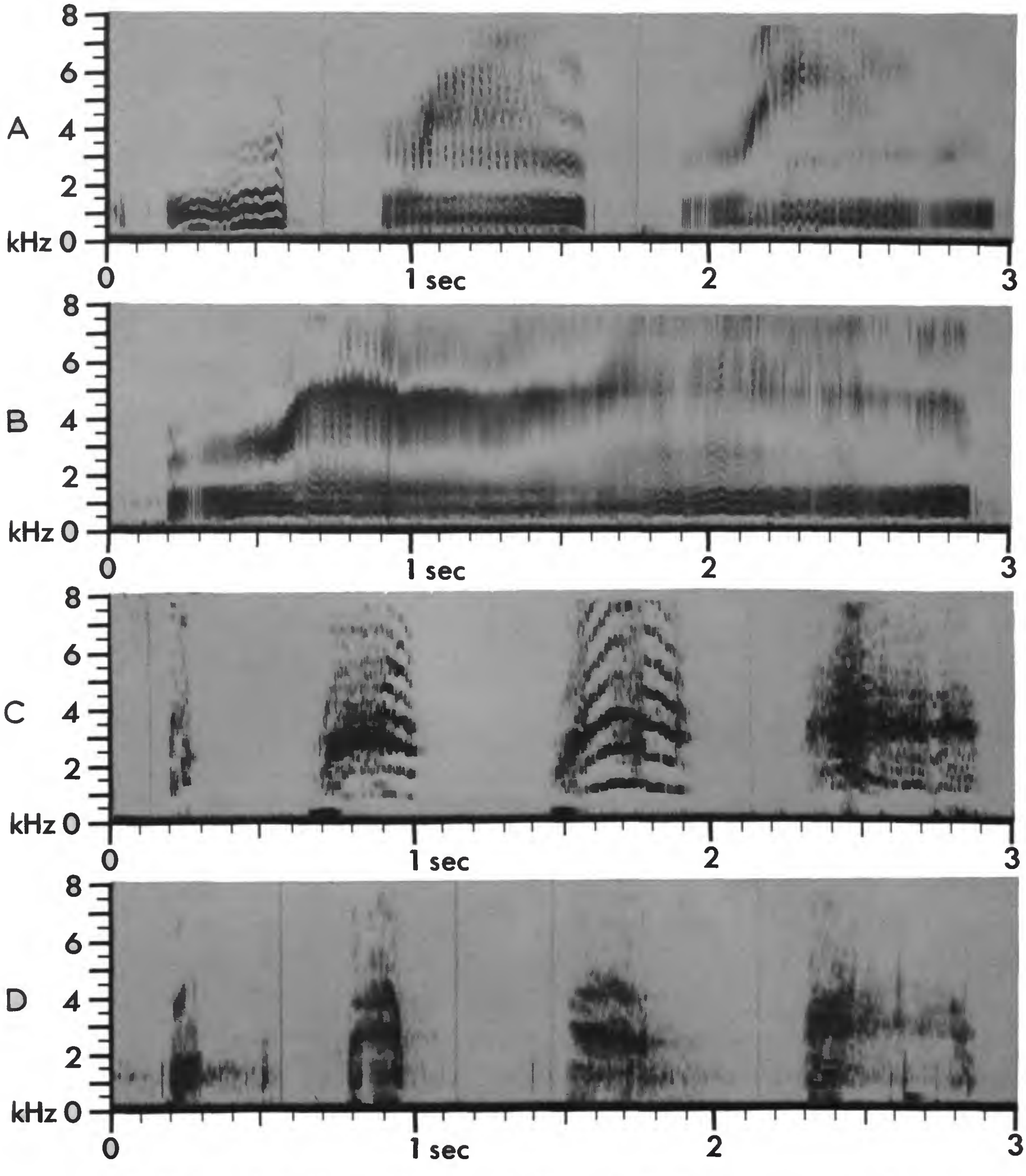


FIGURE 30.—Vocalizations of the fanaloka (*Fossa*) and the African palm civet (*Nandinia*): A–B, four examples of the tremelo groan in *Fossa* (note variation in frequency and temporal structure); C, four examples of screaming calls in *Fossa* (note variation in harmonic detail); D, four examples of bleating in *Nandinia*.

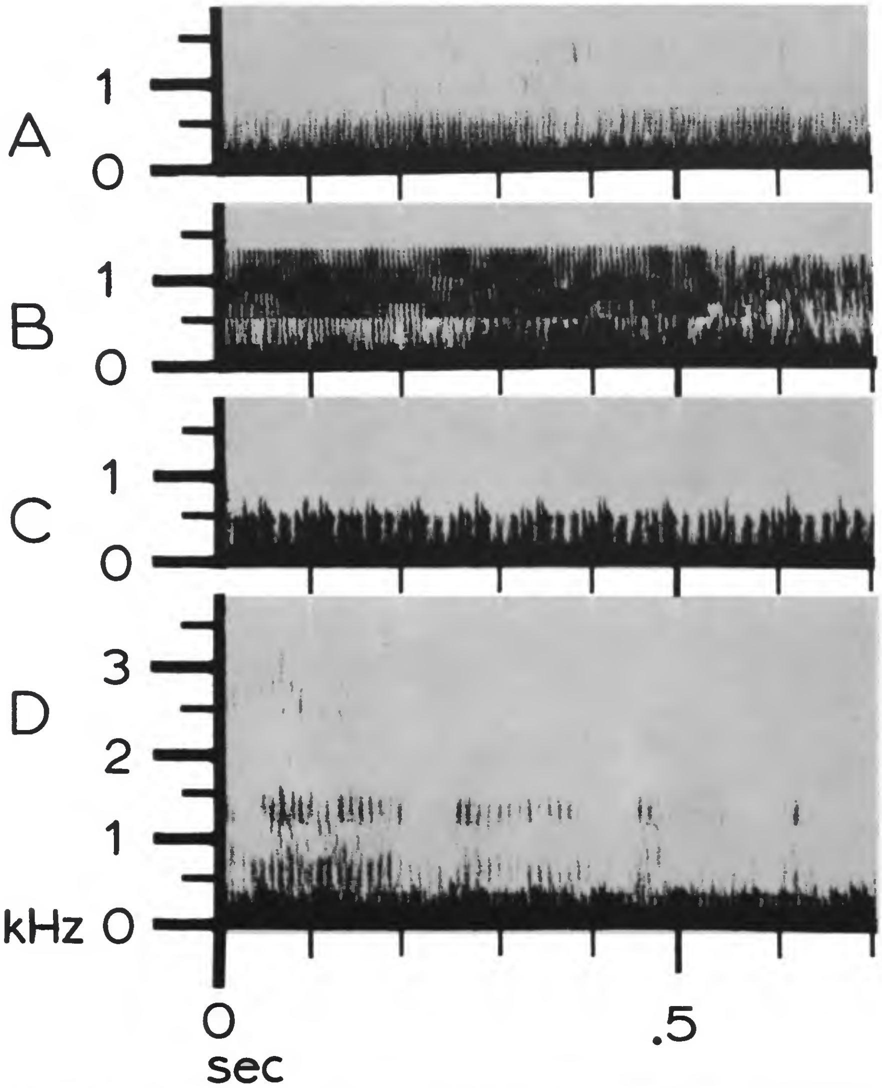


Figure 31.—Growling and humming vocalizations of the genet, the African civet (*Civettictis*), the Formosan masked civet (*Paguma*), and the fanaloka (*Fossa*): A, humming in *Paguma;* B, growling in a juvenile *Genetta* (O); C, growling in an adult *Civettictis* (female); D, growling in a juvenile *Fossa.*

difference in the fundamental frequencies between the fanaloka and genet can be attributed to age difference. Whining was not heard in *Civettictis* but a recording of the female's scream during a fight is presented (Figure 27c). This sonogram is representative of six others. All are characterized by an aharmonic broad frequency scattering of noise. For *Nandinia* Dücker (1971) described a loud, sustained "Fiepen" apparently heard only in young animals. It was not detected in my young male when he was received at the age of about two months. Bleating (Figure 30D), rendered phonetically as "Kräã," refers to a call that may be a variant of whining, though Dücker (1971) recognized them as distinct. It is produced with the mouth open and uttered softly but spontaneously by a motionless or slowly moving solitary animal. Dücker noted that a louder version occurred as a response to "unexpected, sudden contact of the body" (1971:81). Though the male and female *Nandinia* fought on several occasions, a screaming vocalization was not heard.

The tremelo groan and scream in *Fossa fossa* usually differ in their physical properties, but both are uttered with an open mouth and sound like extremes of a graded continuum (Figure 30A–C). Though the groan usually differs from the scream by a more complicated and varied sound structure, groans can have the discrete harmonic organization that characterizes screams devoid of vocal noise (Figure 30: compare A, tracing 1 with C, tracing 3). Most sonograms of groaning consist of unbroken series of tightly spaced pulses having broad zones of frequency emphasis (Figure 30A, tracings 2 and 3, B). These pulses may resolve themselves into deep narrow chevrons (Figure 30A, tracing 2) or thin, broken, superimposed horizontal bands (Figure 30B). The scream of *Fossa* sounds like that of *Genetta:* the fundamental frequency lies in the vicinity of one kHz and the harmonics are tightly packed (Figure 30C, tracings 1–3). Harmonic structure can also be completely disrupted (Figure 30C, tracing 4).

PURRING.—This call was only heard in the male *Nandinia* at the age of 2–3 months. Unlike Dücker's (1957) animals it was not heard in the two adults.

GROWLING AND HUMMING.—Figure 31B–D presents growling vocalizations in *Genetta, Civettictis,* and *Fossa.* Low frequency noise and a repetitive pulse structure are common properties of growling in all three species. The trace of higher frequency pulses in *Fossa* (Figure 31D) and the predominance of these elements in *Genetta* (Figure 31B) are reflections of the young age at which both animals were recorded. It can be seen that the humming vocalization of *Paguma* (Figure 31A) 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 11). Humming, however, is frequency modulated and has a lower sound intensity than growling. In both *Paguma* and *Nandinia* it usually begins at a low frequency (<1 kHz) and then rises 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 male was once heard to "answer" a distant fire engine siren by matching the frequency change pattern remarkably.

HOOTING AND NEIGHING.—These two distinct calls are produced with a partly opened mouth and share the characteristic of high intensity. Hooting was heard in an old male *Nandinia* at the National Zoological Park. Repeated at a rate of about two calls/sec, it 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 that 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 sustained expiration.

Analyses of Interaction

MATERIALS AND METHODS

Data on social interaction in *Genetta* were collected on a socially stable group of three adults (Figure 33), and during encounters between familiar and unfamiliar pairs in a neutral observation cage (Tables 12, 13).

Interactions of three adult genets (K, C, and 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 sixth evening observations began at 2150. Their activities were dictated into a Uher 1000-L tape recorder while the writer sat near 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. Finally, the recorded notes were transcribed for compilation.

Encounters between familiar and unfamiliar animals were staged in a plywood cage measuring 1.2 × 1.2 × 2.4 m (4 × 4 × 8 ft) with a wire mesh top and a 1.2 × 2.4 m plate glass front. Animals were introduced through doors measuring 30 × 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 box on the left. Initially a small entrance was made in each box, but after a pair of animals interacted out of sight, the fronts 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 a series of 10 successive encounters was 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 1). Animals were alternated as the first to be transferred. They 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 viewing the animals through a 30 × 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 targets and duration of contact behavior on the companion's body were recorded (Figure 32). 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.

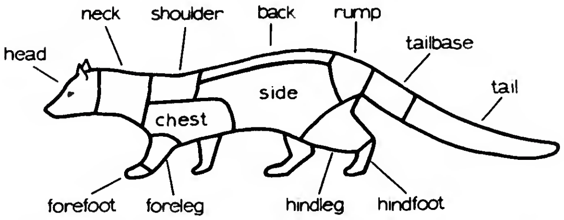


FIGURE 32.—Body topography used in designating the targets of sniffing and head-darting during encounters between genets and African civets (*Civettictis*): the anogenital region lies beneath the tail and between the hindlegs posterior to the penis or vagina; the belly encompasses the ventrum posterior from the chest and anterior of the genitalia.

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

RESULTS

Effects of the Encounter Introduction Schedule on Behavior in Genetta

The order of introduction of the two animals in a series of encounters could affect the conduct of the participants and the outcome of the encounter. Five behaviors were selected to evaluate the effects on animals of the sequence of introduction into the encounter cage. Approaching and sniffing the partner were the two behaviors used to measure social initiative; it was hypothesized that having explored the cage, a resident animal might initiate more social interactions than the more recently introduced one. Alternatively, an animal might become quiescent after exploring an empty cage and exhibit behaviors of a restful state when the partner was introduced. Yawning was used as an index of inactivity. The final two behaviors, sniffing 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 in two categories: introduction into the encounter cage before or after its partner. These paired frequencies for each behavior in which the six animals participated were tested statistically, and only sniffing of the cage exhibited a significant difference (P = 0.025). This suggests that the introduction of one animal into the encounter cage considerably before its partner did not determine the social initiative of the participants.

General Features of Encounters

The types of interaction patterns and their frequency varied greatly between encounters involving different animals, but within a series of encounters for a given pair of animals a certain mode of interaction generally prevailed. The general features of the encounters are outlined below.

Companion-oriented Contact.—Frequencies of contact between the three cagemates (K, I, and C) provide a base for comparison with those in the encounter situation. Social tendencies of these three animals are illustrated in the sociograms of Figure 33. The relative frequencies of the four classes of contact (sniffing, head-darting, licking and nibbling, and fighting) agree with subjective impressions gained over almost three years of daily observation. Contact was most frequently exchanged between the male and females. This is particularly evident in sniffing and body contacts (Figure 33a,d), but it is also seen in licking and nibbling (Figure 33c). Most licking and nibbling was done by the male (K). 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.

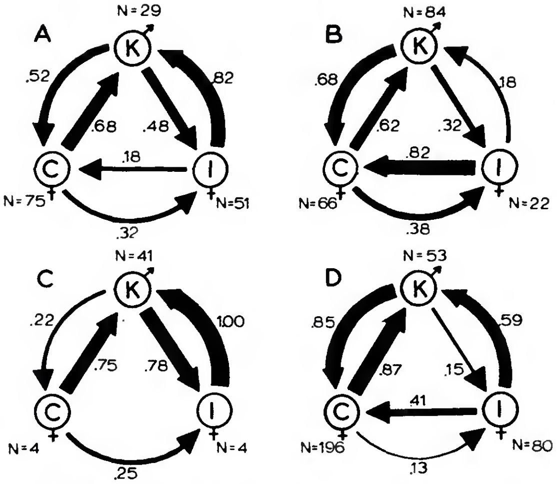


Figure 33.—Sociograms of selected contact patterns between three genet cagemates (animals K, I, and C): a, sniffing (nasal-contacts); b, head-darting; c, licking and nibbling; and d, body contacts (pawing, clasping, standing on, and wrestling; N = number of times each animal performed a given type of contact; arrow thickness is proportional to percentage of occurrence rounded off to nearest 10%; actual percentages in decimals accompany each arrow).

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 two of nine pairings involving unfamiliar animals (Table 12). Protracted sessions of playful interaction occurred between K and Mo and between the two immature males (F and O). Mutual licking and nibbling was exhibited only by K and Mo, and in the three series of encounters involving familiar animals (C and K, I and K, I and C). In all other encounters contact between strange animals predominantly involved sniffing and head-darting. Moreover, in almost all cases these two activities constituted the majority of the contact exchanged between animals.

Fights occurred in 5 out of 12 series of encounters, and were initiated by K and Mo. K initiated a fight with his cagemate C and with the unfamiliar female Mo. 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 male repeatedly clasped and bit the female and finally attacked her violently. The female

TABLE 12.—Number and percentage (in parentheses) of 5 common contact behaviors as observed in a series of encounters involving 12 paired arrangements of 6 *Genetta tigrina* study animals (only pairs 2, 4, and 5 involved animals already familiar to each other)

Animal Pair	Sniffing		Head-darting		Licking and nibbling		Biting and mounting		Limb contact		Total
1 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
2 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
3 Mo ♀....	238	(78.3)	16	(5.3)	8	(2.6)	14	(4.6)	28	(9.2)	304
K ♂....	218	(84.5)	8	(3.1)	19	(7.4)	5	(1.7)	8	(3.1)	258
4 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
5 C ♀....	60	(81.1)	4	(5.4)	1	(1.4)	2	(2.7)	7	(9.5)	74
I ♀....	58	(45.3)	49	(38.3)	5	(3.9)	9	(7.0)	7	(5.5)	128
6 C ♀....	58	(77.3)	17	(22.6)	0		0		0		75
Mo ♀....	64	(74.4)	21	(24.4)	0		1	(1.2)	0		86
7 C ♀....	79	(100.0)	0		0		0		0		79
F ♂....	1	(1.7)	57	(98.3)	0		0		0		58
8 I ♀....	0		9		0		1		0		10
O ♂....	43	(53.7)	30	(37.5)	0		7	(8.8)	0		80
9 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
10 I ♀....	8		4		0		0		0		12
Mo ♀....	30	(75.0)	7	(17.5)	0		3	(7.5)	0		40
11 I ♀....	1		12		0		1		0		14
F ♂....	2		2		0		0		0		4
12 Mo ♀....	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

screamed and attempted to escape for about a minute before the male desisted. Mo initiated three attacks without prior wrestling.

Adult males 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 two occasions the male's excited demeanor caused the resident females to run also. The motion of the two female cagemates and the outsider appeared to confuse the male who then chased a cagemate until he caught and attacked her. For this reason, K was never introduced to either of the other male genets.

NONCONTACT PATTERNS.—While sniffing and head-darting are the most frequent forms of contact, they usually occupy a relatively small amount of the time that two animals are together. An animal's noncontact 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

TABLE 13.—Number and percentage (in parentheses) of companion-oriented locomotion, stances, and movements as observed in a series of encounters involving 12 paired arrangements of 6 *Genetta tigrina* study animals (only pairs 2, 4, and 5 involved animals already familiar to each other)

Animal pair	Approaches					Departures total	Deviation from a proportion of 50:50[2]		Visual fixation	Jaw gaping	Arched-back stance	Tail flaring
	Crouch[1]		Rush		Total		App.	Dep.				
1 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
2 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
3 Mo ♀..	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
4 I ♀..	0	--	0	--	60	51			5	0	0	2
K ♂..	0	--	0	--	38	36	11.2	8.6	12	1	0	1
5 C ♀..	0	--	0	--	28	50	17.4	2.6	7	2	0	1
I ♀..	0	--	0	--	58	45			10	0	0	0
6 C ♀..	10	(12.9)	2	(2.6)	77	59	16.2	11.2	173	12	9	22
Mo* ♀..	58	(38.4)	8	(52.9)	151	93			179	3	0	23
7 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
8 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
9 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
10 I ♀..	11	(15.7)	3	(4.3)	70	53	2.6	0.9	147	58	10	20
Mo* ♀..	4	(6.3)	1	(1.6)	63	55			105	4	6	27
11 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
12 Mo* ♀..	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; asterisk indicates animal that initiated and won fight.

[1] Includes crouched stances.

[2] Calculated by subtracting from 50.0 the lowest percentage an animal contricuted 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.

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 observation ought not be interpreted as "typical," but should illustrate some salient noncontact features. The example is encounter number 5, 1930 hours; the subjects are Mo (female) and I (female) (Appendix 1).

1. Mo leaves nestbox; I reclining within her own nestbox and watching Mo; Mo approaches I, naso-nasal contact, turns, departs, enters nestbox; Mo's tail = ¾ expanded, I's tail = 0.

2. Mo leaves nestbox, smells cage; I watching Mo; Mo returns to nestbox.

3. Mo leaves nestbox, tail = ½ expanded, approaches I to ca. 30 cm, smells cage, departs; approaches I again, looks at her, moves about cage, tail flares to ⅔, enters nestbox.

4. Mo leaves nestbox, tail slightly <½ expanded; I still watching, assumes crouched stance; Mo backs up, turns away, flares tail to ⅔, then to ¾, smells cage, sits, tail = ½; I still staring in crouched stance; Mo stands and enters nestbox; I assumes reclining position; Mo yawns and sits down.

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

6. Mo leaves nestbox and smells cage, tail = 0, climbs on top of I's nestbox, smells it, departs, tail flares to ½, enters her own nestbox and sits.

7. I leaves nestbox and smells floor, tail = 0; Mo watches her; I approaches Mo, sits down and looks at Mo, stands and assumes a weak arched-back stance with a tangential orientation to Mo, flares tail to ¾, departs, climbs on top of her own nestbox, smells cage, tail = ¼, steps down from nestbox; Mo still watching motionlessly; I walks to front center of cage, looks at Mo, flares tail to ⅔, turns away, returns to top of nestbox, tail = ¼; Mo still watching; I yawns and steps to the ground; Mo turns her head slowly while watching I . . . gaze is fixed on her; I approaches Mo to within 30 cm, smells toward her, turns away, departs, tail flares to ¾, walks to front center and back to nestbox 2 times; Mo staring intensely; I's tail is ½ expanded; Mo rushes at I, I departs, Mo chases her about the cage, bites her, they fight, Mo 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 Mo who is smelling urine, anal scent, and tufts of hair on the floor. Mo enters her own nestbox, smells the inside and then sits, tail = ⅞ expanded; I still maintains an arched-back stance and growls. Termination.

There are several notable features of this encounter: (1) the two animals exhibited unequal amounts of activity, (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 two animals during encounters involving minimal contact is usually nonoverlapping 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 elicits activity in the dominant animal. The companion then usually retreats and avoids concurrent activity. It is difficult to make general statements regarding noncontact 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 recorded in Table 13. First, the relative numbers of these actions by each animal may be approximately equal, indicating equal activity. In minimal-contact encounters (pairs 6–12), the activity of the participants is largely out of phase, with neither animal (e.g., Mo or I) predominating. Second, both approaching and departing may be performed primarily by one animal; in the minimal-contact situation this simply reflects that one animal dominates activity to the exclusion of its companion (C and O, I and O, C and Mo). Third, when approaches and departures are most frequent in different animals, the animals may be supplanting each other. In the minimal-contact encounters (C and F, I and F), the inactive animal almost always departed to curtail contact with the active companion.

A comparison of approaching frequencies (Table 13) with sniffing frequencies (Table 12) reveals that in cases where crouching and rushing intimidation occurred (pairs 1–3), the animal who approached the most sniffed and head darted the least. In minimal-contact encounters, with one exception (I and Mo), the approaching animal sniffed the most. This feature of minimal-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 approaching and sniffing suggest there is no correlation between sniffing and approaching.

Crouching and rushing, taken together, appear to be associated with social initiative. Usually animals that most often crouch and rush also sniff their companions the most (compare Tables 12 and 13). In the 2 out of 9 applicable cases 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 the frequencies in Table 13. In any event, animals that maintain protracted stances crouch and rush less frequently than their companions, and hence usually display a low social initiative. Both crouching and the arched-back stance 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, these behaviors are briefer and more frequent than the arched-back stance, and therefore more easily related to other patterns. In 7 out of the 10 applicable encounter series, the animal that stared more than its companion also crouched and rushed more. In instances where this animal also gaped its jaw more, it had been defeated in a fight (Mo by K, and Mo by I).

Visual fixation was generally most common among animals exhibiting minimal contact (Table 13, pairs 6–11) and among animals that fought (pairs 2 and 5: C and K, Mo and K). The lowest frequencies of visual fixation occurred in encounters between the three familiar animals, C and I, I and K. Pair 12 in Table 13 is discounted in this case because encounters were discontinued after the fight.

Jaw-gaping was relatively infrequent in familiar animals that did not fight (I and K, C and I). In the minimal-contact encounters (Table 13, pairs 6–11), a marked disparity in jaw-gaping is evident between the two participants varying in magnitude from 4 (C and Mo) to 14 times (I and Mo). Pair 12 is again discounted for the reason stated above. Among animals that fought, the loser jaw-gaped the most. These were also the animals that approached their companions less frequently (excepting I and Mo).

Flaring of the tail hair occurred in both high- and minimal-contact encounters (pairs 1–5, 6–12). High frequencies of tail-flaring were seen in four of five encounter series where fighting occurred (the exception was the brief discontinued encounter between Mo and F, pair 12). Tail-flaring was infrequent both with familiar animals that did not fight (I and K, C and I) and with 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 usually also tail-flared the most, but the relationship is not significant ($P > 0.05$, Appendix 3). Tail-flaring often occurred as an animal maintained an arched-back stance, but this relationship is not shown in the table.

CONTINGENCIES OF COMMON NONVOCAL INTERACTION PATTERNS IN *Genetta*.—Table 14 gives a rough approximation of some common behavioral associations. The table is an abbreviation of the original matrix, which contains twice as many behavior categories. The consequence of eliminating many of the fine grained behaviors (e.g., closes eyes, ears back, mouth open, etc.) is that some common dyads are obscured. Sniffing and darting is a case in point. This common dyad is not shown in Table 14 because the intention movements of darting were recorded between the occurrence of the sniff and the head-dart. Several contact patterns are presented as having followed depart (e.g., sniff, dart, bite, paw, and stand-on). This resulted from failure to record all approaches, particularly during fast action. In addition, seemingly incongruous sequences like these occurred when an animal attempted to depart. For example, as an animal turned to depart, its tail might be sniffed by the companion.

The simplest form of interaction during encounters consisted of movement toward and away from the companion. Companion-oriented movement was frequently interposed with sniffing by one or both animals. Sniffing and head-darting often occurred in minimal- and maximal-contact encounters and constituted the most common elements of social exchange. For convenience the association between these two patterns will hereafter be referred to as the sniff-dart axis.

The sniff-dart axis and multiple contact exchanges represent the ends of a complexity continuum involving contact. Though it is possible for any two patterns to occur either singly or in repeating and alternating series, sniffing and darting were by far the most common elements in dyadic interaction. Other types of contact (e.g., pawing and biting) had no dyadic integrity.

Biting, pawing, standing-on, and erratic head movements are relatively infrequent behaviors during most encounters, and their contingencies are by no means fixed. Tail-flaring is almost always seen in minimal-contact situations in association with movement away from the companion (Table 13). The arched-back stance tends to repeat itself as an initial response to the visual fixation and approach of another animal. It can be seen that noncontact patterns such as tail-flaring, the arched-back stance, and sometimes erratic head movements are associated with movement toward or away from the companion, but the first two patterns are at times precipitated by fighting. 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.

CONTINGENCIES OF COMMON, NONVOCAL INTERACTION PATTERNS IN *Civettictis*.—The two *Civettictis*

Table 14.—Contingency matrix of interaction patterns in *Genetta tigrina* based on encounters of 12 paired arrangements of 6 study animals; matrix includes behavior patterns from sequences enacted by one animal and/or between two animals (App = walking approach, App^c = crouched approach or stalk, App^r = running approach, SO = stand on or clasp with forelimbs, EHM = erratic head movements, TF = tail flare, ABS = arched-back stance)

Precedes / Follows	App	App^c	App^r	Sniff	Dart	Bite	Paw	SO	EHM	Depart	Follow	TF	ABS	TOTALS
App	19	28	6	241	4	1	3	2	8	97	8	4	2	423
App^c	18	8	2	10				1		12	1	2		54
App^r	12	3	1		1	4		2	1	2				26
Sniff	45	5		323	5	3	4	8	6	177	17	2		595
Dart	2			4	36		1			8	3	1		55
Bite	1			1		3		3		5	1			14
Paw				1	1		1			2				5
SO				3		3		1		2				9
EHM	3			6					2	7	1			19
Depart	84	1		30	6				1	26	9	24		181
Follow	6			18		2			4	3	1			34
TF	9			6	1	1				21	7	7	1	53
ABS	1									1		6	5	13
TOTALS	200	45	9	643	54	17	9	17	22	363	48	46	8	1481

exhibited behavioral contingencies similar to *Genetta* but different by the incorporation of several other patterns. As with genets, departure frequently terminated sniffing, and sniffing and head-darting were both repeated more often than they were followed by other patterns (Table 15). Aside from such repetitions, 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 (turn towards) of a proximate companion. Sparring and clasping were also common antecedents of reclining, but only in the former was reclining associated with a lateral body orientation. It was evident in these two animals that the assumption of either a standing or reclining lateral orientation often precipitated further darting. After the darting animal departed or desisted, the reclining one would stand and move away. Approaching, turning away, departing, 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

TABLE 15.—Contingency matrix of interaction patterns in *Civettictis civetta* based on nine encounters of 2 opposite sex study animals (EHM = erratic head movements, LO = lateral or tangential body orientation, TT = turn towards, TA = turn away, boxed figures = values that account for 20% or more of column totals)

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	73	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

head-darting were more commonly contingent upon themselves than upon any other single pattern of contact. At this level, interaction in *Civettictis* appeared to be more complicated because of 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.

CONTINGENCIES OF VOCALIZATIONS IN *Genetta*.—As mentioned previously, coughing in *Genetta* was usually produced in bouts with intervals ranging from one to several seconds. It is evident in Table 16 that more than half of all coughs were preceded or followed by vocalizations, the majority of which were 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. Although sometimes a response to another animal's contact, an outstanding feature of this vocalization was that it commonly occurred during transitions in gaits, stances, reclining positions, and sniffing. Once an animal produced the sound, it was likely to do so again before a change occurred in its ongoing behavior.

Hissing also occurred most frequently in series; of the 110 times it was contingent upon vocalizations (Table 16), only 10% involved another call type, i.e., growling. There was a fourfold 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 as before. About 25% of the time either visual fixation or jaw-gaping followed the delivery of a hiss; both of these acts were 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 16.—Number and percentage (in parentheses) of selected behavioral contingencies with vocalizations in *Genetta tigrina*

Contingent behaviors	Cough		Hiss		Growl		Scream	
	Preceded by	Followed by	Preceded by	Followed by	Preceded by	Followed by	Preceded by	Followed by
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)
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)	-- --	-- --
TOTALS[3].........	607	606	148	143	60	56	38	33

[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.

Defeated animals also growled as they paced in a stereotyped manner in front of the cage. Growling occurred before as well as after animals visually fixated their companions, or assumed an arched-back stance. These three behaviors accounted for 38% of all antecedent acts and 46% of the succedent acts (Table 16); hissing was the only 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 (Table 16) do not indicate that pain inflicted during biting is the most important stimulus evoking this call. Associated patterns such as clasping and wrestling were never seen to elicit the call by themselves. It appears that once an animal received a painful bite, however, more generalized patterns such as approaching became effective stimuli.

Contingencies of Vocalizations in *Civettictis*.—As in *Genetta,* Figure 34A shows that sniffing the cage and general body movement constituted the vast majority of activities associated with coughing. It can be further seen that in each animal olfactory and (less commonly) gustatory sampling of the cage was quite often an antecedent to vocalization. Less than 20% of all coughing-contingent behavior was nasal contacts. In both animals less than 95% of all nasal contacts was contingent upon coughing. Locomotory transitions were relatively more frequent succedents than antecedents.

More than 70% of the occasions after a call was

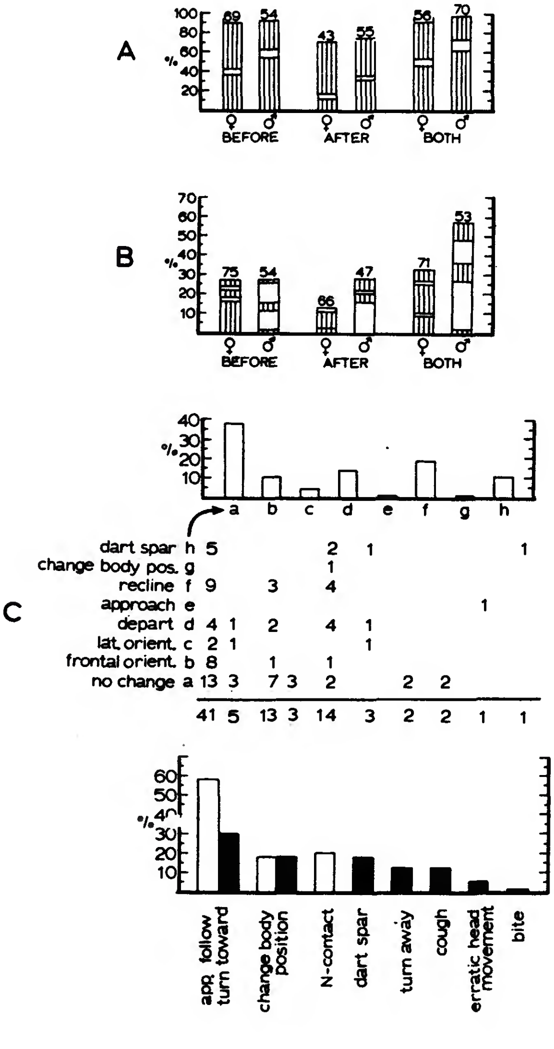


Figure 34.—Behavioral contingencies of vocalizations in the African civet (*Civettictis*):

A, Caller's behavior before, after, and both before and after coughing (the segments of each bar in the graphs 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; difference between bar and 100% indicates percent of calls with no overt contingent behavior; numerals above each bar represent the number of calls from which percentages were calculated).

B, Companion's behavior before, after, and both before and after the caller's 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).

C, Behavior patterns antecedent and succedent to growling by the female (the bottom graph displays patterns of the male—white bars—and female—black bars—that were antecedent to growling by the female; the succedent events in the male are enumerated above each bar; upper graph presents the relative proportions to those succedent events expressed as percentages of the total number of times the female growled, the lower case letters correspond to the behavior patterns listed at left).

given there was no overt change recorded in the companion's behavior (Figure 34B). Antecedent activities of the companion may have evoked the call on some occasions. It is evident that contact by the female was the preponderant antecedent to the male's coughing; and that moving or looking toward or away from the partner was the chief activity of the male preceding the female's coughing. Differences between animals were also exhibited in types of response. In response to the male's coughs, the female sniffed the male 3%, approached 9%, departed 2% of the time, and never coughed back. After the female called, the male 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 female, 80% were apparent responses to actions of the male (Figure 34C, bottom). Female-oriented movements and nasal contacts accounted for 81% of all the male's actions that evoked the female's growling; she also growled when the male simply moved. When there was no change in the male's behavior, the female commonly growled when she moved in his direction.

It is evident that nearly 40% of the time after the female growled there was no change in the male's conduct (Figure 34C, top). 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.

SENSORY CHARACTERISTICS OF SOME NONVOCAL BEHAVIORS.—As a nocturnal forest species having a retina composed solely of rods (Dücker, 1957), *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 noncontact patterns and how they might be perceived by conspecifics. The patterns discussed below can be recognized only visually. Noncontact 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 engaging in it, there would not be selection for behaviors or structures that emphasize this activity to the companion. On the contrary, the patterning of light-colored fields of facial hair provides two characteristics hypothesized as facilitating 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 35 shows 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 two 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 "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 four symmetrical light markings are prominent. Ironically, a similar effect may also be 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 body area to the companion. The tail is concealed or minimally visible and the above-mentioned facial characters predominate. On the other hand, a lateral or tangential position maximizes body exposure in the arched-back stance. The light-colored hair on face and tail delimits the animal's dimensions. Differences between these two patterns may be considered antithetic (Darwin, 1872) and involve both quantitative (head elevation, degree of body exposure) and qualitative differences (visibility or nonvisibility 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 than the tips, erection 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 the overlapping of light and dark hair at band boundaries

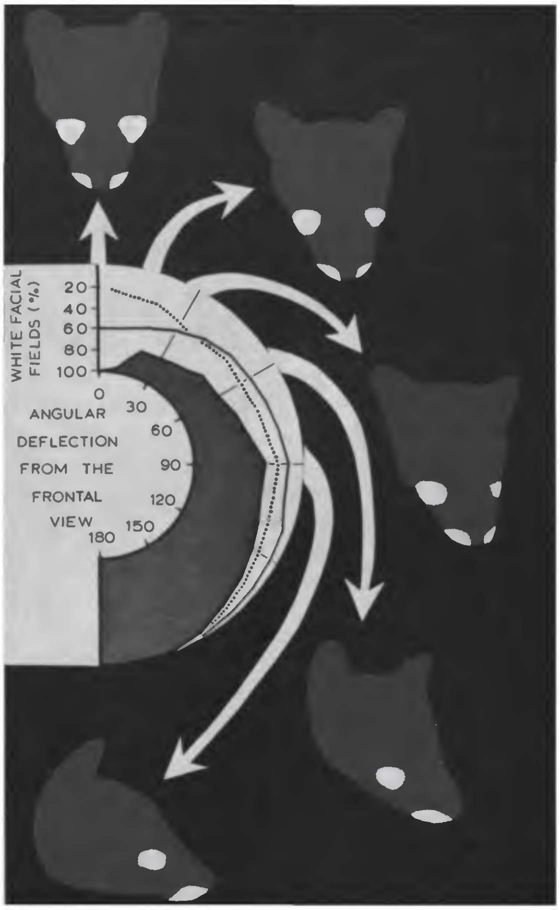


Figure 35.—Appearance of different head positions in the genet and variation in the relative proportions of the white facial markings through a 180° horizontal arc from a frontal position; (gray horizon delimits the area of exposed white hair as a percentage of the amount visible at 0°; approximate percentages of the muzzle and eyespot markings are indicated by the solid and dotted lines respectively, together they equal the percentage expressed by the gray horizon; calculations are based on planimeter measurements from enlarged photos of the horizontally resting head of a dead genet).

produces a more graded effect. In all probability the visual pattern that is produced—a rapid expansion of a series of light-colored bars—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, as well as 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.

Body Targets of Sniffing and Head-darting in *Genetta*.—Figure 36 reveals a bimodal distribution of sniffing frequencies to the fore and hindbody. While the head, nose, and neck were the most commonly sniffed forebody targets, the rump, anogenital region, and tail (including the tailbase) received 45.2% of all nasal contacts, the tail and tailbase accounting for 29%. These common anterior and posterior targets accounted for exactly two-thirds of all companion-oriented sniffing. The side was the remaining most commonly smelled anterior target region; it also constitutes a relatively large surface area. Forty-six percent of all sniffs were directed to targets between the head and side, while the remaining parts of the body, composing slightly less than half the available body surface, received 54% of the total number of sniffs.

The ratio of the frequency to the total duration of sniffiing for any given target varied considerably (Figure 36). Ratios of $\leq 1{:}1.5$ 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 fre-

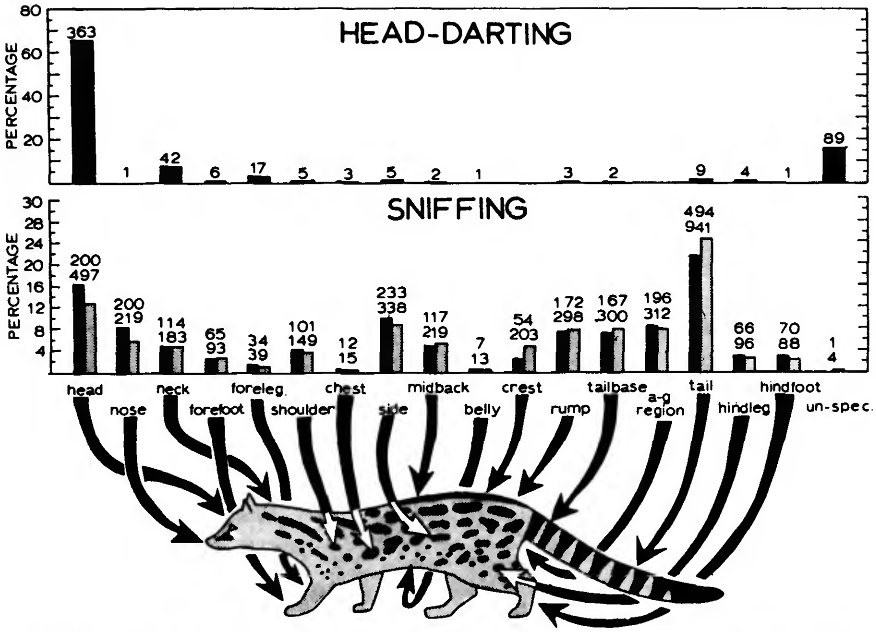


FIGURE 36.—Body targets of head-darting and sniffing in the genet (numerals above bars in head-darting graph and top numerals above bars in sniffing graph = number of observations for that target; bottom numerals above bars in sniffing graph = total duration in seconds of sniffing directed to each target; solid bars = frequency percentages based on total number of all observations for specified and unspecified targets; shaded bars = duration percentages based on total duration of sniffing directed to all specified and unspecified targets).

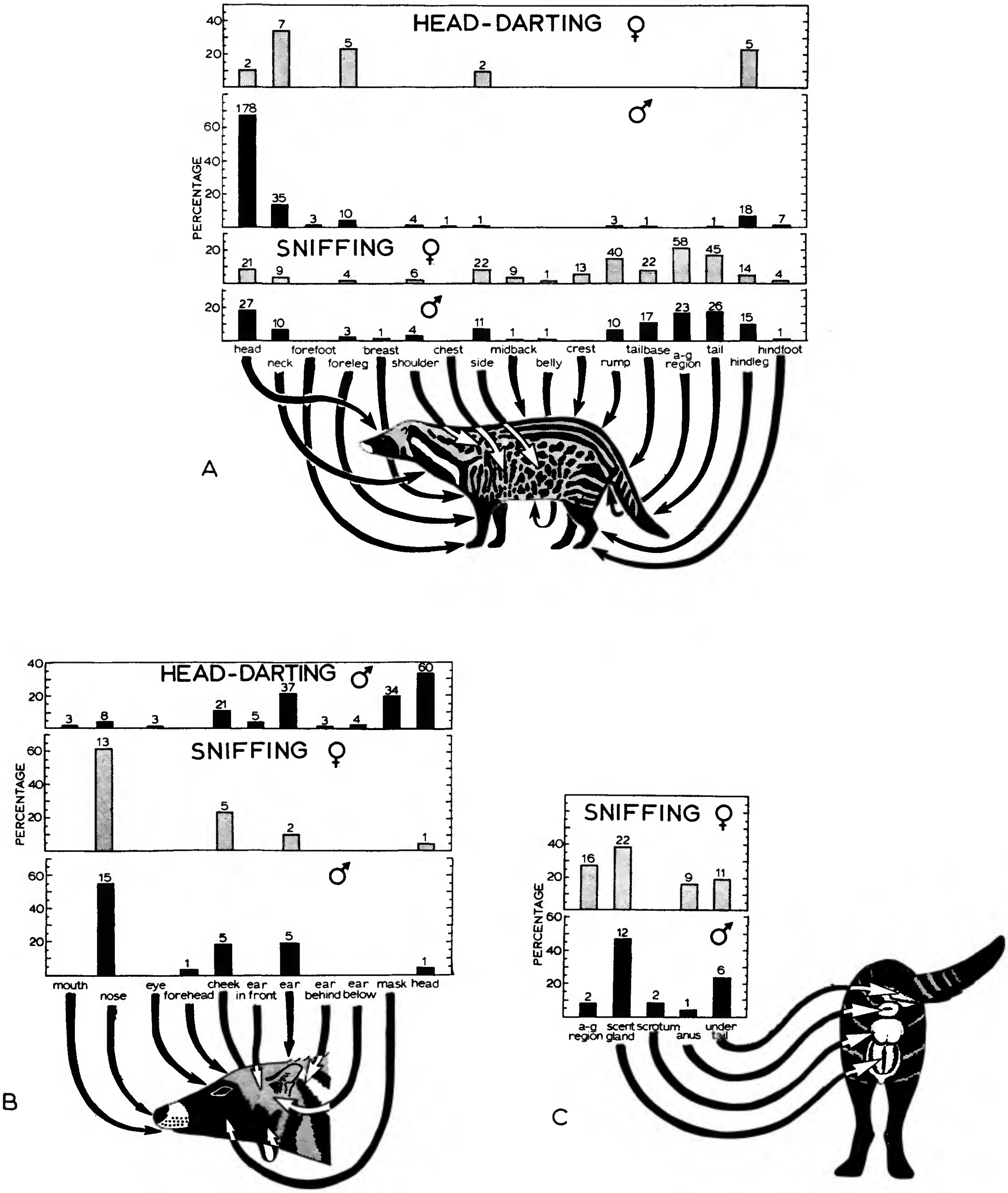
quency:duration ratios of 1:1.5–1.9. The spinal crest had the exceptional ratio of 1:3.75. This clearly demonstrates that duration and frequency of contact are not equally proportional for all targets. Frequently sniffed targets such as the head were sniffed briefly (frequency:duration = 1:1.3), while relatively long periods were devoted to infrequently sniffed targets such as the spinal crest (frequency: duration = 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 vast majority of the time the companion's head was the head-darting target; the neck, forelegs, and tail were struck at less frequently. Other body areas were infrequent targets (Figure 36).

BODY TARGETS IN *Civettictis*.—An interesting comparison with *Genetta* is presented by this species. While the head, neck, and sides were the most commonly sniffed anterior regions, in the pair of *Civettictis* the majority of sniffing was directed to posterior body targets. The female directed 60% of all nasal contacts to the male's hindquarters, while the male addressed 65% to this area of the female's body (Figure 37).

In a number of instances it was possible to determine the precise orientation of sniffs to specific body

FIGURE 37.—Body targets of head-darting and sniffing in the female and male of *Civettictis* (each category exclusive of others): A, general body targets of head-darting and sniffing in the male and female; B, specific targets of head-darting and sniffing on the head of the male and female; C, specific targets of sniffing on the anogenital region of the male and female (female not shown here to conserve space; because body targets were not always noted specifically during an encounter, general targets such as head and anogenital region have been duplicated in B and C, e.g., the undertail category of C was included as part of the anogenital category in A; numerals accompanying each segment of the graph represent the number of observed instances from which the percentages are calculated).



HEAD-DARTING ♀
40
20
2
7
5
2
5
♂
PERCENTAGE
60
40
20
178
35
3
10
4
1
1
3
1
1
18
7
SNIFFING ♀
20
21
9
4
6
22
9
1
13
40
22
58
45
14
4
♂
20
27
10
3
1
4
11
1
1
10
17
23
26
15
1
head
neck
forefoot
foreleg
breast
shoulder
chest
side
midback
belly
crest
rump
tailbase
a-g region
tail
hindleg
hindfoot
A
HEAD-DARTING ♂
40
20
3
8
3
21
5
37
3
4
34
60
SNIFFING ♀
PERCENTAGE
60
40
20
13
5
2
1
♂
60
40
20
15
1
5
5
1
mouth
nose
eye
forehead
cheek
ear in front
ear
ear behind
ear below
mask
head
B
SNIFFING ♀
PERCENTAGE
40
20
16
22
9
11
♂
60
40
20
2
12
2
1
6
a-g region
scent gland
scrotum
anus
under tail
C

parts (Figure 37B,C). Based on a limited number of observations, the nose, cheek, and ear received the majority of nasal contacts to the head. Sniffing targets of the hindquarters differed only slightly between the two subjects. Targets in this area on the female can be ranked in decreasing frequency from scent-gland, under-tail, to anus. On the male's body, the order of the first two 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 areas were also struck in the genets, the relative proportion of darts to them was less, particularly in the case of the hindleg (Figure 36). There is an obvious difference in targets between animals. The male darted primarily at the neck, foreleg, and hindleg (totaling 80% of 21 darts), and the head and side were infrequently struck. The female directed over 65% of 262 darts to the male's head and struck at the neck less than 15% of the time. The neck, hindleg, and foreleg were the next most common targets (Figure 37A). Thirty percent of the male's darts directed to the head struck the ear region, while the mask and cheek were less common targets.

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 male and female). In *Genetta* 33% of all sniffs to the tail were directed to the base while in the civets 54% of all such sniffs were aimed at the base (male = 48%, female = 65%). Thus in *Civettictis* the proximal portion of the tail and the anogenital region seem to be more preferred or accessible targets for sniffing. From the standpoint of hair patterning these areas are quite distinctive (Figure 37C). The scent gland is a visually and physically prominent attribute comparable in its alternating pattern of white and black to the sides of the neck. The tail of *Civettictis* differs from *Genetta* in that most of the white hairs are concentrated on the sides and ventral 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.

Interaction through Sniffing and Head-darting: the Sniff-Dart Axis

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's sniffing or attempting to sniff its companion's body.

ROLES OF "SNIFFERS" AND "DARTERS".—Table 12 reveals that if a series of encounters is considered the animal with the highest sniffing score may or may not have the highest darting score. The meaning of these summated values, though, is difficult to interpret because the relationship between two 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 six animals exhibited statistically significant differences (Appendix 4). Animal K, for example, darted significantly less frequently than his companions when he dominated sniffing ($P < 0.005$). Animal C also darted less during encounters with F ($P < .05$). There was no significant difference in her darting frequency, however, 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 ($P = 0.025$). The remaining three 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 Mo the level of darting bore no consistent relationship to frequency of sniffing. Similar results were found in the two African civets. The male, who dominated sniffing in eight of nine encounters, darted significantly less than the female ($P<0.01$, Appendix 5).

Appendix 6 records the darting scores of both animals in 21 encounters in which only one genet sniffed its companion. In 15 out of 21 cases the sniffer received darts but did not dart itself. In the remaining 6 encounters, both sniffer and nonsniffer darted and the nonsniffer predominated. There appears to be a tendency for the sniffer to refrain from darting, but this is not a statistically significant pattern ($P > 0.05$). On the other hand, of 68 encounters in which both animals sniffed, on only 10 occasions (14.7%) did the less sniffed animal refrain from darting. When the less 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 confines its activity to darting but does not smell back.

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. Also, 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 introduction of different companions, sniffing and head-darting targets were grouped into four 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 four 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 (Appendices 7 and 8).

Though the head and neck were the predominant targets, the absence of scores for the other regions resulted in rank ties that produced insignificant variance. The null hypothesis for sniffing was rejected at a probability of ≤ 0.017 for four of the six animals (K, C, I, and O). For head-darting only animals C and I deviated from a random variance ($P \leq 0.054$). These results indicate that though most animals darted and sniffed more often at certain regions than others, the relative frequencies to these regions were not necessarily consistent with different companions. Thus, while almost all animals exhibited disproportionate contact distributions to their companion's body regions only two of the six animals were inconsistent in the way they sniffed their companions, and only two were consistent in head-darting at their companions.

SNIFF-DART RATIO AND TARGET SELECTION.—Tables 17 and 18 summarize the relationship of head-darting to sniffing and sniffing targets in *Genetta* and *Civettictis*. The frequencies of these two 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 higher rates shown by the genets. The overall darting rate in the female civet was two times greater than the highest rate displayed by a genet; the male displayed a darting rate comparable to the lower 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 is not correlated with any fluctuation in 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), the predominance of tail and hindbody sniffing appeared to be a strategy permitting maximum olfactory sampling at a minimum risk of sustaining a dart.

To test this hypothesis, the body was divided into three sections that maximally reflected the longitudinal polarity of sniffing distribution (Tables 17 and 18) and the frequency distribution of sniffs to these three body parts was tested for low and high sniff:dart ratio encounters with the Friedman two-way analysis of variance (Appendices 9 and 10). In genets exhibiting sniff-dart ratios $\leq 1:0.5$, there was a highly significant variance of the sniff distribution to the three regions ($P < 0.001$). When the same genets had sniff:dart ratios $\geq 1:0.33$, 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, low 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 although 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

TABLE 17.—Relationship of sniffing to head-darting frequency and to sniffing body targets (percentage in parentheses) in *Genetta tigrina*

Animal Pair		Sniff		Head-dart		Sniff:Dart ratio[1]	Sniffing Body Targets[2]			Total duration of encounters per pair (hr:min:sec)
		Total	per 10 min.	Total	per 10 min.		Forebody	Midbody	Hindbody	
1	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)	
2	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)	
3	Mo ♀..	238	7.7	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)	
4	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)	
5	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)	
6	C ♀..	58	1.4	17	0.4	1:0.36	15 (25.9)	9 (15.5)	34 (58.6)	6:41:20
	Mo ♀..	64	1.5	21	0.5	1:0.26	25 (39.1)	6 (9.4)	33 (51.6)	
7	C ♀..	79	2.4	0	--	1:0.72	6 (7.6)	9 (11.4)	64 (81.8)	5:29:40
	F ♂..	1	0.3	57	1.7	----	0 --	1 --	0 --	
8	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)	
9	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)	
10	I ♀..	8	0.2	4	0.9	1:0.87	6 (75.0)	2 (15.0)	0 --	6:45:39
	Mo ♀..	30	0.7	7	0.2	1:0.13	5 (16.6)	5 (16.6)	20 (66.6)	
11	I ♀..	2	<0.1	12	0.3	1:2.00	1 --	0 --	1 --	5:52:44
	F ♂..	1	<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 ≥30.

the three 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 (Appendix 10), the forebody ranked second highest in high ratio encounters and lowest in low ratio encounters. So while there was no difference in variance between the two 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.

DISCUSSION

Vocalizations among Viverrids

Table 11 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

TABLE 18.—Relationship of sniffing to head-darting frequency and to sniffing body targets (percentage in parentheses) in *Civettictis civetta*

Encounter and animal	Sniff		Head-dart		Sniff:Dart ratio[1]	Sniffing Targets[2]			Duration (Min:sec)
	Total	per 10 min.	Total	per 10 min.		Forebody	Midbody	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	1 --	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[3] ♂	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). Percentages calculated only when sniffing frequency $\geq$ 30.

[3] Entries in columns 2 and 4 are means.

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

Hooting and neighing are unique to the two palm civets (*Nandinia* and *Paguma*) and no repetitive sound having equivalent intensity has been heard in any other species. Eisenberg (pers. comm.) heard a whinnying call in wild Ceylonese *Paradoxurus* that approximates my description of neighing in *Paguma.* All three 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 three species of palm civets also have perineal scent glands, an examination of animals and museum specimens indicated low secretory rates of relatively weak scents. If it is assumed that the paradoxurines evolved from semiarboreal 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 broadcast over long distances, its transmission is dependent on and enhanced by air current, and it is doubtful that all parts of civets' living volume are equally accessible for scent 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 make a small, ground-living species more vulnerable 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 two-dimensional than three 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, and the interval distribution is 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 three 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. In mother-infant associations, however, 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. Although responsiveness to the call does not disappear, Ewer noted that it gradually becomes more and more conditional upon other factors in the situation (Ewer and Wemmer, 1974).

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 that elicit this call. When an animal is sufficiently aroused, the coughing may be spontaneous and bear no clear relationship to ongoing activities. Prior to copulation, for example, male genets coughed repeatedly while following the female.

Coughing in volleys probably arises 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 expulsion of volleys of coughs during expiration in *Civettictis* could have arisen from the doublet and triplet condition seen 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, 1971). It is probable that the call arose independently in this species. Curiously, like *Civettictis, Fossa* is strictly a ground-living species.

Nonvocal Interaction in Genetta *and* Civettictis

A large number of behavior patterns are shared by both *Genetta* and *Civettictis;* a small number 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 unidirectional 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, sniffing may be unidirectional or reciprocal; sniffing and head-darting are frequently distinct roles, 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 consists 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 additional 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) or scruff-shoulder orientation (Fox, 1971). In the golden jackal, for example, 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 (1967:324) 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 the 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 *Genetta* and *Civettictis* 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 two 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 deduced 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 visible only during crest erection and the white perineal gland is often concealed by the tail; only the gland receives oriented contact. Neither marking's configuration 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 different 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 for 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 numbered for convenience, but the separation does not imply a lack of causal relationship between them.

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

2. 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.

3. Origin of lateral body orientation with 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.

4. 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 terrestial 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 facilitates transition from sniffing and darting to maximal contact interaction.

Addendum

Shortly after this manuscript was revised for publication two important papers appeared dealing with the natural history and behavior of the small-spotted genet, *Genetta genetta*, in Europe. They are B. Gangloff and P. Ropartz, Le Repertoire Comportemental de la Genetta, *Genetta genetta* (Linné), *La Terre et la Vie* (1972) 26(4):489–560; and M. Delibes, Sobre Alimentacion y Biologia de la Geneta (*Genetta genetta* L.) en España, *Doñana, Acta Vertebrata* (1974) 1:143–199.

Gangloff and Ropartz' study is a lengthy description of the social, nonsocial, and predatory behavior of captive animals. It is evident that the social behavior of this species is qualitatively similar or identical to that of *Genetta tigrina;* however, quantitative data on social interaction are not presented on which to base further comparisons. Delibes' analysis of feeding habits reveals the preponderance of small vertebrates and insects in this species' diet. This is the only large contribution available on this aspect of genet ecology.

Appendices

ENCOUNTER SCHEDULES AND STATISTICAL PROCEDURES

Appendix 1: Encounter Schedules for *Genetta tigrina*

Encounter number	*Date*	*First animal introduced*	*Duration in cage prior to encounter (hrs:min)*	*Second animal introduced*	*Encounter duration (min:sec)*
		Male-Male Encounters: F and O			
1	6 Sep 69	F	3:30	1900	52:53
2	8 Sep 69	O	3:50	1940	45:47
3	10 Sep 69	F	3:50	1915	31:24
4	12 Sep 69	O	4:10	1910	34:20
5	14 Sep 69	F	3:45	1645	34:09
6	16 Sep 69	O	3:25	1630	33:35
7	18 Sep 69	F	4:00	2010	40:24
8	20 Sep 69	O	4:15	1935	46:10
9	22 Sep 69	F	4:10	1945	31:39
10	24 Sep 69	O	4:20	1930	33:45
		Female-Female Encounters: C and I (familiar)			
1	20 Jun 69	I	4:15	2030	30:58
2	9 Jul 69	I	—	1900	33:44
3	17 Jul 69	I	3:50	2010	32:56
4	25 Jul 69	C	3:45	1930	32:22
5	31 Jul 69	C	2:45	1900	32:55
6	7 Aug 69	I	3:40	2040	33:11
7	15 Aug 69	I	2:05	2000	31:19
		Female-Female Encounters: C and Mo			
1	18 Aug 69	C	4:30	2130	34:57
2	20 Aug 69	Mo	3:15	1945	40:50
3	22 Aug 69	C	1:15	1630	36:31
4	24 Aug 69	Mo	2:30	1845	33:34
5	26 Aug 69	C	4:47	1855	34:45
6	28 Aug 69	Mo	2:45	1930	49:22
7	30 Aug 69	C	3:12	1930	46:15
8	1 Sep 69	Mo	4:05	2000	35:55
9	3 Sep 69	C	3:50	1910	39:01
10	5 Sep 69	Mo	4:50	2020	50:10
		Female-Female Encounters: I and Mo			
1	25 Sep 69	Mo	3:20	1950	35:25
2	27 Sep 69	I	4:25	2050	37:17
3	28 Sep 69	Mo	3:00	1905	37:27
4	1 Oct 69	I	3:00	1900	41:01

Appendix 1—Continued

Encounter number	*Date*	*First animal introduced*	*Duration in cage prior to encounter (hrs:min)*	*Second animal introduced*	*Encounter duration (min:sec)*
5	3 Oct 69	Mo	3:35	1915	45:19
6	5 Oct 69	1	2:40	1930	39:42
7	7 Oct 69	Mo	3:00	1615	45:23
8	9 Oct 69	1	3:20	1940	48:38
9	11 Oct 69	Mo	3:30	1630	36:34
10	13 Oct 69	I	3:30	1930	38:53
MALE-FEMALE ENCOUNTERS: K AND MO					
1	9 Jun 69	Mo	4:00	2100	29:54
2	16 Jun 69	Mo	3:10	2010	30:06
3	23 Jun 69	K	3:30	2030	31:22
4	30 Jun 69	Mo	3:50	1620	36:16
5	7 Jul 69	K	3:45	1915	32:11
6	14 Jul 69	Mo	3:00	1930	33:06
7	21 Jul 69	Mo	2:25	1715	22:32
8	28 Jul 69	K	6:50	1630	27:04
9	4 Aug 69	Mo	2:15	1915	32:49
10	11 Aug 69	K	3:15	1930	33:19
MALE-FEMALE ENCOUNTERS: K AND C (familiar)					
1	14 Oct 69	K	3:00	1635	35:14
2	16 Oct 69	C	3:40	1940	35:44
3	18 Oct 69	K	3:40	2030	34:04
4	20 Oct 69	C	4:05	2050	36:21
5	22 Oct 69	K	3:05	1940	36:11
6	24 Oct 69	C	3:25	2040	35:31
7	26 Oct 69	K	3:30	2000	39:47
8	28 Oct 69	C	4:00	2000	34:24
9	30 Oct 69	K	3:20	1940	33:44
10	1 Nov 69	C	4:05	2010	31:57
MALE-FEMALE ENCOUNTERS: F AND 1					
1	2 Nov 69	F	3:45	1925	39:10
2	4 Nov 69	I	2:50	1620	33:32
3	6 Nov 69	F	6:20	1950	36:36
4	8 Nov 69	I	3:00	1615	31:16
5	10 Nov 69	F	3:15	1645	33:06
6	12 Nov 69	I	3:22	1652	39:48
7	14 Nov 69	F	3:50	1940	34:14
8	16 Nov 69	I	3:25	1655	33:14
9	18 Nov 69	F	5:05	2030	38:38
10	20 Nov 69	I	4:30	2100	33:10
MALE-FEMALE ENCOUNTERS: O AND C					
1	21 Nov 69	O	3:00	1850	39:32
2	23 Nov 69	C	2:55	1625	36:39
3	25 Nov 69	O	2:55	1840	34:55
4	27 Nov 69	C	4:10	1740	31:39
5	29 Nov 69	O	3:48	1658	30:23
6	1 Dec 69	C	3:00	1920	33:56

7	3 Dec 69	O	3:55	2015	28:11
8	5 Dec 69	C	4:00	1930	32:18
9	7 Dec 69	O	3:00	1630	35:24
10	9 Dec 69	C	4:20	2020	31:19

MALE-FEMALE ENCOUNTER: F AND Mo

1	11 Dec 69	F	3:00	1600	11:40

MALE-FEMALE ENCOUNTERS: O AND I

1	30 Dec 69	O	3:30	1930	32:14
2	1 Jan 70	I	3:20	1905	34:44
3	3 Jan 70	O	3:35	1935	52:50
4	5 Jan 70	I	4:05	2040	32:54
5	7 Jan 70	O	3:50	1950	35:08
6	9 Jan 70	I	4:50	2050	33:16
7	11 Jan 70	O	2:40	1940	33:01
8	13 Jan 70	I	3:40	1940	34:16
9	15 Jan 70	O	3:00	1900	32:43
10	17 Jan 70	I	3:10	1610	32:56

MALE-FEMALE ENCOUNTERS: F AND C

1	18 Jan 70	F	3:30	1915	32:11
2	20 Jan 70	C	2:20	1845	32:58
3	22 Jan 70	F	3:05	1930	35:40
4	24 Jan 70	C	3:20	1650	34:42
5	26 Jan 70	F	3:15	1845	29:45
6	28 Jan 70	C	4:10	2010	32:27
7	30 Jan 70	F	3:00	1845	28:20
8	1 Feb 70	C	4:25	2020	33:35
9	3 Feb 70	F	4:15	2015	36:03
10	5 Feb 70	C	4:05	2000	33:59

MALE-FEMALE ENCOUNTERS: K AND I (familiar)

1	6 Feb 70	K	3:00	1945	32:57
2	8 Feb 70	I	3:30	2000	27:21
3	10 Feb 70	K	4:15	2015	30:32
4	12 Feb 70	I	3:20	1640	29:42
5	16 Feb 70	K	4:00	2000	35:20
6	18 Feb 70	I	3:30	2000	33:30
7	20 Feb 70	K	4:00	2000	33:27
8	22 Feb 70	I	3:45	1845	36:27
9	26 Feb 70	K	3:30	1630	29:56
10	2 Mar 70	I	3:00	1900	29:12

Appendix 2: Encounter Schedules for *Civettictis civetta* (male-female encounters)

Encounter number	*Date*	*Encounter onset time*	*Encounter duration (min:sec)*
1	2 Nov 70	1500	44:00
2	3 Nov 70	1530	34:39
3	4 Nov 70	1445	53:54
4	5 Nov 70	1500	59:24

Appendix 2—Continued

Encounter number	*Date*	*Encounter onset time*	*Encounter duration (min:sec)*
5	9 Nov 70	1530	36:30
6	10 Nov 70	1515	33:15
7	12 Nov 70	1500	38:30
8	13 Nov 70	1500	48:24
9	16 Nov 70	1530	40:25

Appendix 3: Statistical Procedures for Tail-flaring Frequency in *Genetta tigrina*

Wilcoxon matched-pairs, signed-ranks test; N = number of series 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): 0.05

Jaw-gaper		*Companion*		*d*	*Rank*	*Statistics*
K	7	C	13	−6	−4.0	
Mo	5	K	19	−14	−8.0	
I	20	Mo	27	−7	−5.5	
C	22	Mo	23	−1	−1.5	
I	2	O	11	−9	−7.0	N = 8
F	1	C	8	−7	−5.5	T = 4.5
I	3	F	1	+2	+3.0	P = >0.05
I	2	K	1	+1	+1.5	

Appendix 4: Statistical Procedures for Head-darting Frequency in *Genetta tigrina* (between Sniffers)

Wilcoxon matched-pairs, signed-ranks test; N = number of single encounters in which (1) each animal sniffed its companion, and (2) at least one animal head-darted; sniffer = animal that sniffed more frequently than its companion; variable: head-dart frequency; significance level: 0.05

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	Mo	4	−4	−5.5	N = 9
	0		1	−1	−1	T = O
	2		5	−3	−3	P = <0.005
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	Mo	8	−8	−10.5	
	0		2	−2	−4	
	8		4	+4	+6	

Sniffer		*Sniffed*		*d*	*Rank*	*Statistics*
	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 = >0.05 (n.s.)
C	0	F	7	−7	−4	
	0		6	−6	−3	
	0		9	−9	−5	
	0		11	−11	−6	
	0		1	−1	−1	N = 7
	0		14	−14	−7	T = O
	0		5	−5	−2	P = 0.05
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	Mo	3	−3	−5.5	N = 9
	3	C	0	+3	+5.5	T = 17.5
	0		37	−37	+9.0	P = >0.05 (n.s.)
Mo	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 = >0.05 (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 = 0.025
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 = >0.05 (n.s.)

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

Appendix 5: Statistical Procedures for Head-darting Frequency in *Civettictis civetta*

Wilcoxon matched-pairs, signed-ranks test; N = number of encounters; variable: head-dart frequency; significance level: 0.025

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 = <0.01 >0.005

Appendix 6: Statistical Procedures for Head-darting Frequency in *Genetta tigrina* (between Sniffers and Nonsniffers)

Wilcoxon matched-pairs, signed-ranks test; N = number of single encounters in which only one animal sniffed its companion, and at least one head-darted; variable: head-dart frequency; significance level: 0.05

Encounter number	*Nonsniffer*		*Sniffer*		*d*	*R'*	*R"*	*Statistics*
1	I	1	F	0	+1	+2.0	+3.5	
8	I	1	Mo	0	+1	+2.0	+3.5	
10		1		0	+1	+2.0	+3.5	
4	C	2	Mo	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	−4	−5	−12.0	
4		0		2	−2	−2	−8.5	
5		2		9	−7	−6	−17.5	
6		1		5	−4	−3	−12.0	N = 21
8		1		0	+1	+1	+3.5	T = 68.0
10		1		6	−5	−4	−14.5	P = >0.05

Appendix 7: Statistical Procedures for Testing Distribution of Nasal Contacts to Four Body Regions in *Genetta tigrina*

Friedman two-way analysis of variance; conditions = 4 general body targets (I = head and neck, II = trunk, III = legs, IV = tail); variable: nasal contact frequency; significance level: 0.05

Animals encountered	Conditions I N	I Rank	II N	II Rank	III N	III Rank	IV N	IV 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	
Mo	47	2.0	79	3.0	9	1.0	82	4.0	$Xr^2 = 8.2$
		6.0		10.0		3.0		11.0	P = 0.017
Individual C									
K	44	2.0	52	3.0	27	1.0	97	4.0	
Mo	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	$Xr^2 = 6.6$
		13.0		16.0		5.5		15.0	P = <0.01
Individual I									
Mo	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	$Xr^2 = 11.7$
		13.0		13.0		5.5		10.5	P = <0.001
Individual Mo									
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	$Xr^2 = 6.3$
		11.0		10.0		5.0		14.0	P = 0.094
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	$Xr^2 = 8.4$
		7.0		7.0		5.0		12.0	P = <0.017
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	
Mo	1	4.0	0	2.0	0	2.0	0	2.0	$Xr^2 = 1.5$
		11.0		12.0		8.0		9.0	P = 0.754

Appendix 8: Statistical Procedures for Testing the Distribution of Head-darting to Four Body Regions in *Genetta tigrina*

Friedman two-way analysis of variance; conditions = 4 general body targets (I = head and neck, II = trunk, III = legs, IV = tail); variable: head-darting frequency; significance level: 0.05

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	
Mo	6	4.0	0	1.0	1	2.5	1	2.5	$Xr^2 = 6.6$
		12.0		4.0		7.0		7.0	P = 0.075

Appendix 8—Continued

Animals encountered	*Conditions*								*Statistics*
	I		*II*		*III*		*IV*		
	N	*Rank*	*N*	*Rank*	*N*	*Rank*	*N*	*Rank*	
Individual C									
K	135	4.0	12	3.0	9	2.0	3	1.0	
Mo	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 = 0.033
Individual I									
Mo	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 = 0.054
Individual Mo									
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 = <0.148
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 = 0.148
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 = 0.175

Appendix 9: Statistical Procedures for Testing the Distribution of Nasal Contacts to Three Body Regions in *Genetta tigrina*

Friedman two-way analysis of variance; conditions = 3 general body targets (1 = forebody, II = midbody, III = hindbody); first test: encounter series in which the sniff-dart ratio was ≤ 1:0.5, second test: ≥ 1:0.36; variable: nasal contact frequency, significance level: 0.05

Animal and companion		*Conditions*						*Statistics*
		I		*II*		*III*		
		N	*Rank*	*N*	*Rank*	*N*	*Rank*	
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	(Mo)	47	2.0	44	1.0	126	3.0	
Mo	(K)	54	2.0	52	1.0	132	3.0	
Mo	(I)	5	1.5	5	1.5	20	3.0	
C	(Mo)	15	2.0	9	1.0	34	3.0	
Mo	(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	≤ 1:0.5
F	(O)	129	2.0	149	3.0	122	3.0	$X_r^2 = 19.1$
			19.0		21.0		34.0	P = <0.001

K	(C)	24	1.0	50	2.0	86	3.0	
I	(Mo)	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	≥ 1:0.36
I	(F)	1	2.5	0	1.0	1	2.5	$X_r^2 = 2.3$
			14.0		14.5		19.5	P = <0.30 (n.s.)

Appendix 10: Statistical Procedures for Testing the Distribution of Nasal Contacts to Three Body Regions in *Civettictis civetta*

Friedman two-way analysis of variance; conditions = 3 general body targets (I = forebody, II = midbody, III = hindbody); first test: encounter series in which the sniff-dart ratio was ≤ 1:0.5, second test: ≥ 1:0.33; variable: nasal contact frequency; significance level: 0.05

Encounter and animal		*Conditions*						
		I		*II*		*III*		
		N	*Rank*	*N*	*Rank*	*N*	*Rank*	*Statistics*
2	♂	1	1.0	10	2.0	34	3.0	
2	♀	0	1.0	3	2.0	17	3.0	
3	♂	0	1.0	7	2.0	11	3.0	
4	♂	0	1.0	2	2.0	6	3.0	
4	♀	0	1.5	0	1.5	3	3.0	
5	♂	6	2.0	5	1.0	12	3.0	
6	♂	2	2.0	1	1.0	11	3.0	
6	♀	2	3.0	0	1.0	1	2.0	
7	♂	2	1.0	11	2.0	32	3.0	≤ 1:0.5
8	♂	0	1.0	1	2.0	15	3.0	df = 2
9	♂	1	3.0	0	1.5	0	1.5	$X_r^2 = 9.8$
			17.5		18.0		30.5	P = <0.01
1	♂	18	1.5	18	1.5	62	3.0	
1	♀	19	2.0	15	1.0	29	3.0	
3	♀	0	1.5	0	1.5	1	3.0	≥ 1:0.33
5	♀	11	3.0	1	1.0	8	2.0	df = 2
7	♀	3	2.0	1	1.0	17	3.0	$X_r^2 = 6.4$
			10.0		6.0		14.0	P = <0.05

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