Z. Tierpsychol., 34, 359—394 (1974)

ISSN 0044-3573 / ASTM-Coden: ZETIAG

Department of Zoology, University of Ghana, and National Zoological Park, Washington, D.C.

The Behaviour in Captivity of the African Civet, *Civettictis civetta* (Schreber)

By R. F. Ewer and C. Wemmer

With 9 figures

Received 20. 12. 1972

1. Introduction

The African civet, *Civettictis civetta,* is the largest of the African viverrids: the head and body length of an adult ♂ may be as much as 80 cm, with a tail not quite as long as the body, but the ♀ is distinctly smaller. The species is widely distributed through both forest and savanna regions, wherever long grass or thickets are sufficient to provide daytime refuges, from the southern fringes of the Sahara southwards to northern Zululand, Botswana and northern South West Africa. Nevertheless, the civet's solitary, nocturnal habits and its timidity make observations in the wild difficult and little is known of its behaviour.

The present observations were made on one pair of animals obtained as juveniles from Jersey Zoo, kept at the National Zoological Park, Washington (♂ W and ♀ W), another pair kept at the University of Ghana (♂ G and ♀ G), which were captured from the wild when they were judged to be about 12 days old and on the subsequent progeny of the latter pair. The Washington animals were housed in adjoining cages 6 × 12 ft (approximately 1.8 × 3.6 m), separated by a sliding door so that they could be allowed together or kept separate as desired. The Ghana animals were at first kept indoors in a laboratory and as their locomotory powers developed a gangplank was provided giving them access to a window bench, previously wired off as a cage for rats. A little later an outlet was made from this bench cage to an outdoor enclosure measuring approximately 6 × 7 m, of which the inner 2.3 m was formed by a covered veranda. The rest of the enclosure contained grass and a few shrubs and creepers. A sleeping box was provided on the veranda and another in the open part of the enclosure: the former was rarely used and the civets preferred to sleep in the latter. After the birth of the first litter, a second similar enclosure was added alongside the first, access from one to the other being by a doorway on the veranda. At first the animals were free to continue using the laboratory but ultimately they acquired the ability to jump from the floor to the benches (78 cm high) and their destructive habits necessitated restricting them to the outdoor enclosures and the window bench cage in the laboratory.

Civets do not possess highly sectorial carnassial teeth and are known to be omnivorous, eating fruit and carrion as well as a wide variety of small vertebrate and invertebrate prey. The basic diet of the Washington animals consisted of daily horsemeat with an added vitamin supplement, rats and mice twice weekly and fish now and then. Bananas and oranges were given several times a week and apples, pears, grapes, melons and strawberries when in season. The diet of the Ghana animals comprised fruit (mainly bananas and paw-paw), meat and fish and a milk and cereal mixture with added vitamin supplement. This was varied by the addition of small vertebrates and insects as available and eggs were given once a week either scrambled or mixed in the milk. The animals were fed at about 17.00 hrs, but when the ♀ was lactating she was often given extra milk in the morning. Boiled rice with added fat or gravy and any type of sweet cake were much relished occasional delicacies but chocolate was refused. Grass was frequently eaten in considerable quantities but, was not chewed effectively and appeared in the faeces virtually unaltered. The animals' own hair in the droppings tended to be concentrated together with the grass, which suggests that the main function of grass eating may be to prevent the formation of hair balls in the stomach.

2. Colour Patterning

The civet's colour patterning is highly distinctive and a number of features are of interest in relation to the animal's behaviour.

(i) General body pattering. There is considerable individual variation in colouring (Allen 1924): the Ghana animals came from a cocoa farming area where the natural vegetation is moist semi-deciduous woodland and are much lighter in colour, with more grey and less black spotting on the body than the Washington animals which are descended from a stock obtained from Sierra Leone. In the former, the forequarters are predominantly grey and the spotting is very obscure, becoming strongly marked only from behind the shoulders back. They in fact look as though an artist had finally made up his mind to provide a spotted coat only after the forequarters had been completed (Fig. 1 a). The young showed the same general patterning but there was some variation, some being rather paler than others. The result of the irregular patterning

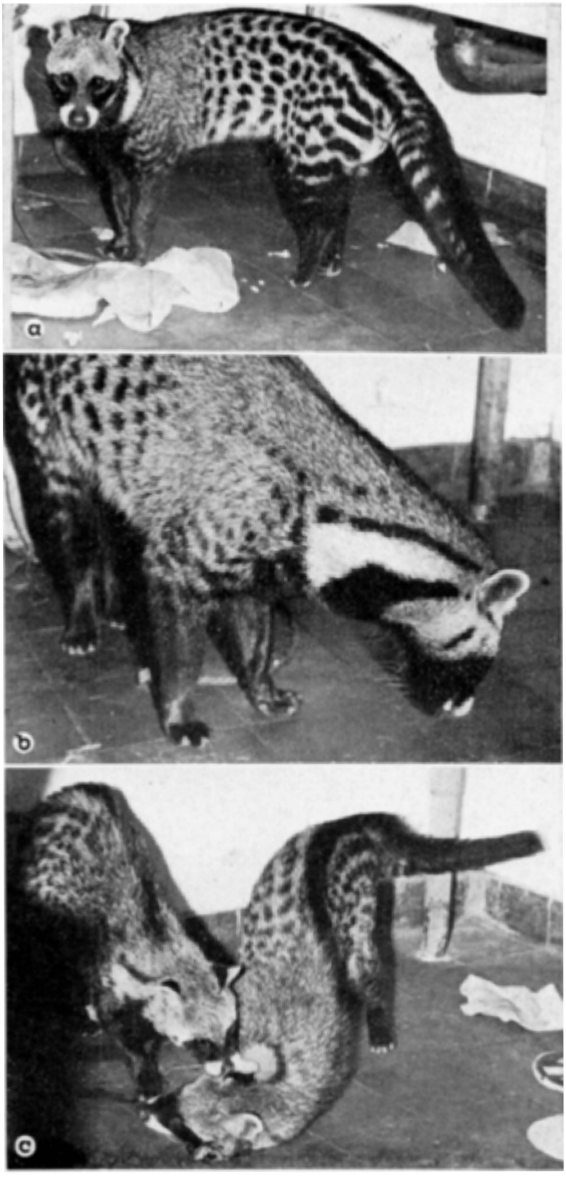

Fig. 1: (a) ♂ G, showing details of colour patterning. (b) The same animal, showing the neck stripe. (c) ♂ G scent-rubbing on a piece of food while ♀ G snaps at his neck stripe

is extremely cryptic even in relatively open terrain. The eye does not register an outline corresponding to "spotty animal" and, despite the fact that grass is green and brown and the civet grey and black, the animal shown in Fig. 1 can become virtually invisible in a clump of grass. Certainly one could pass within a metre or two and fail to notice him. In the Washington animals the black spotting is more intense and the spots have fused to form diagonal stripes on the shoulders and flanks and are almost rosette-like on the sides (Fig. 2 a).

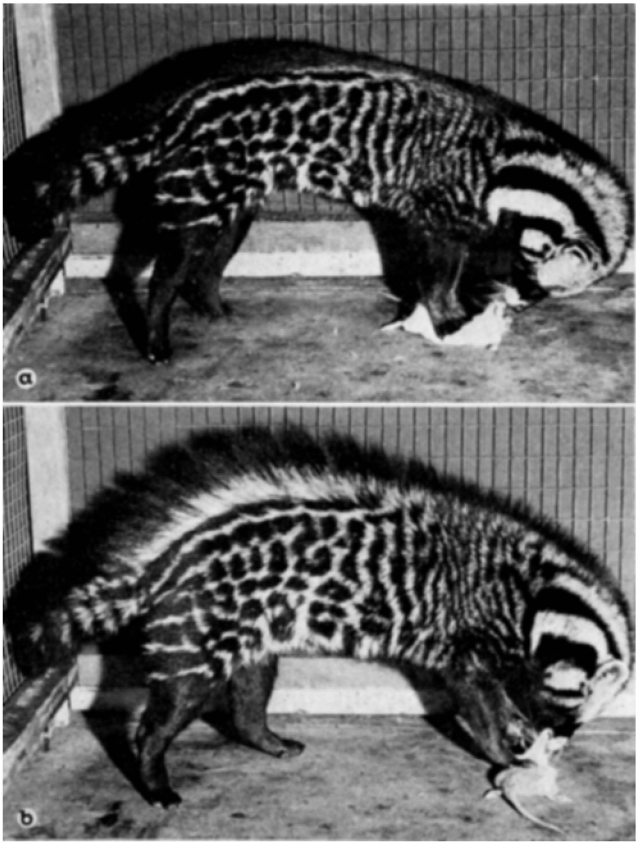

Fig. 2: ♂ W eating a rat (a) without and (b) with erection of the dorsal crest

(ii) The neck stripe (Fig. 1 b, c). This consists of a band of white, sloping back from behind the ear to the front of the shoulder, accentuated by black borders above and below. Civets are not social animals: even between juveniles playful fighting tends to go over into earnest rather easily and the preliminaries to mating frequently include aggressive snapping by both sexes. Such attacks, however, are highly stylised; bites are generally partly inhibited and are directed predominantly at the side of the neck. Often the two thrust and lunge with their noses at each other, each seeking to launch a bite at the other's neck. Such "neck fencing" is particularly characteristic of juvenile squabbles which have started as play. It therefore seems likely that the neck stripe acts as a bite director, ensuring that attacks are focussed on an area where little damage will be done, even if the bite is a genuine one and not a mere token.

It is not known whether the skin is particularly thick in the region of the neck stripe. Functions of this type, directing social responses to particular regions of the body, have previously been suggested both by KLEIMAN (1967) and by FOX (1969) for distinctive markings in other species of carnivore.

(iii) The ear spots (Fig. 1 c, 6 b). The upper and outer half of the posterior surface of the pinna is white, contrasting sharply with the black basal portion. It has been suggested that similar ear spots in the Felidae may serve to facilitate following of the mother by her young (SCHALLER 1967). It seems doubtful if the civet's ear spots could in fact be easily seen by young kittens: possibly, however, they may serve a similar function between adults, making it easier for sexual partners to keep track of each other during the prolonged locomotory activity which often precedes mating.

(iv) Facial markings. KLEIMAN (1967) has suggested that the dark facial markings in *Nyctereutes* and in *Otocyon* serve as signals directing social grooming. In the civets, however, allogrooming was directed mainly to the perineal region and the nape of the neck and they were never seen to groom each other's faces. The only social interaction in which the face mark may have played a role (see p. 387) seems quite inadequate to account for the evolution of such distinctive patterning. One can therefore only suggest that the white muzzle, which is certainly very visible in dim light, may serve as a species recognition mark in face to face encounters.

3. Special Senses

The sense of smell is extremely acute and clearly plays a very important part in the civet's life. General testing of the olfactory environment is a normal accompaniement of rousing up from rest: the animal stands with the neck extended, the head raised and the nose pointing upwards and moves the head gently up and down through a small arc, sniffing the while. The presence of an unfamiliar person is quickly detected by smell and food which is not moving is usually located by smell rather than by sight: even if, to the human eye, a piece of food is clearly visible, the civet will sniff about and move slowly towards the source of the smell. If a small piece of meat it concealed in a clump of grass a civet passing by will check abruptly, sniff and cast about until it finds the food. A cricket or grasshopper is similarly located and an unfamiliar object, if not very large, may also be first detected by smell. A number of other aspects of behaviour dealt with later also reflect the importance of olfactory stimuli in the civet's world.

Hearing is acute, particularly for high pitched sounds. The ability to distinguish sounds is also reasonably well developed, since ♂ G and ♀ G soon learnt to respond to their individual names.

The eyes possess a tapetum lucidum giving an extremely brilliant eye shine, with a pale orange tint. One would therefore expect vision to be of the normal nocturnal type, with high sensitivity but low acuity. The animals' general behaviour is in accord with this assumption. The animals move about at night in very dim light with complete assurance and movement is quickly noticed but, as already mentioned, sight is of little importance in locating food that neither moves nor emits any sound. In general, their behaviour suggests that scent and sound are more important than sight in alerting them to the presence of prey, which seems reasonable in a species that hunts by night and takes mainly small prey, easily concealed by vegetation.

4. Gaits, Postures and Expressive Movements

In captivity conditions, the main gaits used were the walk and the gallop. The walk varies from a relaxed leisurely progression to a surprisingly fast action at a speed equalling moderately energetic human walking. Particularly towards the beginning of one of the ♀'s periods of heat, ♂ G and ♀G would often walk to and fro in their enclosures for considerable periods of time. The gallop usually appeared as an escape response, if the animals were alarmed, and was also sometimes seen during sexual chasing. Civets can jump well and when galloping will bound over obstacles up to half a metre high without interrupting the gait. The trot was seen mainly as transitional between the walk and the gallop and, in the restricted cage conditions, did not appear as a gait of importance in its own right.

Civets are terrestrial animals and the compact, blunt-clawed, digitigrade feet are suited neither for climbing nor for digging. Although attempts are sometimes made to use the paws to scrape out an insect or a frog from a refuge on land or in water, these attempts are made only after efforts to reach the prey with the mouth have failed and they are soon abandoned if not immediately successful. ♂ G was never seen to climb but the lighter ♀ G and the juveniles would occasionally scramble up sloping branches in a manner suggesting that birds' nests in low bushes may now and then be rifled in this way. Climbing as escape behaviour is dealt with later (p. 385).

Civets are nocturnal and become active only towards dusk. The greater part of the day is spent resting in cover, but sunbasking is not uncommon in the morning or late afternoon. The usual sleeping posture is lying on the side, with the body either fully extended and the head resting on one cheek, or curled up, with the head near the base of the tail (Fig. 3 a). It is not uncommon for an animal resting on its side to roll over on its back and remain for a few moments lying thus, extremely relaxed with all the legs in the air but flexed at knee, elbow and wrist. Another posture commonly adopted when resting but not deeply asleep is to lie virtually symmetrically on the belly with the fore paws tucked neatly under the chest, the neck fully extended and the chin resting on the ground (Fig. 3 b).

Compared with cats and dogs, civets show a very restricted range of facial expressions. Although the ears may be directed forwards or rotated laterally in response to auditory stimuli, they cannot be folded back and their movements do not reflect the animal's mood. The lips too show restricted mobility and the degree to which the snout can be pulled back and the nose wrinkled is very slight. Narrowing of the eyes does make a noticeable change in expression but general body carriage reflects mood more obviously. When at ease and alert, the civet moves with the head held higher than the shoulders and the legs well extended. In anxiety or fear the head is lowered, the legs are flexed and the whole body sags. The eyes are narrowed and the erectile hair of the dorsal crest is more depressed than usual, giving a peculiar flat-topped look to the back. The general contour is long, low and flat or even slightly concave above and when the animal moves, it does so at a slow slinking walk. The same tendency to lower the body in anxiety is reflected in a very characteristic response to a slightly startling stimulus. The animal, previously standing erect, promptly lowers its hindquarters to a sitting posture, pauses for about two seconds, looking towards the source of stimulation and then lowers the head. Presumably in natural cover this gives concealment while the animal ascertains the location and extent of the potential danger. Another posture commonly adopted is the "indecision alert"

(Ewer 1968 a) in which the animal stands with one fore paw raised and looks towards whatever has attracted its attention.

Erection of the long hair of the dorsal crest and tail produce a most dramatic effect (Fig. 2). The crest is not present on the neck but from behind the shoulders back, the hair along the mid-dorsal line is considerably longer than elsewhere, reaching a length of up to 105 mm. When erected, it produces a knife-edge effect, the contour over the hindquarters is convex and the apparent dorso-ventral depth of the body is suddenly increased. The whole contour is the antithesis of that characteristic of pure anxiety or fear. Piloerection occurs mainly in defensive threat. The animal usually keeps the face directed towards the source of alarm but the body turned sideways; the change in size and contour produced by crest erection is therefore fully visible to the opponent.

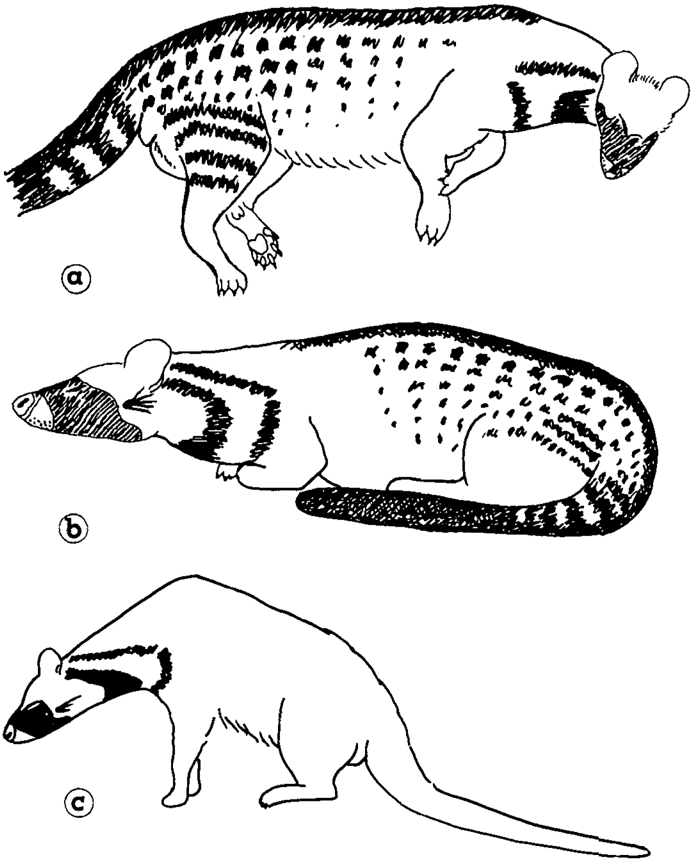

Fig. 3: Resting postures (a) lateral, (b) ventral. (c) A posture adopted by ♀ G in face of ♂ G, reflecting mixed motivations. The lowered hindquarters indicate anxiety or timidity but the high shoulders with head lowered and extended towards the ♂ reflect readiness to bite him. Sketches from life

This lateral orientation was very clearly shown in the following incident. The position of a nest box in the Washington animals' cage had been changed and ♂ W approached it cautiously, sniffed it and then seized it in his mouth and pulled it over. Both animals then fled to the opposite side of the cage and erected their crests maximally. ♀ W then turned broadside on to the box and walked briskly to and fro several times. After each turn she retraced her steps with extreme accuracy, maintaining a very uniform speed of progression as well as a uniform lateral orientation: finally she paused in the indecision alert posture and stared at the box. The whole procedure had such precision that she looked almost like a mechanical toy moving on a set of rails.

Defensive threat involves mixed motivation: a tendency to escape combined with readiness to attack if further molested. Piloerection is also a common accompaniment of attacks on prey with intimidatory qualities. There is, however, another context in which crest erection occurs, apparently as a result of a rather non-specific high level of general arousal, in which conflicting motivations are not easily discerned. If scent rubbing (vide infra) becomes very intense, it is accompanied by piloerection. Often this is followed by biting or worrying the object being rubbed, which may indicate some arousal of aggressive tendencies but nothing in the animal's behaviour suggests fear or anxiety. There are, however, some indications (mentioned later) that sexual tendencies may also be aroused.

One very distinctive movement which has clear signal value is the adoption of an appeasement posture. This consists of quickly lying down on the side, one shoulder being first lowered and the rest of the body following. Appeasement was frequently shown both by ♂ G to ♀ G and vice versa. Either the ventral or the dorsal surface of the body might be turned towards the partner but the dorsal presentation was more usual: out of 16 cases where the orientation was noted, only 4 were ventral. In a hostile encounter one animal might appease in response to a snap (or intention movement of snapping) from the other or the attacking animal might follow its snap by appeasement, as if to disarm any possible retaliation. Sometimes both attacker and attacked appeased simultaneously, which might then result in the rather ludicrous situation of the two lying symmetrically back to back, neither prepared to take the initiative and make the next move: indeed, they occasionally remained lying thus and relapsed into sleep after such an incident. Appeasement appeared to be extremely effective and an appeasing animal was never attacked. It should, however, be noted that this refers only to the context of minor hostilities between a familiar ♂ and ♀. Whether appeasement is used and, if so, how effective it is, in serious altercations between animals of the same sex is not known.

5. Vocalizations

Although rather silent animals in general, civets have several distinct vocal signals. Three of these are agonistic.

(i) The growl: a prolonged low rumbling growl. Growling by ♀ G in defence of her kittens frequently occurred if one approached the nest box in which she was lying with them. Only rarely did the adults growl at each other in defence of food, the usual response to an attempted theft being merely to try to keep the piece of food out of reach.

(ii) The cough-spit: an explosive spit at so low a pitch as to sound almost like a cough. This is the "last ditch" threat vocalization, normally heard when a terrified animal is approached. When the ♀ growls in defence of her young, she may follow this with a cough-spit, if one refuses to withdraw or if one makes a sudden movement. The Washington animals also gave the cough-spit when startled by sudden movements. It was then accompanied by jumping upwards, all four feet leaving the ground at once and the dorsal crest was maximally erected.

(iii) The scream: a screaming cry was given several times by ♀ W in the course of serious fights with ♂ W. What was probably a lower intensity version of the same vocalization was heard once only from the Ghana animals. The ♀

had become extremely hostile to the ♂ following the birth of her first litter and frequently chased him. During one particularly violent pursuit a strange cry, half yelp, half bark, was heard. The animals were out of sight at the time but the quality of the cry suggested panic rather than aggression and it seemed probable that it was given by the ♂.

During agonistic encounters another sound may be produced which, although not a vocalization, may have some communicatory value. When one animal snaps at another, the teeth meet with a loud click. An animal can thus be aware of being snapped at, even if he is not looking in the direction of his opponent.

There are three different types of mew or miau.

(i) The distress mew of a young kitten: a sound much like the corresponding call of a domestic kitten. The mother on numerous occasions was seen to respond to this call by going to the mewing kitten; frequently she would lick it briefly but she did not pick it up and carry it back to the nest box. On one occasion a kitten mewed while it was being measured. The mother, who had watched the process up to that point without signs of alarm, promptly growled and cough-spat. Spectrographic analysis showed that in a 19 day old kitten the mew lasts just under 300 msec and consists of three parts. An initial note at a frequency of 2 kHz is followed after a brief pause by one falling in pitch from 1.5 to just over 1 kHz. This goes over without a pause into a slightly wavering note at approximately 1 kHz. The initial and final notes last about 70 msec, the middle one twice as long.

(ii) The cat-like miau: made by the ♀ during copulation and followed by moving forward as though trying to get free of the ♂.

(iii) The ♀ sex call: as one of her heats approached, ♀ G moved about more than usual during the daytime and emitted a call, best described as between a moan and a miau at low intensity and as a hoarse miau at highest intensity. When she emitted this cry, the lips were parted more at the corners than at the front of the mouth. Sometimes the miau occurred in isolation, sometimes it was followed by the contact call. It was heard on two successive days during this oestrus and subsequently on another occasion just before a mating took place. Although it has therefore tentatively been called a sex call, its significance is not fully clear. On neither occasion did the ♂ make any visible response to it.

The most frequently heard vocalization is the contact call. This is a short repetitive sound, usually delivered 3 or 4 times in succession but there may be as many as 7 notes in a sequence. It can be imitated by saying "ha-ha-ha" with the lips closed instead of open. The pitch varies with the size of the animal, being higher in small kittens and lower in adults. Spectrographic analysis of calls made at 19 days old showed that the main sound energy is concentrated in a band from 0.5 to 1.0 kHz, with a less intense "tail" of higher frequencies. The individual notes begin abruptly but end slightly less sharply and they are somewhat irregularly spaced, with a tendency for the first two or three notes in a sequence to follow each other more rapidly than the subsequent ones. There is also some diminution in intensity in the notes at the end of a series. In a call consisting of 3 notes, the intervals between the starts of successive notes were 114 and 144 msec and in one of 7 notes they were 106, 129, 159, 144, 144, and 159 msec. The individual note is brief, lasting no more than 30 msec and the total duration of the 7-note call was 848 msec. The call is most frequently heard from kittens and is given by an individual who finds himself alone. The littermate at once responds by repeating the call and moving to join the caller. The characteristics of the call, with abrupt onset and repeated several times, make it very easy to locate and the responder went accurately in the direction of the first caller. The response of young kittens is automatic and virtually invariable and no call was heard that failed to evoke the response. ♀ G, as a kitten was once ill with a severe digestive upset and she remained in the nest box. Her brother, exploring the laboratory, suddenly finding himself alone in a strange place, called: the ♀ promptly replied and tottered weakly out of the nest box to join him. Furthermore, both kittens responded at once to an imitation of the call. As the animals grow older and more assured in their environment, calling becomes less frequent and the response to it less predictable. It appears that they no longer respond automatically and other factors in the situation can now decide whether the response will or will not occur.

When ♀ G had her first litter, the kittens called and responded in the same way as the parents had done at the same age. The mother, however, now behaved in a different manner. She used the call to summon the kittens and they responded to her call in the same way as to each other's. When the kittens called, the mother replied; she did not, however, go to the calling youngster but merely waited for him to come to her.

Once she called when the kittens happened to have climbed on top of the sleeping box. They called in reply but were unable to climb down and go to her, since the end of the box nearest to her was also its highest point. One kitten became so agitated that it emitted a loud mew. The ♀, who had not moved in response to the kittens' contact calls, instantly went to the box, climbed up beside them and down again. They failed to follow her and in fact did not succeed in joining her until she moved over to the lower end of the box, apparently by chance.

When the kittens were a month old, chasing play started quite abruptly. This at first greatly worried the ♀ and she called them back to her repeatedly. They responded and ran to her but would be off in a new direction a moment later: sometimes, indeed, they merely ran beneath her belly between her fore and hind legs and continued their chase on the other side. Despite this, her calling did serve to restrict the radius of their activities and prevented them from ever getting very far from her. It also illustrated very clearly how the contact call system between mother and young operates, all members replying to a call but only the young moving to the caller. This ensures firstly that the litter does not get dispersed, secondly that the young can find their mother and lastly that the mother can summon her young to her when necessary. If the ♀ herself were to go to any calling kitten, the situation would merely be further complicated and getting the family together would be no easier. The fact that she will come at once in response to a distress mew makes provision for situations where the mother's presence is urgently required.

Amongst adults, the contact call may be used in any situation where contact with a conspecific is desired but definite responses to the call are not easily seen. The use of the call in association with the sex call by the oestrous ♀ has already been mentioned. In the early stages of the ♀'s heat, when she is not yet prepared to permit the ♂ to contact her, he will often lie near her and call now and then, much as a tom cat uses the entreaty vocalization to his ♀. Once the young of the second litter, aged approximately 6 months, were separated from the parents in one of the enclosures and the door between them was closed. Both mother and juveniles were extremely upset by this and she ran up and down the dividing wire netting, calling repeatedly. On one occasion when ♂ G and ♀ G were four months old, they were given a live snake inside the laboratory. They were at first very hesitant in their attacks on it and twice they retreated to the window bench cage and called to each other repeatedly, apparently seeking reassurance from each other. Fully adult animals also often call after having been alarmed by some disturbance.

Two other vocalizations which probably reflect different intensities of a single type of utterance were each heard once only. The first was a puppy-like "wuff", emitted by a juvenile when excited at the approach of feeding time. The second was a soft, almost unvoiced "wah", sounding like a puppy with laryngitis trying to bark. It was emitted twice during a bout of chasing and wrestling play when ♂ G and ♀ G were 38 days old. It appeared to reflect a high level of excitement but whether it had any communicatory function was not clear. Young *Genetta pardina* make a rather similar panting noise during excited play.

6. Comfort Movements and Toilet Behaviour

Comfort movements include yawning, stretching and shaking the body, much as a dog does, with the maximal movement in the region of the shoulders. In yawning, the mouth is opened much less widely than is characteristic of the Felidae. Yawning may occur in isolation or may precede or follow stretching. A common form of stretching is a cat-like arch-back stretch. The animal stands with the fore and hind limbs a little closer together than usual, then extends the limbs and spine, so that the back is thrown up into a convex arch, after which one or two steps forward are usually taken. The Washington animals commonly stretched in a dog-like manner, lowering the forequarters and extending the fore limbs, thus throwing the back into a sigmoid curve.

A certain amount of grooming may be performed at any time when the animal is resting but a prolonged toilet in which the whole of the body was cleaned in a single session was not seen. Three methods of cleaning are used.

(i) The paws and limbs and the greater part of the body from the shoulders back, including the tail, are cleaned with the mouth, using a combination of licking and nibbling with the incisor teeth. The tongue is soft and lacks the keratinised spines characteristic of felines and herpestines. It is therefore not an efficient comb and when the longer-haired parts of the coat, along the dorsal crest and the tail are being dealt with, nibbling predominates, whereas with the shorter-haired areas, licking is more important. Special attention is devoted to the region of the perfume gland. This area is cleaned in a lying position: sometimes the head is bent right round and contact with the gland established from behind the hind leg, sometimes the leg is merely raised sufficiently to permit the nose to reach the gland from in front but sometimes the cat-like posture is adopted, with the hind leg held stiffly up in a near vertical position.

(ii) The toes of the hind foot are used to clean from the cheek back to the shoulder. Although scratching with the hind foot is sometimes carried out in a lying position, more usually the animal stands on three legs. A brief series of scratches is made and the action then terminates and is not followed by licking the toes. Occasionally after a slight pause, a second series of scratches may be made, usually involving a slightly different part of the body from the first.

(iii) In addition to the cleaning done by scratching with the hind foot, the face is also cleaned with the inner surface of the wrist. After a few rubs with the wrist, the latter area is then licked clean. The action is very similar to the cat's face washing technique except that it is not repetitive and comprises only a single sequence of rubbing the face and licking the wrist.

Allogrooming between adults occurred now and then, grooming of the ♀ by the ♂ being much commoner than vice versa. If either animal had scent rubbed on food, the partner would often lick off the blood but, apart from this, the areas which the ♂ most often groomed were the ♀'s neck and ears and her anogenital region, particularly round the scent gland. Grooming of her flanks and near the root of her tail was often, in fact, an attempt to reach this area.

7. Defaecation, Micturition and Scent Marking

While defaecating, the animal stands with the back slightly arched and the tail held out horizontally or sloping slightly downwards. The tail may be moved up and down if any straining accompanies the passing of the faeces. Each individual uses the same place each night to deposit its droppings and a large pile would thus normally accumulate. Although the droppings were in fact cleared away each day, the animals always used the same places. ♀ G and ♂ G each had their own lavatory site, close together but distinct. Their enclosure contained a log wedged in a sloping position against a wall. Both animals made use of this, ♂ G climbing up it a short distance to deposit his droppings over the side while ♀ G went right to the top. When ♂ G was separated in the second enclosure, he backed up and defaecated over the edge of the veranda. This preference for defaecation from a height would facilitate the accumulation of a large compact dung pile. The kittens did not use the parental sites but selected their own: they defaecated separately but not far from each other and in each litter the place chosen was only a short distance from the favourite sleeping place.

The adult droppings are strongly scented and it seems highly probable that the accumulated pile has some significance in marking. Kleiman-Eisenberg (1972) has pointed out that in a solitary species which ranges over a wide area, the value of droppings in information transfer may be greater if they are concentrated in one particularly significant spot — usually close to the refuge or sleeping place — than if they are widely distributed. The dung pile certainly would constitute an important topographic feature in the olfactory landscape but it is not clear whether its significance relates mainly to its author, to a potential mate or in a more general way to other conspecifics.

♀♀ and juveniles micturate in a slightly squatting posture with the hind legs a little spread apart and the stream of urine is directed vertically downwards. In the adult ♂, however, the tip of the penis is bent round as the urine is voided and the stream is directed backwards between the hind legs at an angle of about 60° to the horizontal. He also usually shifts position during the process, so that the urine is widely distributed on shrubs, grass tufts or whatever vertical objects are available. During micturition ♂ W often but not invariably made backward kicking movements with the hind feet as he walked. ♂ G was not seen to do this. Presumably this micturitional procedure has some significance in marking but the ♀ and juveniles were not seen to make any response to the ♂'s urine. The ♂, however, if he was close by when the ♀ micturated, or if he came on her urine within a few seconds of its being voided, would sniff it and flehm. ♂ G invariably flehmed on smelling fresh ♀ urine, regardless of whether she was in oestrus or not but only once was he seen to do so in response to urine over one minute old. ♂ W was seen to flehm 32 times after sniffing ♀ W's urine, once after sniffing her scent gland and once after sniffing one of her scent marks.

In flehmen the ♂ first sniffs the urine and may also lick at it; he then raises his head with the lips slightly parted and the nose drawn back but the wrinkling of the snout produced is so slight that it is not noticeable from a distance of over a metre or two. The nose is then usually moved up and down several times, through a distance of up to 5 cm and finally, the tongue is protruded and the snout licked briefly (Fig. 4 a). ♂ G usually flehmed twice in succession in response to the ♀'s urine and very frequently he himself then micturated. In ♂ W the preliminary sniffing lasted from 3.5 to 35.0 sec with a mean of 12.3 sec (N = 34) while the flehmen itself was of shorter duration, 2.0 to 13.0 sec, with a mean of 7.5 sec (N = 49). As may be seen from Fig. 4 b, there is no clear relationship between the duration of the flehmen and of the sniffing that preceded it.

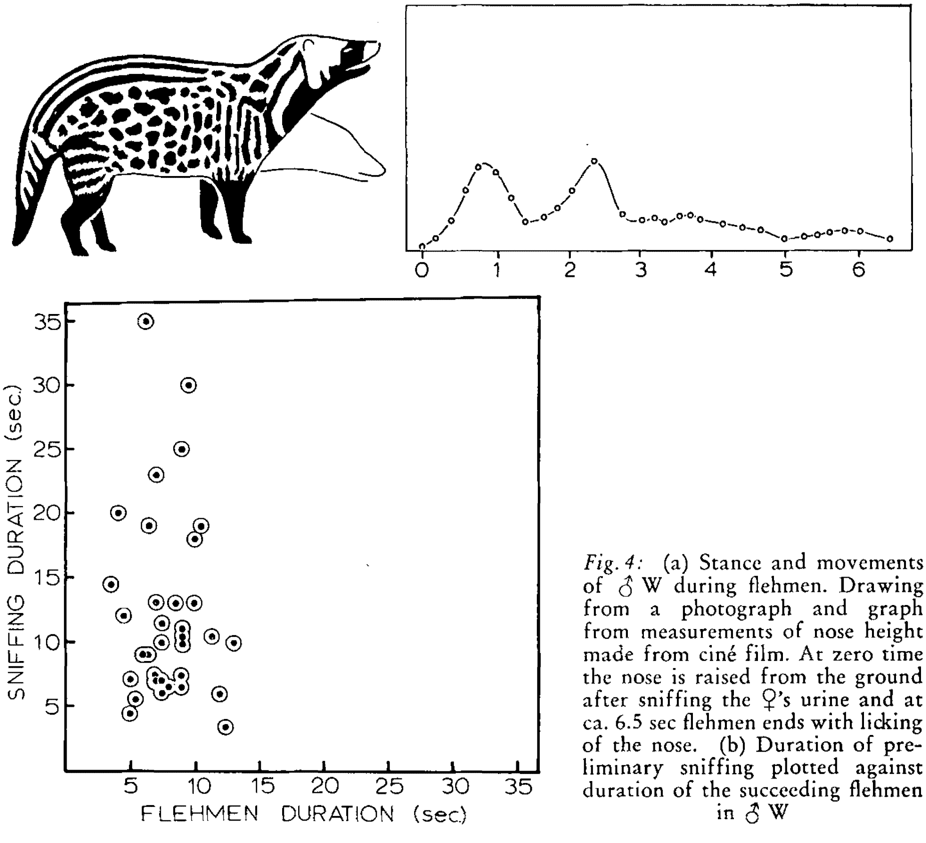

Fig. 4: (a) Stance and movements of ♂ W during flehmen. Drawing from a photograph and graph from measurements of nose height made from ciné film. At zero time the nose is raised from the ground after sniffing the ♀'s urine and at ca. 6.5 sec flehmen ends with licking of the nose. (b) Duration of preliminary sniffing plotted against duration of the succeeding flehmen in ♂ W

The large perfume gland is situated between the anus and the vulva or penis. Its structure has been described by Pocock (1915) and it is figured by Allen (1924). The inner pockets containing the secretion are enclosed by antero-posteriorly elongated lips which are everted when the secretion is being applied. If a horizontal object is to be marked, the animal squats down and presses the gland on the substratum. Vertical objects, such as tree trunks, are also marked and to do this the animal backs up, raises the tail vertically, everts the lips of the gland and presses it firmly against the object. The height of the mark is thus a reflection of the size of its author and the marks of ♂ G and ♀ G on such things as walls and table legs were easily distinguishable, his being some 5 cm higher than hers. The gland is larger in the ♂ than in the ♀ and although both sexes mark, the ♂ does so much the more frequently: moreover, the ♀ marks on horizontal surfaces more often than on vertical ones, whereas in the adult ♂ the reverse is the case. Young animals mark only in the squatting posture and the backing up technique to mark a vertical object is used only by adults. The size difference between ♂ and ♀ glands was already quite clear in ♂ G and ♀ G when they were first received (Fig. 5).

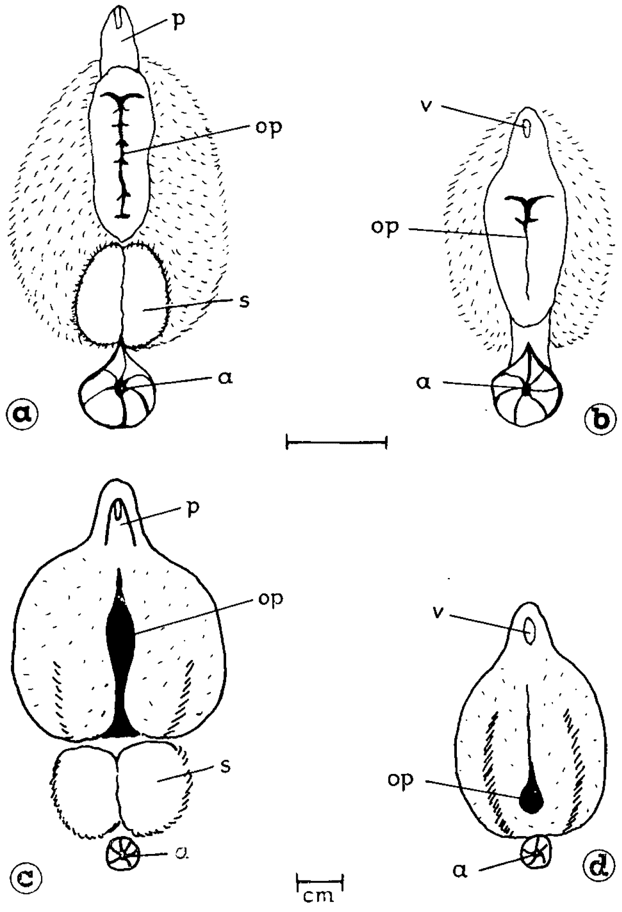

Fig. 5: Perfume glands of (a) ♂ G and (b) ♀ G, aged 21 days. (c) and (d) glands of the same pair aged 7 months. a, anus surrounded by area of naked skin; op, opening of gland; p, penis; s, scrotum; v, vulva

In the captivity situation, the only marks which could be encountered apart from the animal's own, were those of the familiar cage mate, to which one would not expect any great response. It was, noted however, that if one adult marked, it was not uncommon for the other to smell the mark and add its own. Adults sniffed the marks made by kittens but did not follow this by marking themselves. Since only one adult ♂ and one adult ♀ were kept together, it was not possible to see whether an animal would also add its own mark to one made by another of the same sex. Between the sexes such behaviour could clearly assist ♂ and ♀ to find each other, since the addition of a new mark to a routine marking point would be noticed on the next visit. Counts of the number of marks made each night on table and chair legs in the laboratory failed to provide any clear evidence of changes in the frequency of marking by ♂ G in relation to ♀ G's heats but there was some indication that she was more inclined to mark vertical objects around the time of oestrus than at other times.

The animals did not emit musk when alarmed but they did sometimes mark in association with other forms of behaviour indicative of anxiety or insecurity. The herpestines *Suricata* and *Crossarchus* will both mark unfamiliar objects or smells with anal sac secretion directly when they are discovered but the civets did not respond in quite the same way. An unfamiliar object or a familiar one carrying the scent of a stranger would almost always be found marked by the following morning but in their first approaches to such objects the civets showed great caution and the marking was not normally performed directly when their presence had been detected. It seemed that strange objects were disquieting and produced a need to establish security by the setting of "own mark" but the intimidatory characteristics of the unfamiliar were at first too strong to permit this and some degree of habituation was required before the marking could be performed.

8. Prey Capture

Civets are not recorded as killers of large prey and the biggest prey species offered were rats and guinea pigs, an almost full grown domestic hen and snakes a little over a metre long. The paws are not used in prey capture but the repertoire includes a number of different forms of attack with the jaws.

(i) The Run-away bite: a quick nip without precise orientation, delivered on any part of the prey's body, followed by instant release and retreat; typical of the initial attack on intimidatory prey. The run-away bite may be preceded by "biting at", in which the animal makes a quick snap in the direction of the prey but without actually contacting it.

(ii) Bite-and-throw: a bite, again without precise orientation, which is held only long enough for the prey to be thrown to one side with a quick movement of the head. This is usually the second stage in an attack on intimidatory prey: it is often accompanied by a quick leap in the air, all four legs leaving the ground at once.

(iii) Bite-and-shake: here the grip is retained and the head shaken from side to side with extreme violence. The shaking is sufficient to smash a small rodent's backbone and rupture the major blood vessels, and a 42 cm long snake, after being shaken, was found to have its vertebral column broken in 6 places. At the end of the shaking, the prey may be thrown aside with considerable force, or it may merely be dropped. If a snake is being dealt with, the civet usually leaps aside as the prey is released, apparently to avoid any chance of being reached by a return strike.

(iv) The killing bite, in which the grip is retained and the jaws bite home firmly. If the resistance encountered is considerable, the bite may be repeated in rapid succession, without the teeth ever being fully withdrawn from the skin, or with some shifting of grip between bites. Leyhausen (1965) calls these two variations 'Nachbeissen' and 'Nachschnappen' respectively, which we translate as iterant biting and iterant snapping.

With small prey such as a mouse or a small lizard, a killing bite will be lethal, regardless of its orientation on the body of the prey. When dealing with larger things, an aimed killing bite, directed specifically at the skull of the prey, was sometimes used and the civet always paused for a moment and looked carefully at the prey before biting in this way, so that the deliberate aim was very obvious. With rats and snakes the aimed head bite was used as the coup-de-grace, administered after the prey had been disabled by preliminary attacks. If provided with a freshly killed rat, the civets often "killed" it with a head bite and the deadness of prey which they had themselves killed was also sometimes assured by their giving it a head bite before starting to eat. The aimed head bite might be single or iterant, depending on the hardness of the prey's skull and it was also sometimes accompanied by shaking.

The way in which a particular prey is attacked reflects the civet's degree of confidence or timidity. As one would expect, the intimidatory features of prey include its size and any attempts it makes to defend itself. Unfamiliarity also affects the civet's behaviour very strongly and any prey species encountered for the first time is treated with great circumspection. Olfactory characteristics are important here and even a dead rodent is approached with caution if its smell is strange. The quality of the smell is also important: prey which is not very palatable, as shown by subsequent failure to eat it readily, is usually attacked with hesitation, whereas prey that is devoured with enthusiasm also evokes attack more readily. This was particularly clear with snakes. File snakes (*Mahelya crossi*) smell disagreeable to the human nose and the civets would either refuse to eat them or, at most, pull off a few pieces: green tree snakes (*Philothamnus sp.*), sand snakes (*Psammophis sibilans*) and herald snakes (*Crotaphopeltis hotamboei*) were eaten readily. The file snake, even if extremely passive, was attacked in a very hesitant manner, the other three species with much more decision. The difference in treatment is not related to venomousness for none of these species is dangerous.

The following account of the first kill of a full grown rat by ♀ G at the age of 5 months illustrates a typical hesitant attack. The rat crouched in a corner without moving and the civet approached slowly with the dorsal crest erected. She made several bites at the rat without contacting it, her teeth meeting with a loud snap and after each bite she withdrew before renewing the attack. It took 5 min for the first run-away bite to be made, after which she retreated hastily and again began a gradual approach with 'bites at'. This time contact was established more quickly and the rat was bitten and thrown aside a short distance, the civet at the same time leaping in the air. The rat, now injured, crawled out of reach under a cupboard and had to be pulled out. Again the civet went through the sequence of bite at, bite throw and leap aside and finally she bit, held her grip and shook, repeating this several times with increasing vigour. The first full scale shake broke the rat's back and although it was dead and motionless, the civet shook and threw the corpse several times more. The first attacks on live mice, made when the civets were two months old, followed a very similar course. In contrast, the experienced adults seize a rat by the middle of the body without hesitation, shake it violently, put it down and then, although it is usually already dead, they end by crunching the head with a few iterant bites. Indeed, ♂ G may kill a rat with a single bite on the head combined with shaking, without any preliminaries beyond a careful look before lunging forward to attack.

The cautious progressive attack is particularly effective in dealing with snakes. The initial run-away bites and bites with throwing are usually directed towards the tail; they may injure the snake slightly and can certainly prevent its escape. The civet's withdrawal after a bite is so fast that the snake has no chance to turn and strike and the leap aside after a throw serves to avoid any strike that might be made, should the snake happen to land in a favourable position. Once the stage of bite and shake is reached, the contest is virtually over: the snake is helpless while being shaken and once its back has been broken in a few places, it can no longer raise its head from the ground and is powerless to strike. At this stage the civet may pause, look carefully and make the kill with an aimed bite on the head or may simply continue the process of bite, shake and release until the snake is dead and, indeed, will usually shake the dead snake a few times before starting to eat it.

Birds were killed in much the same way as mammals: one or two initial bites without precise orientation combined with shaking sufficed to break the back and the final kill was usually a head bite. ♀ G, for instance, attacking a hen, first seized it by the rump as it tried to run away and shook it, without inflicting much damage beyond the loss of a few feathers. The hen again ran and she gripped it by the middle of the back, shook it and laid it down. The hen was now virtually dead: its back was broken and the abdomen was also broken open but after a moment it gave a slight flutter. The civet at once took it by the head and with a few iterant bites, crushed the skull.

Small fish, frogs and aquatic insects placed in the water dish were caught very quickly. The civets had no hesitation about putting their faces in the water and caught the prey with a quick scooping bite. The paws were used only to chase out prey which had got into a position where it could not be reached with the mouth. Pieces of meat put in the water dish were caught in the same way. The civets, however, never took to dowsing their food, and although on one occasion ♂ G placed the wing of a bird in the water dish and took it out again, this was the only time such behaviour was seen.

9. Eating, Scent-rubbing and Drinking

Without specialised carnassials, the civets cannot easily cut through anything tough; the skin of an adult rat, for instance, presents considerable difficulty. Large prey cannot therefore be dismembered simply by slicing pieces off with the carnassials and the technique adopted is to hold it down with the fore paws and tear pieces off by gripping with the incisors and pulling upwards, a method commonly adopted by species lacking a specialised carnassial shear amongst the herpestines as well as the viverrines (see Fig. 2). Once the prey, or a part of it, has been taken into the mouth, it is not at once swallowed but chewed for some time, using the left and right sides of the jaws in alternation. The head is held tilted to one side so that the chewing side is downwards and as the change to the other side is made, the head is rotated to tilt in the opposite direction. This is done so expertly that one almost gets the impression of the piece of flesh remaining where it is, while the civet's head moves from one side of it to the other. The number of bites made on each side is highly variable, usually from 4 or 5 up to 12 or 14 but counts of up to 20 have been made.

The feathers of birds present a problem but the civet has no special method of plucking. The incisor tearing technique is used to begin with and the animal has some trouble in getting rid of the feathers in its mouth. Once a few bits of skin have been torn away and the flesh exposed, further pieces can be torn off more easily but the civet cannot cut through the bases of the feathers as a cat can and a young animal usually swallows most of them. With experience, however, although the smaller feathers are still eaten, the civets become adept at getting rid of tail and wing feathers by plucking the meat from the feathers, rather than vice versa. Using the technique normally adopted for dealing with tough prey, one or both fore paws are placed firmly on the feathers and the meat is then torn away from them with the incisor teeth.

The poison glands of anurans are more highly developed on the dorsal than on the ventral surface and the usual method of dealing with this type of prey is to open it from the ventral surface and pull out the viscera. Some species are completely devoured but with others little more than the viscera and the ventral body wall are eaten and toads are generally refused. The civet sometimes uses one paw to turn the prey over on its back but sometimes it merely picks it up and throws it a short distance. If it lands belly up, then the throat or abdomen is bitten but if not, it is simply thrown again.

Mammals, snakes and large lizards are eaten from the head down but with very small species, such as mice, which can be taken into the mouth whole, there is no particular orientation of eating. Indeed, an adult civet makes virtually no distinction between killing and eating a mouse: it simply grasps the prey in its jaws and starts to chew it. When skinned rats were offered, these too were eaten from the head down and the empty skin was also eaten head first.

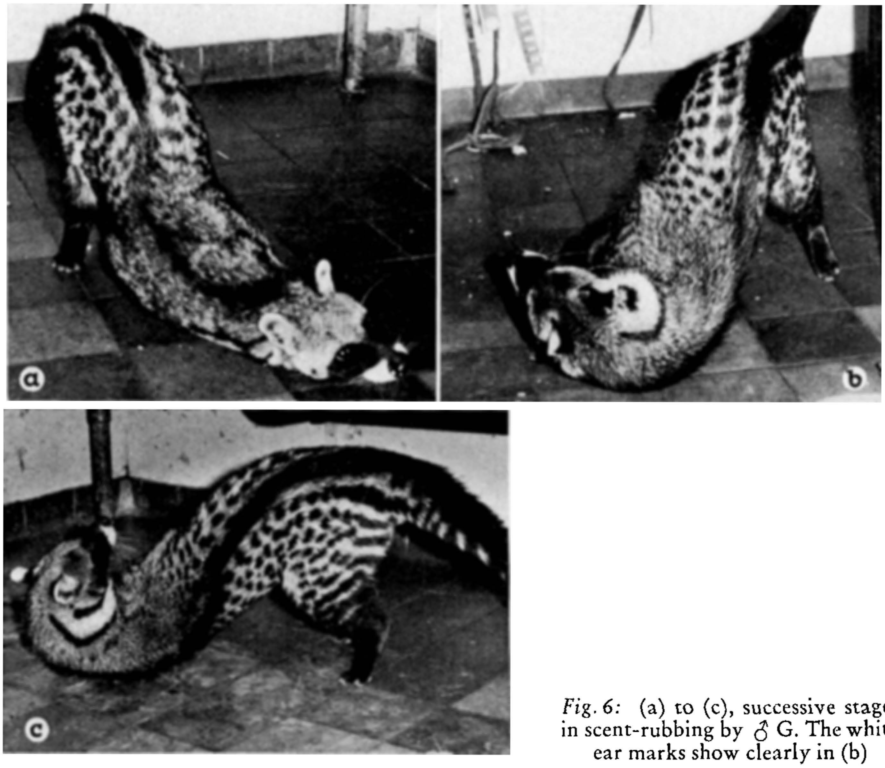

Fig. 6: (a) to (c), successive stages in scent-rubbing by ♂ G. The white ear marks show clearly in (b)

Eating may be preceded or punctuated by scent rubbing on the food (Fig. 6). In scent-rubbing the chin is first lowered and laid on the food, usually slightly on one side but sometimes virtually symmetrically. The body is then pushed forward, the fore legs flexed and the head turned sideways so that the chin, the side of the neck and the shoulder are successively rubbed along the food. Having rubbed the shoulder, the animal usually rights himself, stands up and may repeat the whole procedure. If the rubbing continues, erection of the dorsal crest usually occurs before long and sometimes there is opening and closing of the jaws, together with licking movements of the tongue which give the impression that the animal is salivating and preventing itself from dribbling. Sometimes in an intense bout of rubbing, the animal does not right himself after rubbing the shoulder but rolls right over on his back. The back is fully extended and he usually rolls right over on the other side before getting to his feet again. It is unusual for him to roll back again onto the original side but this does happen now and then. The impression given is that genuine rubbing does not go further than the shoulder and that the complete roll over is a sort of overshoot; indeed it often looked like involuntary overbalancing. Rubbing was performed by both sexes and even young kittens on their first encounters with meat or fish will rub on it, usually before trying to eat. Rubbing is evoked by any unfamiliar or particularly strong smelling animal food, especially anything slightly rotten, but vegetable foods were never rubbed. The gut of any prey species, too, is particularly prone to evoke rubbing, even if the prey is the animal's own kill and therefore perfectly fresh. It was common for the civets, having killed prey, to start to eat and then, once the abdomen had been reached, to stop eating and rub on the exposed gut. Both sexes responded in the same way to different types of food but ♂ G could be induced to rub by a number of unnatural odours which had no such effect on ♀ G. The mosquito repellants 'Off' and 'Flypel', for instance, could be relied upon to send him into a frenzy of rubbing. He was also prone to rub on one's arms and legs, whereas ♀ G did not do this. The tendency for rubbing to be followed by biting or worrying is not related to subsequent eating for it is not restricted to food: a piece of tissue impregnated with 'Off' was worried and it was necessary to discourage ♂ G's attempts to rub on arms and legs, since if allowed to persist, he would follow the rubbing by biting.

The significance of scent-rubbing is obscure. It is not concerned with setting an ownership mark on food which is not going to be consumed at once, for there is no correlation of rubbing with failing to finish a meal. Moreover, there was no tendency for one animal to avoid taking food already rubbed by the other: on the contrary, the fact that one animal was rubbing its food instead of eating it often gave the other an easy opportunity to steal it. If ♀ G had rubbed on food, her kittens would often rub on the side of her neck and lick at it. Possibly this helps to familiarise them with the smells of locally available prey species but it is difficult to believe that this is more than an incidental function of the rubbing behaviour.

Rubbing on carrion or dung is widespread amongst the Canidae and the palm civet, *Nandinia binotata* rubs on food very much as the civets do. Van Lawick Goodall and van Lawick (1970) have described similar behaviour in the spotted hyaena, *Crocuta crocuta.* In the latter species carrion and dung are frequent objects of rubbing but the favourite one is the mass of undigested hair which is often vomited up after a meal. There appears to be some connection between scent-rubbing and the acceptance of carrion as food, for this behaviour is not recorded in species which will eat only fresh meat. The converse is not true for the larger Felidae are not known to indulge in scent-rubbing but will eat rotten meat. Acceptance of carrion, however, is not characteristic of the Felidae as a whole and appears to be a secondary habit, correlated with the ability to kill prey large enough to provide more than a single meal. Felid rubbing on catmint appears to be something different, related to sexual behaviour rather than to food (Palen and Goddard 1966) and the civets when offered catmint showed little interest and were not stimulated to rub. Nevertheless, there may be some connection between their scent-rubbing and sexual arousal for if ♂ G rubbed on one's legs, he would sometimes combine this with clasping in a manner reminiscent of his attempts to mount an unreceptive ♀. Moreover, on one occasion, the kittens of litter 5, aged 58 days, rubbed intensively on a dead rat and followed this by a bout of fighting and wrestling play which continually switched over into mounting attempts. Mounting during play had not been seen previously and a little later on the same evening, they played again without any mounting.

Civets drink with a noisy dog-like lapping, in contrast to the silent lapping characteristic of cats and mongooses. They appear to be taking and swallowing a mouthful of water with the assistance of the tongue rather than using the tongue alone to convey fluid into the mouth.

10. Mating Behaviour and Reproduction

♀ G's periods of heat were usually preceded and accompanied by a number of changes in the animals' general behaviour. The ♀, previously much more amicable towards the ♂, became more inclined to snap at him if he approached her closely and growled at him more often in defence of food. He made no retaliation but became more aggressive towards his keeper. His increased tendency to give the contact call has already been mentioned. Both animals showed increased locomotor activity and, around 21.00 hours, after they had fed and rested for some time, would start persistently walking round and round their enclosure. During this 'roaming' the ♂ often held his mouth slightly open, a habit not seen at other times.

In the restricted cage conditions, where there could be no possibility of losing track of the partner, it was not easy to assess the reactions of the pair to each other during this activity. The ♂ was not following the ♀ closely and the two often passed and repassed, apparently oblivious to each other's presence: nevertheless, he was rarely far from her and if it happened that he did leave her immediate vicinity, for instance by entering the inner windowbench cage, the ♀ would promptly join him and pass close by him paying no overt attention but behaving in such a way to ensure that contact was reestablished. In the wild there would be no reason for the animals to circle about and following may then be a much more definite procedure.

The duration of the ♀'s heats was variable. Sometimes sexual behaviour was seen only on a single night, on other occasions on several successive nights, the maximum observed being six. During these longer heats, the ♂ often made mounting attempts before the ♀ was ready to accept him. She then did not take up the crouched mating posture but remained standing and he was therefore forced to mount in an abnormal manner, clasping her round the body with his fore limbs. Sometimes he mounted from behind, sometimes he stood beside her and slipped one paw over her body just behind the shoulders. Having clasped her with his paws, the ♂ then laid his chin on the ♀'s neck but sometimes, particularly when she tried to move away from him, he would grip her fur in his teeth. These attempts were always unsuccessful and although the ♂ often had an erection, intromission was not achieved. Usually the ♀ simply walked away from under the ♂ but sometimes she turned and snapped at him which caused him to dismount.

During prolonged heats, locomotor activity gradually increased and the ♀'s receptivity was finally shown by her breaking into a run and inciting the ♂ to pursue by approaching him and running past close beside him. On three occasions she picked up a piece of discarded food in her mouth, apparently using this as an added incentive to make him give chase. When he did so, she would pause and adopt the mating posture for a moment but instead of permitting him to mount at once, would run off again. Most of these courtship chases occurred at night and mating took place out of sight but on two occasions the full procedure was seen. On the first of these the animals had been showing sexual excitement on the previous evening but the ♀ had refused to allow the ♂ to mount. When they first roused up from the day's rest just before dusk, the ♀ moved off and the ♂ ran after her. Two or three times she sank down, so that she was almost lying prone with her body fully extended but as the ♂ approached she again ran. Finally she lay with her hindquarters slightly raised and permitted him to mount. His fore paws were on either side of her shoulders and supported most of his weight while his hind legs made treading movements on either side of her flanks and pelvic thrusting took place. There was no neck grip at this stage but the ♂'s chin was resting on the ♀'s neck. After a few moments she gave a low miau and five seconds later she moved forward away from him. When he followed, she turned and snapped at him and he promptly took up the appeasement posture. She then moved on and he followed and once again she sank down into the mating position. The ♂ mounted as before and again the ♀ miaued and moved forward slightly. This time the ♂ moved with her and gripped her fur between her shoulder blades: the ♀ miaued once more, moved forward again and the ♂ then dismounted. Pelvic thrusting was fast (ca. 2 per sec) during the period before the first miau, then slowed down and was not apparent during the final stages. Treading occurred during the initial stages before the ♀'s first miau, which was probably when intromission took place. The time from this moment until the ♂ dismounted was 40 sec. When the copulation terminated both animals licked their genitalia, the ♂ (still with an erection) quite calmly but the ♀ was at first greatly excited and turned a complete somersault as she bent her head down to lick her vulva.

The second mating that was seen took place after dark at 19.45 hrs. Shortly before this, the ♀ entered the window-bench cage, giving the 'sex call' and closely followed by the ♂. The pair went to and fro between inner and outer cages several times and once there was a brief mount or attempted mounting on the veranda where the animals were not fully visible, after which they once more came in and went out. A mating then took place on the veranda in full view. The ♀ crouched as before and the ♂ mounted in the same manner. The ♀ then attempted to crawl forwards and he gripped her by the neck and restrained her. The mating lasted 70 sec in all but since it was not possible to hear if the ♀ miaued, the moment of intromission could not be determined. When the ♂ dismounted there was a bout of wildly excited post-copulatory rolling by the ♀ but he remained calm and merely licked his genitalia briefly. Both of these matings were successful and were followed by pregnancy.

The ♂ of litter 2 first attempted to mount the mature ♀ when he was 6 months old but with the original pair, the first mounting attempts were seen when the animals were 7 months old. The ♀, however, was totally unresponsive and it was not until a month later that she showed signs of sexual excitement. The first effective mating occurred during a heat lasting from 18th to 23rd Sept. 1970, when the pair were just over a year old and the first litter of two young was born on Nov. 25th. This gives a gestation period of between 63 and 68 days. Mating occurred when the young of this litter were 106 days old but unfortunately about a month later the ♀ miscarried. She mated again 13 days later and a second litter, also of two young, was born after 79 days. The first mating after the birth of this litter took place when they were 100 days old and a third litter of two young was born 66 days later. After the first 48 hours, however, the ♀ began to neglect them and they became chilled and died. Since the young of the previous litter had not been removed, it seemed possible that their presence might have been responsible for the ♀'s neglect of the new litter. She came on heat 13 days after parturition, mated and 80 days later gave birth to a litter of three. Since the first two litters had been successfully reared in the presence of the ♂, it was not thought necessary to remove him. At first the ♀ cared for the kittens adequately but when they were 16 days old she showed signs of coming on heat and began to neglect them. The kittens were removed and fed and the ♀ mated the following evening. Several attempts were made to return the kittens to her but she remained unresponsive to them and they were therefore hand reared. The ♀ gave birth to a litter of three kittens 81 days after mating. In view of the two previous failures to rear young in the presence of the ♂, the pair were separated a few days before parturition was due, one in each of the two enclosures. Although she was still in visual, vocal and olfactory contact with the ♂, the ♀ reared this litter successfully.

From these data it appears that the female civet is sexually mature at one year old, the ♂ possibly a little earlier and the first litter is born when the ♀ is about 14 months old. The ♀ comes on heat again when her young are about 3½ months old and there thus may be two litters in a year. If a litter is lost she will come on heat again within a fortnight and births are therefore not strictly seasonal. The data for the five litters born are given in Table 1.

Table 1: Details of 5 litters born to ♀ G

Date born	Gestation (days)	No in litter	Sexes
Litter 1 26 / 11 / 70 (reared)	63 - 68	2	1 ♂, 1 ♀
Miscarriage on 4 or 5 / 4 / 71			
Litter 2 6 / 7 / 71 (reared)	79	2	1 ♂, 1 ♀
Litter 3 19 / 12 / 71 (not reared)	66	2	2 ♂
Litter 4 30 / 3 / 72 (not reared)[1]	80	3	3 ♂
Litter 5 7 / 7 / 72 (reared)	81	3	1 ♂, 2 ♀

[1] Removed and hand reared.

The original Ghana pair of animals from the wild were born in early September and small youngsters captured in the wild came into the possession of acquaintances on 1/11/69 and 20/2/72. These must have been born in October and late January or early February. Litters born in the wild in late July or early August and in September have also been recorded by S. M. JEFFREY (pers. comm.). This gives records for Ghana of births in July (captive), late July or early August (wild), September and October (wild), November and December (captive), January or early February (wild), March (captive).

The data for gestation periods are of some interest. The first and third litters were born after gestation periods of approximately 65 days, the three others after 79, 80 and 81 days, roughly a fortnight longer. There was no difference in the stage of maturity at birth of the kittens of the long and short gestation litters. The two with the shorter gestation period were ♀ G's first litter and one born after the successful rearing of the previous litter. The three with the longer period were each conceived following some departure from the normal cycle: in one case, a miscarriage, in the other two the loss of litters at an early stage through maternal neglect. This suggests that in these latter three cases, although oestrogen secretion had reached levels sufficient to produce behavioural oestrus, it had not yet brought about the uterine changes necessary for the establishment of gestation and a delay in implantation resulted. The duration of the delay corresponds with the normal length of an unmated cycle. The litter is born no sooner than it would have been, had the ♀'s heat been a fortnight later and had there then been no delay in implantation but there may nevertheless be some advantage in what happens. By her coming on heat as soon as possible the ♀'s chances of finding a mate are doubled, since she has two potential heats instead of one between the loss of one litter and the commencement of true gestation of the next.

MALLINSON (1969) gives the duration of two gestations of animals kept at the Jersey Zoo as 45 and 60 days. The former seems surprisingly short and unfortunately he does not state whether the kittens were normal at birth.

11. Development of the Young

Absence due to illness made it impossible to watch the development of litter 2 and the following account is based mainly on ♂ G and ♀ G and on their first pair of offspring. Ages given for ♂ G and ♀ G are based on the assumption that they were 12 days old when received. The two sets of observations are complementary since with the hand-reared young it was easy to note the earliest times at which various forms of behaviour appeared and to test their responses to various types of food, including live prey. With the naturally reared litter less detailed observation was possible since the mother became worried if long periods were spent close to her kittens; moreover, if the young showed hesitation about attacking prey, it was sure to be snatched by one or other parent before their full responses could be seen. On the other hand, it was possible to watch the progressive development of the interactions between parents and young. In addition, a few observations were made on litter 3 during the few days that they survived, on litter 4 up to the age of 12 weeks and on litter 5 from the age of 8 weeks.

The newborn kittens were not weighed but the first kitten of litter 3 to die, at 6 days old weighed 162 g and at an estimated age of 17 days ♂ G weighed 540 g and ♀ G 480 g. The weights of litter 4 were as follows:

17 days	21 days	33 days
540 g	550 g	810 g
530 g	550 g	800 g
440 g	480 g	680 g

Although the kittens are born fully furred, the adult colour pattern is not fully developed at birth. The neck stripe is present but is pale greyish and is therefore less conspicuous than the adult white stripe. The inside of the ears is white but the white hair ends at the edge of the pinna and the white mark on the posterior surface is absent. This develops slowly, first as a thin rim and it is three weeks before a small oblique white area is clearly visible on the posterior surface. The facial patterning is at first very indistinct (Fig. 7). The forehead is darker than in the adult, so that the contrast with the black areas is reduced. The two white muzzle marks are present but the black mask at first consists of two patches which do not meet in the mid line. These gradually extend, meeting first at the tip of the nose and the line of fusion then extends towards the forehead. The point at which extension of the black finally ceases varies from individual to individual and the line of black may therefore run virtually straight across the bridge of the nose or a distict V may remain. The genal vibrissae arise from a black spot which may be distinct from the face mask or

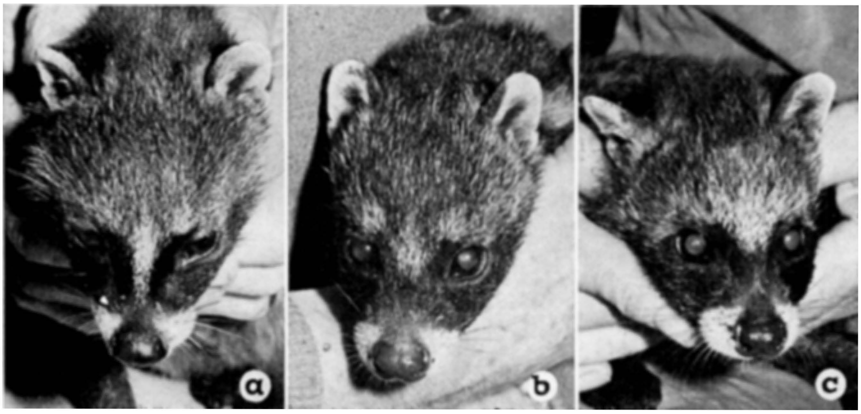

Fig. 7: (a) and (b) individual variation in facial markings of littermate kittens aged 21 days. (c) the same kitten as in (b) aged 32 days. The forehead has become lighter and the black face mask is now more distinct

confluent with it. The changes which are in progress by the age of three weeks presumably reflect the fact that by this time the replacement of the birth coat by the first juvenile pelage is under way.

In small kittens the perfume gland is rather genet-like in appearance (Fig. 5). The pouch is marked out by an area of pale hair, in the centre of which the naked lips of the gland are visible. In the ♀ these lips are linked by a hairless isthmus with the patch of naked skin round the anus: by the age of a month this connection has been obliterated and the lines of dark hair which traverse the white of the adult pocket have started to appear. Further growth of the pocket soon conceals the naked lips which are then visible only when everted in preparation for marking and the lines of dark hair on either side of the opening become longer and more obvious.

The kittens are born at a relatively advanced stage. The eyes are open at birth (litter 3) or within a few days (litter 1: 4 days, litter 4: 2—3 days) and the kittens are capable of crawling, although the hind legs do not fully support the body until about the 5th day. Although they may stray about slightly and make their way back to the mother, apparently guided by smell, it is not until the age of 17 or 18 days that active exploring outside the nest area makes its appearance. During the 5th month, a number of changes take place, presumably associated with the onset of maturation of the gonads. Although the smell of musk is detectable in the glands of young kittens, the marks they make do not carry much odour but during the 5th month they become much more strongly scented and the droppings too begin to smell strongly of musk. During the same period the ♂ first flehms in response to fresh ♀ urine, his retromingency makes its first appearance and he begins to mark vertical objects by the backing up technique. His testes also become noticeably larger at about this time. The young of the first litter ceased suckling at 14 weeks old, those of litter 5 at 16 weeks and those of litter 2 at 20 weeks.

Table 2 gives the ages at which various forms of behaviour were first seen but it is necessary to say a little more about the development of responses to food and prey, about play and about defensive responses.

Table 2: Age in days at which various forms of behaviour were first seen

	♂ G and ♀ G	Litter 1	Litter 4
Contact call	-	5	5
Walk firmly	-	5	8
Olfactory testing (Witterung)	-	6	12
First signs of play	14	21	14
Eating earth	17	21	14
Taking cover and freezing	-	18	14
Exploring outside nest area	18	17	23
Unaided micturition	17	25	17
Run and jump	20	23	23
Accept raw meat	23	21	23
Scent mark	25	25	-
Scent rub on food	27	33	-

(i) Food and prey. Many young mammals eat small quantities of earth shortly before they begin to eat solid food, very likely as a means of establishing the normal gut flora (Ewer 1968 b). ♂ G and ♀ G ate earth the first time they encountered it, when they were provided with an earth box at 17 days old. Both they and the young of litters 1 and 4 first ate small quantities of raw meat early in the fourth week of life but at this stage the teeth have not erupted sufficiently for effective chewing. The first response to live prey was seen at 23 days old, when ♂ G sniffed at a moving insect and made intention movements of biting at it but did not actually bite. The next day he again followed a live termite, keeping his nose in contact with it as it moved. When it paused he remained with his nose touching it for 2 seconds, then quite abruptly bit at it, ate it and promptly ate two more.

By the age of 1 month, the teeth have erupted sufficiently for small pieces of meat to be eaten readily and the meat is shaken as it is picked up. At 6 weeks old, a small lizard proved to be too tough to chew up but was tackled in the normal manner by holding it down with the forepaws and tearing pieces off with the incisors (Fig. 8 b).

Fig. 8: (a) Play in six weeks old kittens: the ♂ is climbing and the ♀ in pursuit takes the opportunity to worry his tail. (b) Six weeks old kitten holds down a lizard with its paw and tears it apart

♂ G killed a mouse on the first occasion it was offered, when he was 72 days old, going through the entire normal sequence of bite at → run-away bite → bite-and-throw → bite-shake-and-throw. Once it was dead, he became very excited and indulged in a frenzy of shaking and throwing the corpse before eating it from the head down. The ♀ responded similarly to her first mouse with an inhibited bite at. The ♂, who had by this time made his own kill, then snatched the mouse, bit and threw it. It was replaced, now motionless, close to the ♀ who sniffed at it and, exactly as with the ♂'s first insect, the smell appeared to release the appropriate response. After a short pause, she suddenly bit with lightning speed, threw the mouse aside and leapt in the air as she did so. Further experience with live prey was merely a matter of increasing confidence in attack. ♂ G, for instance, killed his fifth mouse very swiftly and without hesitation with a single bite combined with violent shaking and by his seventh, he had reached the stage of making virtually no distinction between killing and eating. The young of litter 4 were first offered a mouse at the age of 55 days, when the most enterprising of the three killed in the same way as ♂ G did his first mouse.

Mice were one of the civets' favourite foods and the young of litter 1 were never given a chance to kill a mouse: while they hesitated, one or other parent always captured it. They were given their first opportunity to deal with live vertebrate prey at the age of 154 days, when the parents permitted them to kill a rat — prey much less relished than mice. The young made the kill in the usual manner, a timid approach with some piloerection leading to bites at → run-away bite → bite-and-throw (with leaping aside) → bite-shake-and-throw.

It has already been noted that the adults ate skinned rats in the usual way, from the head down. In this they differ from the mongoose *Crossarchus* and the marsupial *Dasycercus*, in both of which the normal orientation of eating is completely disrupted if the prey is skinned. In *Crossarchus* skinning the head alone is sufficient to cause disorientation. Mice with the head skinned were offered to litter 4 at the age of 84 days, by which time they had already had live mice three times. One kitten promptly 'killed' the dead mouse by biting and shaking it several times, then sniffed it over, made a tentative bite at a hind leg, sniffed it again and ate from the head down. The second kitten at once started to eat his mouse from the head down in the normal way. The third and most timid kitten was still 'killing' his mouse by shaking and throwing it when the first stole it and ate it without hesitation from the head down. The young of litter 5 were offered head-skinned mice without their having had any previous experience of mice, live or dead. They nevertheless showed the normal orientation of eating.

(ii) Play. The first indications of play were seen in ♂ G and ♀ G at the age of 14 days and took the form of biting at each other and at one's fingers when one encouraged them to do so. Once exploration outside the nest had started, play became much more active and included running, chasing, jumping at each other followed by biting, usually directed at neck or ear and wrestling (i.e. clasping each other, usually round the shoulders, often followed by both falling over). They also bit at and shook any suitable objects, trouser legs and the littermate's tail being the favourite recipients of this treatment. Associated with this type of play, litter 4 showed another pattern related to the treatment of prey. Gripping and shaking such objects as dusters was sometimes followed by holding them down with the forepaws and tearing at them with the incisor teeth. By the fourth week, the main form of play in ♂ G and ♀ G was wild chasing, interspersed with bouts of tail worrying, biting at each other and wrestling. Climbing up and down from various objects in the laboratory, particularly an armchair, also became part of routine play sessions (Fig. 8) and at a similar age the kittens of litter 1 climbed onto the roof of their nest box and down again. By about 6 weeks old, play fighting sometimes went over into earnest and it was noticeable that when this happened, bites were directed almost exclusively at the side of the neck. The kittens continued to play, although with decreasing frequency, until they were nearing sexual maturity and at the age of three months, elements of sexual behaviour first became apparent in play. Once the animals had become excited, wrestling play often went over into mounting attempts, one clasping the other round the waist, sometimes combined with a neck bite. Most commonly it was ♂ G who mounted ♀ G but she also mounted him now and then. In the Washington animals, however, it was the ♀, who was the younger of the pair, that performed most of the mountings seen during play.

Play with live prey was never seen but the shaking and throwing of the corpse which often followed a kill appeared to be at least partly playful.

At the age of approximately four months, for instance, two live mice were given to ♂ G and ♀ G and were rapidly killed, the ♀ giving hers such a violent throw that it flew from one side of the room to the other, over the top of a desk. This was followed by an outburst of wild activity in which the pair ran hither and thither, finding a mouse and throwing it high in the air, dashing after it again, losing it and finding it repeatedly before they finally settled down to eat.

With litter 1, although the same types of play were seen, there were some quantitative differences. Although there was some running and jumping from 24 days onwards, true chasing began rather suddenly at 31 days old. This was accompanied by the usual biting, wrestling and worrying of each other's and their mother's tails and also of bits of grass. Chasing and running play, however, did not persist as it had done in the parents, whose youth was spent in the laboratory. At 5 weeks old, wild chasing or sometimes merely contagious running, was a common form of play but at 6 weeks it was being replaced by a new activity — hunting for insects among the clumps of grass in the enclosure. From this time onward, fighting play and tail worrying were almost the only forms of play seen and, apart from suckling, hunting for insects became the kittens' other main activity. In fact, one could say that in the more nearly natural environment, the serious business of life had begun and play activities showed a corresponding decline. Fighting play showed a strong tendency to go over into earnest in the second month of life and declined in frequency. The parents did not normally join in the games of the young, although they were tolerant of having their tails worried but with litter 5, the mother occasionally became sufficiently excited by the kittens' chasing play to join in very briefly.

(iii) Defensive behaviour. Very young kittens in the nest will spit defensively in response to any strange object approaching them rapidly but no attempt was made to find out when this behaviour makes its first appearance. At 9 days old, the kittens of litter 1 showed another form of protective behaviour; that of 'freezing' or remaining absolutely motionless for some time after any sudden disturbance. At 18 days old ♀ G was inadvertently disturbed while she was nursing the young. She sprang up suddenly, dislodging the kittens: one froze

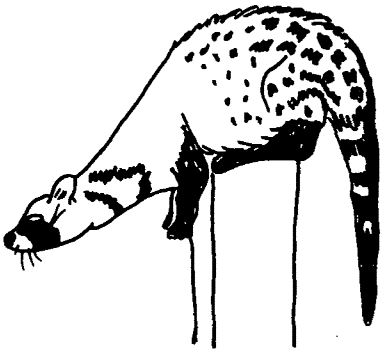

Fig. 9: Alarmed kitten, having taken refuge on top of fence post. Sketch from life

where it fell, the other crawled into the nearest cover before doing so. From then on moving under cover and then freezing was the normal response to sudden alarm and was seen on a number of subsequent occasions. Litter 4 showed this response at the age of 14 days.

Another escape response was seen twice in litter 1, at 42 and 53 days old. On both occasions the kittens were scared by the sudden clatter caused by the mother killing a rat with violent shaking: the female kitten hid in the grass and then froze as usual but the ♂ ran up the nearest vertical object, which happened to be an old fence post a little over a metre high. On reaching the top, he froze in a seemingly very awkward posture (Fig. 9) and on the second occasion remained thus immobile for 15 minutes before making any move to climb down again. A kitten of litter 5 on three occasions (aged 57, 61, 72 days) climbed the wire netting of the cage wall (ca. 2 m high) when alarmed. It was unable to climb down and having attempted to turn round to do so head first, it fell down. On one occasion when repairs had to be made to the cage, the 2 year old ♀ G was panic stricken and sought refuge by climbing but this was the only time an adult was seen to behave thus. Since fleeing upwards is commonly regarded as the hallmark of an arboreal species, one can hardly avoid interpreting this behaviour as the survival of a response first evolved during a more arboreal ancestral stage.

12. Parental Behaviour

The second enclosure had not been built when litter 1 was born and it was therefore not possible to separate off ♂ G. Immediately after the birth of her kittens, ♀ G became very hostile to him, chased him and snapped at him viciously. He made no attempt to retaliate but fled at once and ran up and down the edge of the enclosure, seeking for a means of escape. It seemed clear that in the natural situation, he would have left and the ♀ would have remained alone while rearing her young. Within a few days, however, the ♀ became less antagonistic and by the fifth day permitted ♂ G to lie beside her and the kittens during the daytime resting period. At feeding time, however, the sight of him with a piece of meat in his mouth would trigger off an attack and for some days all the food was therefore cut into pieces small enough to be swallowed quickly. The ♂ made no attempt to attack the kittens and before long he permitted them to lie in contact with him and the family group usually rested as a unit, the ♀ often with her head resting on the ♂'s body and the kittens nestling against whichever parent happened to be in the more convenient position. Indeed, the ♀ would sometimes move away, leaving the kittens with the ♂ and it was no uncommon sight to see him lying extended or slightly curled with the two kittens resting against his abdomen. He also licked the kittens, including toilet licking of the perineal region. It seems very improbable that such ♂ parental behaviour would ever be shown in a natural situation. It appears to be comparable with the parental behaviour which may be shown by adult ♂ rats as the result of prolonged exposure to the presence of young pups (ROSENBLATT 1970). ♂ G remained tolerant of the youngsters, even when they were approaching sexual maturity and allowed the ♂ of litter 2 to make mounting attempts on ♀ G without interference.

By the time ♀ G had her third litter, her hostility to ♂ G following their birth was more violent and more persistent than previously. As already mentioned, she failed to rear this and the next litter, which may have been the result of the disturbance caused by the presence of the ♂ and he was separated from her during the rearing of litter 5. It is therefore not possible to say whether as he became older, his parental responsiveness to the kittens would have waned or not. However, he gave no signs of hostility towards the young of litter 5, although he and ♀ G would occasionally snap at each other through the wire netting.

Parturition was never witnessed and the kittens when first seen had always been licked dry, the surrounding area was clean and there was no trace of embryonic membranes or placentas. The advanced stage of the young at birth makes it unnecessary for the ♀ to retrieve them if they happen to crawl away from her slightly but ♀ G moved the kittens of litters 3 and 4 from one enclosure to the other on the day they were born. She was seen carrying a kitten 7 times in all: 3 times it was held gripped by the neck, once by the shoulders, once by the middle of the back and twice by the lumbar region. On another occasion, when she was worried by the fact that an older kitten was playing with the senior author, she made a half-hearted attempt to retrieve it and picked it up by the nape of the neck but put it down again after moving it only a very short distance. If picked up by the nape of the neck, the kittens gave the "carry passivity" response, hanging limp and motionless until set down again.

♀ G showed the usual toilet care of the young, licking them all over with special attention to the perineal region and consuming the urine and faeces voided as a result of such stimulation. This continued beyond the age at which external stimulation had become unnecessary and the kittens were not given the opportunity to micturate independently until they were 25 days old. During the immediately following period the ♀ licked up their urine as soon as they had voided it. She was able to detect by smell that they had urinated, for on one occasion a kitten micturated out of her sight and she at once alerted, sniffed, went to the spot and licked up the urine. At first the kittens micturated wherever they happened to be when the need arose, which was usually in or around the favourite resting places, but at 49 days old they began to use a specific lavatory site some distance away and the ♀ did not clean up the urine voided there. A further week elapsed before the kittens began to defaecate at their lavatory site and dung piles started to accumulate there.

The ♀ lay on her side to feed her young and was not seen to adopt any other nursing position. Young mammals have various methods of inducing milk let-down by mechanical stimulation of the mammary area. Cats use a kneading movement of the fore paws, the 'milk tread', whereas puppies use the snout. The civet kitten uses a combination of paws and snout. It starts to feed standing on all four paws, pushes in with its snout and then pulls back, tugging on the teat: there are several alternations of boring in with the snout and tugging back but the movements are not made in a regular rhythm. Once sucking is under way, the kitten closes in slightly, rests on its hind quarters only and starts to use the milk tread. This is a much less smooth action than that of the domestic kitten and consists of a series of rather jerky alternating punches with left and right paws, rather than a regular kneading movement. After a little while the tread ceases and sucking continues without further use of the paws. A feed generally lasted 10—12 min and purring was not heard during suckling.

Teat ownership has been recorded in domestic cats (Ewer 1959) and also in pigs (Donald 1937; McBride 1963). It also exists in a modified form in the viverrid *Suricata* (Ewer 1963 a). The civet's claws are not sharp and fights over a teat would not be likely to cause injury and there therefore seemed little reason to expect that they would show teat ownership. Instances of one teat being taken in succession by each kitten or of one being displaced by the other were seen during the first fortnight and feeding positions were therefore not at first recorded. By the third week, however, it was obvious that of the ♀'s four teats only the posterior pair were being used and on several occasions each kitten was seen using the same teat. Recording of feeding positions was therefore started when the kittens were 27 days old. It was not always possible to see what was going on, since too close an approach disturbed the ♀ but the results obtained suffice to show that ownership had indeed been established by the time recording started. The ♂ kitten fed from the left teat 25 times and from the right only twice: the ♀ kitten fed 27 times from the right teat and was never seen to use the left one. Although they were not weaned until about 14 weeks old, suckling became increasingly infrequent and difficult to see. Regular recording stopped when the kittens were 53 days old but after the mother's miscarriage the juveniles, aged 133 days, were seen to suckle once and each chose the correct teat. It thus appears that teat ownership is shown but is not established as quickly as in the domestic cat.

Licking of maternal saliva (mouth suckling) is a common phenomenon in rodents but the only carnivores in which it has so far been recorded are the genet (DÜCKER 1957) and the long-tailed weasel (HAMILTON 1933). It was seen in the civets for a brief period when they were 35—40 days old and once later on, when the ♂ kitten (aged 61 days) was being groomed by the mother, he made a desultory attempt to lick at her mouth but she did not cooperate and his attempt was unsuccessful. In mouth suckling the kitten pushes up the ♀'s upper lip with his snout at approximately the level of her canine tooth, which is in the middle of the white facial mark. One would expect such behaviour to be guided by olfactory rather than by visual stimuli and it is difficult to believe that the white mark could actually be orienting the action, still less that this could be the main function of the mark.

For a carnivore, providing the young with solid food is a problem and, if the prey is difficult to kill, it may also be necessary for the parent to provide the young with the opportunity to gain experience in killing and hunting. It was therefore of interest to see whether the civet would show any behaviour related to these functions. However, it seemed undesirable to risk leaving the full responsibility to the mother, especially since the ♂ was present as a potential food thief. The kittens' diet was therefore supplemented by giving them such foods as raw meat, insects, rice and cake, which they began to accept at 21 days old. It was difficult to give them very much, since the adults usually managed to steal most of what was provided for the youngsters. Attempts by the young to catch live insects were seen during the second month and they reacted to any rustling noise in the grass and went to investigate. Although they caught and killed insects during this period, they were rarely given a chance to eat them: one or other parent often filched their prey from under their noses as they hesitated about eating and when attempts were made to give large pieces of meat to the kittens, these were also stolen. Clearly in a natural situation the young would, at this stage, have been supplementing their diet more effectively by catching insects: not only would the ♂ not have been present but they could also have hunted further away from the mother.

It was not until the kittens were 42 days old that the ♀ first took steps to provide them with food. She and ♂ G had each been given a rat. Despite the fact that it was dead, ♀ G shook hers violently, which alarmed the young. The ♂ attempted to steal her rat several times but she drove him off. She then began to eat the rat but, as she did so, kept working her way towards where the kittens were hiding and then summoned them to her with the contact call. The ♀ kitten came first and began to scent rub on the remains of the rat, which further alarmed her brother. The mother called him repeatedly until he finally joined in, scent rubbed too and then both kittens ate a little.

Although the mother called the young to her, she continued eating herself and by the time the young actually got there, there was not a great deal left for them. ♀ G was never seen to give the whole of a prey animal to the young; she always ate some of it herself. She did, however, carry it towards them and call them to her; she permitted them to take pieces from her as she ate and furthermore, she left scraps lying about where she had been eating, which was not her normal habit. She also sometimes called the kittens to her while she was drinking from the milk bowl. She still sometimes stole a piece of meat which a kitten was trying to eat but she then allowed it to be taken back by the youngster. Somewhat later, when the kittens were in their third month, she usually stopped eating once the kittens had come to her and left the food to them. Once when half a domestic fowl had been provided, the parents tore it apart between them. This scared the kittens, who took refuge in the nest box and the ♀ then took up a piece of the meat, carried it to them and laid it down beside them. Thus although the mother did not give whole prey to the young, she called them to share her kill and her eating behaviour became modified in two ways. Firstly, although her tendency to defend her food was still in operation in relation to ♂ G, it was in abeyance in relation to the kittens: secondly, she showed progressive inhibition of eating in the presence of the kittens; at first it was merely a question of leaving scraps for them but later she stopped eating once they had started.

The kittens continued to be alarmed by the violent movements made by the adults in killing prey but their ability to cope with the remains made available by the mother showed a dramatic change. At first they were hesitant to start eating and would push scraps of food about with their noses before biting at them and if the mother took the piece they were trying to eat, they merely sniffed about where the meat had been and did not seem to understand where it had gone. At 54 days this changed abruptly: they now searched for bits of meat when summoned by the ♀, snapped them up the moment they were found and refused to permit either the mother or the littermate to steal them.

No indication of regurgitation of food for the young was ever seen. On one occasion a week was allowed to pass without any food that had hair on it being provided. ♀ G was then given two mice, which she devoured completely. If she subsequently regurgitated for the kittens, it seemed likely that mouse hair would appear in their droppings or, at least, if it did, there would be no means for it to have got there, other than the consumption of regurgitated mouse. Careful search of the droppings, however, failed to produce any such evidence. ♂ G never showed any tendency to share his food with the young.

The young were thus solely dependent on the mother's milk for approximately the first six weeks of life and thereafter their diet was increasingly supplemented by insects which they caught for themselves and by sharing the mother's food. No attempt by the mother to provide them with opportunities to make a kill was seen but the extreme caution shown in first responses to prey made it clear that there was little chance of their running into danger if left to themselves and furthermore, all the normal killing behaviour was shown in the first encounters with live prey. Since the range of foods taken includes not only invertebrates but also any kind of small vertebrate — frogs, lizards and birds as well as mammals — it is clear that during the long period of mixed nutrition, there should be ample time for them to develop their confidence and skill in killing, even without direct assistance.

13. Discussion

Apart from their propensity for scent-rubbing, whose significance remains obscure, a number of features in the behaviour of the civet are of interest either because of their functional interrelations or because they serve to throw some light on the possible evolution of more complex patterns in the Felidae.

The mating posture will be considered first. This is extremely similar to the posture characteristic of the Felidae and the mating of genets is also of the same type (DÜCKER 1957). In the majority of mammals the ♀ remains standing during mating and the ♂ mounts clasping her round the waist or lumbar region with his fore limbs: the very different felid type of mating procedure therefore requires some explanation. The most obvious suggestion is that it first arose as an adaptation to arboreal mating, where it would clearly be necessary for the ♀ to lie flat on the branch and clasp it firmly with her fore limbs. Arboreal mating of this type has been described in one viverrid, *Cryptoprocta ferox* (ALBIGNAC 1970) and although genets have not been seen mating in the wild, it would be surprising if such arboreal animals did not mate, at least sometimes, on a tree branch.

If this suggestion is correct, then it is necessary to account for the retention of an arboreal mating posture in terrestrial felids and civets. In the case of the Felidae, the relevant factor may be the existence of a highly specialised killing bite. The bite is very accurately oriented and according to LEYHAUSEN (1965) death results from the forcing apart of two vertebrae by the laterally flattened canine teeth. Although the paws are used to restrain the prey or to bring it into a suitable position, the kill is made with a single bite. The usual male method of mounting with clasping is not unlike the felid method of attacking prey but in the felid type of mating, the ♂'s posture and in particular his balance, with the fore paws planted firmly on the ground and taking most of his weight, is completely different from the attacking position. The felid mating posture may therefore serve to obviate the danger of the ♂'s accidentally switching over from mating to attack and treating the ♀ as prey instead of as a sexual partner. In view of the specialised nature of the killing bite, any such mistake could well be lethal and the advantage of reducing the chance of errors is obvious. It is less clear why the crouched mating posture should have been retained in the civets, who do not possess a highly specialised killing bite. It is, however, worth noting that attempts by the ♂ to mount a standing ♀ were frequently seen and this may possibly indicate that the crouched mating posture is actually in the process of being lost in the civets. Both this and the fact that climbing as an escape response is shown by such otherwise essentially terrestrial animals suggests that the civets' adoption of terrestrial habits may be of relatively recent date.

Civets are not specialist killers of large prey. The difficulty they experience in cutting through the skin of an adult rat suggests that larger mammalian species are not normally attacked. Birds as large as a domestic hen are killed but how big a snake a hungry adult civet would be prepared to tackle in the wild is not known. The technique of killing using preliminary bite-and-shake, however, seems particularly suited to coping with this type of prey. In this connection, some of the characteristics of the play of young civets are of interest. As is normally the case, their play embodies actions which will later be used in earnest in prey capture and in fighting. Being essentially terrestrial animals, it is natural that running and chasing should also be important components of play. The most striking characteristic of civet play, however, is the frequency of worry play. This corresponds with the fact that in prey killing, biting and shaking play a major role. It is also worth noting that although the kittens shook all sorts of substitute objects, the laboratory reared pair were not seen to pick up objects and throw them aside in play, although small things which they could have thrown were available. This suggests that in the civet's repertoire, biting and shaking is a basic movement pattern and the bite-and-throw an inhibited and curtailed version of the shake.

The prey killing repertoire includes a bite directed at the head but this is not used unless the civet is confident that the prey is not capable of retaliation. Correlated with this 'play-safe' killing technique goes the fact that there is no complex education of the young and the mother's behaviour in providing them with their first solid food is relatively simple. This, however, means that the lactation period must be prolonged to ensure that they receive sufficient nourishment for long enough to permit them to gain prey catching experience with little maternal assistance. VAN LAWICK-GOODALL and VAN LAWICK (1970) have pointed out that the extremely long lactation period of the spotted hyaena (up to as much as 18 months) is similarly related to the absence of any very effective provision of solid food for the young.

Teat ownership in the civets is probably also related to the long lactation period. Unlike young domestic kittens and piglets, civet kittens are not initially provided with any dangerous weapons and squabbles of the very young over a teat would be no more damaging than those of puppies. The civet kittens, however, will still be suckling when their teeth are fully erupted and serious fights are liable to break out now and then. If, at the age of 3 or 4 months, they were to attack each other in competition for nursing positions, the results could be highly unpleasant and a weaker youngster might be excluded from feeding. It seems reasonable therefore to suggest that teat ownership is more important towards the end of lactation than at the beginning and its slow establishment in comparison with the domestic cat is not surprising. The domestic kittens' ability to direct their responses to one particular teat at a very early age, apparently on the basis of olfactory cues, would appear to be a more complex and more highly evolved type of behaviour than that of the civet kittens, who do not establish ownership until after all their sensory abilities are fully developed. This must make it easier for them to learn the characteristics and location of their own teat and it seems likely that in its initial evolutionary stages, teat ownership developed late, as in the civets.

The civet's prey catching behaviour and the mother's methods of providing the young with solid food are also of interest in relation to the evolution of the more specialised behaviour shown in the Felidae. The accuracy and lethal qualities of the felid killing bite have already been mentioned. It is not at once apparent how an initially less precisely oriented and less immediately lethal attack could have evolved into this extremely effective single bite technique. The civet's use of the aimed head bite as a coup-de-grace, however, suggests an answer. It is not necessary for the initial attack to have gradually evolved into the death bite: instead, there may have been gradual evolution of a more effective coup-de-grace, administered earlier and earlier in the attack sequence as its lethal qualities improved. The initial stages of attack, whose function is to disable the prey, could then be progressively curtailed and finally eliminated, apart from the use of the paws to manipulate the prey into a suitable position. In fact, the felid killing bite need never have been anything other than the terminal action of the attack sequence. It is not intended to suggest that the ancestral felid used the same killing technique as the modern civet — merely that it may also have had the combination of an initial attack which rendered the prey relatively helpless and a killing bite on or near the head, which could then be made without the predator endangering itself if it came within reach of the prey's jaws. In particular, the ancestral felid must have made much more use of the paws than do the civets, whose paws are adapted to terrestrial life and are of little value as weapons. The same combination of an initial disabling, followed by an aimed coup-de-grace is also shown by another not very specialised and certainly not closely related killer — the dasyurid marsupial *Dasycercus cristicauda* (EWER 1969 a).

As pointed out elsewhere (EWER 1969 b), the domestic cat's complex behaviour in providing her young with solid food and with live prey involves a progressive inhibition of the hunting, killing and eating sequence. The civet's much simpler behaviour involves the same sort of inhibition but here it does not progress beyond the initial stage of partial inhibition of eating. It is, nevertheless, not difficult to see how from such beginnings the complexity of the cat's behaviour could have been evolved by gradual elaboration.

The significance of mouth suckling is not certain. The behaviour of the young civets, however, suggests that its function in this species is not directly nutritional. It is shown over a short period only and the bouts of licking are so brief that it is difficult to believe that a significant transfer of fluid or nutrients is taking place. It is restricted to the period immediately preceding the mother's first providing the young with solid food and in DÜCKER's (1957) genet too, mouth suckling was seen just before the young began to eat solids. It therefore seems reasonable to suggest that it acts as a signal from young to mother and has the function of stimulating her to begin sharing her prey with them. It is reminiscent of the food begging pattern characteristic of the Canidae but since regurgitation of food for the young has not been definitely shown to occur in any of the Feloidea, a derivation from food begging does not seem plausible. Possibly the sequence should be read in the reverse direction. Licking at the mother's mouth, initially reflecting developing responsiveness to the smell of food on her lips, may have started as the primary signal that the young now require solid food, regardless of the method used to supply their need. Where the means adopted is regurgitation, an elaboration of the same pattern could serve as a food begging signal, inducing regurgitation. If, however, the food given to the young has not been swallowed but is simply carried in the mouth, then the signal is no longer required, once the mother's food bringing or food sharing behaviour has been initiated.

Before leaving the question of behaviour connected with feeding, one point about the civets' readiness to catch aquatic prey deserves consideration. Although they show this ability, they do not in captivity develop the habit of dowsing their food as do the raccoon (*Procyon lotor*), the marsh mongoose (*Atilax paludinosus*) and the Cape clawless otter (*Aonyx capensis*). If LYALL-WATSON (1963) is right in regarding dowsing as a form of behaviour in which the captive animal gives itself an opportunity to perform elements of its prey catching repertoire which are otherwise deprived of outlet, then the failure of civets to dowse is easily understood. The three species known to dowse all catch aquatic prey using skilled movements of their sensitive long-fingered paws: the civet merely snaps up aquatic prey in its mouth and the motor pattern involved does not differ significantly from its method of catching small prey on land. There is therefore no specific prey catching pattern which in dowsing could find an outlet otherwise unavailable and thus no particular reason why they should readily take to dowsing.

The responses of the young to the contact call are of some interest. Exactly the same transition as the civet kittens show from an automatic, seemingly compulsive response to a facultative one is seen in the development of young *Suricata* (EWER 1963 b). The adaptive significance of the change is clear.

It is when the young first become capable of effective locomotion outside the nest or burrow that they are in greatest danger of getting dispersed and lost. It is therefore essential that they have behaviour which can be relied upon to prevent this. As they explore and become familiar with their surroundings, however, the need to keep together diminishes and an automatic response would soon begin to interfere with individual exploration and with first attempts to catch insects. Although responsiveness to the call does not disappear, it gradually becomes more and more conditional upon other factors in the situation.

A contact call very like that of the civets is given by the young of genets and also by the fanaloka *Fossa fossa* (Wemmer 1971): young *Helogale* (Zannier 1965) and *Suricata* (Ewer 1963 b) also have a repetitive contact call. It is thus clear that amongst the viverrids a juvenile contact call having characteristics making it easily located is widespread, although only in the civets and in *Suricata* have the responses of littermates and parents been described. In the civets the call is retained by the adults and is used by the mother to summon the young. In *Suricata* the call is given only by the young and serves to keep the litter together but has apparently disappeared from the adult vocabulary and in this species the use of a comparable vocalization by the mother to summon the kittens has not been reported. In the Felidae, the reverse seems to have happened: the cheetah uses a repetitive vocalization to summon her cubs which, from Adamson's (1969) description, sounds very like the viverrid contact calls and both lioness (Adamson 1960) and tigress (Schaller 1967) use a repetitive low grunting call. The cubs of these species, however, are not known to use the calls to maintain contact with each other.

In conclusion, the possible existence of facultative delayed implantation must be mentioned. Delayed implantation is common amongst the Mustelidae and Ursidae but has not so far been recorded in any of the Feloidea. The present observations are merely suggestive and do not provide any direct evidence for the occurrence of delayed implantation. It is therefore clearly desirable that they should be extended and that other related species should also be studied.

Summary

The behaviour of two pairs of African civets (obtained as juveniles and at approximately 12 days old) and of the latter pair's subsequent progeny is described.

It is suggested that while the general colour patterning is cryptic, the distinctive white markings may have social functions.

Expressive postures and movements are described, including an appeasement action. In addition to defensive and distress vocalizations, there is a socially positive contact call and another believed to be a ♀ sex call.

Comfort movements, grooming, micturition and defaecation and scent marking by means of the perfume gland are described.

Scent and hearing are the senses most important in alerting to the presence of prey. The methods of killing mammals, reptiles and birds are described. Great caution is shown in dealing with unfamiliar prey. Violent shaking is an important component of the attack and may be followed by an aimed coup-de-grace, once the prey has been disabled. Eating of prey is normally from the head down and with a rat this orientation is not dependent on the presence of the skin. Strongly smelling foods very frequently evoke scent-rubbing, the chin, neck and shoulder being repeatedly rubbed along the food.

The posture adopted by the ♀ during mating is similar to that of the domestic cat. The gestation period in normal circumstances is about 65 days but three litters conceived following miscarriage or early loss of a litter had gestations of approximately 80 days. It is suggested that this may represent a facultative delayed implantation.

The development of the young is described, including defensive responses, play and ontogeny of prey capture. In the one litter in which observations were possible, teat ownership was shown but developed later than it does in the domestic cat. The ♀'s methods of providing the young with solid food are described: their rudimentary nature is correlated with a prolonged lactation period. It is suggested that in this species mouth suckling may act as a signal to the mother that the young now require solid food.

The possible significance of civet behaviour in relation to the evolution of more complex patterns characteristic of the Felidae is discussed.

Zusammenfassung

Zwei Paare der afrikanischen Zibetkatze kamen in unseren Besitz, ein Paar war 12 Tage alt, das andere etwa halbwüchsig. Ihr Verhalten sowie dasjenige der Nachzucht des einen Paares wird im folgenden beschrieben.

Das Zeichnungsmuster der Tiere dürfte generell schutzfarbig sein, doch sind wohl vor allem die auffallenden weißen Flecke und Binden soziale Signale.

Die Tiere besitzen eine Reihe von Ausdrucksbewegungen und -stellungen, auch eine Beschwichtigungsgebärde. In Abwehr und Bedrängnis lassen sie je besondere Laute hören, außerdem besitzen sie einen sozialen Kontaktlaut und einen weiteren, der anscheinend ein weiblicher Sexualruf ist.

Komfortbewegungen, Körperpflegehandlungen, Harnen und Koten werden beschrieben. Geruchsmarkierung erfolgt mit Hilfe von perinealen Duftdrüsen.

Dem Auffinden der Beute dienen in erster Linie der Geruchs- und Gehörsinn. Sie töten Säugetiere, Vögel und Reptilien auf verschiedene Weise. Gegenüber ihnen noch unbekannten Beutetieren sind sie sehr vorsichtig. Wesentlicher Bestandteil des Angriffs auf Beute ist heftiges Abschütteln, dem ein gezielter Tötungsbiß folgen kann, sobald die Beute keiner Gegenwehr mehr fähig ist. Die Tiere verzehren die Beute normalerweise vom Kopf an. Versuche mit toten Ratten zeigten, daß zumindest bei diesen Beutetieren diese Orientierung nicht vom Fell abhängt. Auf stark riechender Nahrung reiben die Tiere häufig Kinn, Hals und Schulter.

Die Begattungsstellung des ♀ gleicht der der Hauskatze. Die normale Trächtigkeitsdauer beträgt etwa 65 Tage. Drei Trächtigkeiten, die auf eine Mißgeburt bzw. den frühzeitigen Verlust eines Wurfes folgten, dauerten etwa 80 Tage. Vermutlich kann es unter solchen Bedingungen zu einer verzögerten Implantation kommen.

Die Jugendentwicklung der Jungtiere ist beschrieben, besonders das Abwehrverhalten, das Spiel und die Entwicklung des Beutefangs. Ein genau beobachteter Wurf zeigte Zitzenkonstanz, allerdings später als bei den Würfen der Hauskatze auftrat. Während der Entwöhnungsperiode zeigt das ♀ nur wenig Neigung, die Jungen mit fester Nahrung zu versehen; dafür aber ist die Laktationsperiode relativ lang. In diesem Stadium beginnen die Jungen mit Leckbewegungen am Maul der Mutter, was für diese wahrscheinlich das Signal ist, feste Nahrung anzuschleppen.

Möglichkeiten der Deutung des Verhaltens der Zibethkatzen im Hinblick auf die Evolution komplexerer Verhaltenssysteme der katzenartigen Raubtiere werden erörtert.

Literature cited

Adamson, J. (1960): Born free. Collins & Harvill Press, London • Adamson, J. (1969): The spotted sphinx. Collins & Harvill Press, London • Albignac, R. (1970): Notes éthologiques sur quelques carnivores malgaches: le *Cryptoprocta ferox* (Bennet). Terre et Vie **24**, 395 bis 402 • Allen, J. A. (1924): Carnivora collected by the American Museum Congo Expedition. Bull. Amer. Mus. nat. Hist. **47**, 73—281 • Donald, H. P. (1937): Suckling and suckling preference in pigs. Emp. J. exp. Agric. **5**, 361—368 • Dücker, G. (1957): Farb- und Helligkeitssehen und Instinkte bei Viverriden und Feliden. Zool. Beitr. Berl. **3**, 25—99 • Ewer, R. F. (1959): Suckling behaviour in kittens. Behaviour **15**, 146—162 • Ewer, R. F. (1963a): A note on the suckling behaviour of the viverrid, *Suricata suricatta* (Schreber). Anim. Behav. **11**, 599—601 • Ewer, R. F. (1963b): The behaviour of the meerkat, *Suricata suricatta* (Schreber). Z. Tierpsychol. **20**, 570—607 • Ewer, R. F. (1968a): A preliminary survey of the behaviour in captivity of the dasyurid marsupial, *Sminthopsis crassicaudata* (Gould). Ibid. **25**, 319—365 • Ewer, R. F. (1968b): Ethology of mammals. Logos Press, London • Ewer, R. F. (1969a): Some observations on the killing and eating of prey by two dasyurid marsupials: the mulgara, *Dasycercus cristicauda* and the Tasmanian devil, *Sarcophilus harrisi*. Z. Tierpsychol. **26**, 23 bis 38 • Ewer, R. F. (1969b): The 'instinct to teach'. Nature, Lond. **223**, 698 • Fox, M. W. (1969): The anatomy of aggression and its ritualization in Canidae: a developmental and comparative study. Behaviour **35**, 242—258 • Hamilton, W. J. (1933): The weasels of New York. Amer. midl. Nat. **14**, 289—344 • Kleiman, D. G. (1967): Some aspects of social behavior in the Canidae. Amer. Zool. **7**, 365—372 • Kleiman-Eisenberg, D. G. (1972): Social behaviour in the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. J. Mammal. **53**, 791—806 • van Lawick-Goodall, J., and H. van Lawick (1970): Innocent killers. Collins, London • Leyhausen, P. (1965): Über die Funktion der relativen Stimmungshierarchie (dargestellt am Beispiel der phylogenetischen und ontogenetischen Entwicklung des Beutefangs von Raubtieren). Z. Tierpsychol. **22**, 412—494. • Lyall-Watson, M. (1963): A critical re-examination of food "washing" behaviour in the raccoon (*Procyon lotor* Linn.). Proc. zool. Soc. Lond. **141**, 371—393 • Mallinson, J. J. C. (1969): Notes on breeding the African civet, *Viverra civetta*, at Jersey Zoo. Int. Zoo Yb., **9**, 92—93 • McBride, G. (1963): The 'teat order' and communication in young pigs. Anim. Behav. **11**, 53—56 • Palen, G. F., and G. V. Goddard (1966): Catnip and oestrous behaviour in the cat. Ibid. **14**, 372—377 • Pocock, R. I. (1915): On the feet and glands and other external characters of the Viverrinae, with the description of a new genus. Proc. zool. Soc. Lond. **1915**, 131—149 • Rosenblatt, J. S. (1970): Nonhormonal basis of maternal behavior in the rat. Science **156**, 1512—1514 • Schaller, G. B. (1967): The deer and the tiger. University of Chicago Press • Wemmer, C. (1971): Birth, development and behaviour of a fanaloka, *Fossa fossa*, at the National Zoological Park, Washington, D. C. Int. Zoo Yb. **11**, 113—115 • Zannier, F. (1965): Verhaltensuntersuchungen an der Zwergmanguste, *Helogale undulata rufula*, im Zoologischen Garten Frankfurt am Main Z. Tierpsychol. **22**, 489—496.

Authors addresses: R. F. Ewer c/o D. W. Ewer, Centre for Overseas Pest Research, Wright's Lane, London W 8. — C. Wemmer, Chicago Zoological Park, Brookfield, Illinois, 60513, U.S.A.

Requests for reprints should be addressed to Dr. C. Wemmer.